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# Pathways to Autopoiesis

*A Computational Study of the Emergent Properties of  
Self-Producing Systems*

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By

RICHARD J.CARTER



Bristol Centre for Complexity Sciences

and the

School of Chemistry

UNIVERSITY OF BRISTOL

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## ABSTRACT

The theory of autopoiesis (auto - self, poiesis - producing) suggests that a living system distinguishes itself from non-living matter by its ability to generate and maintain itself. With the increase in systems thinking and complexity science at the turn of the twenty-first century this idea has been steadily gaining traction in fields as diverse as biology, the social sciences, law and architecture. The theory has been adopted most widely in the field of synthetic biology and chemistry where it provides a conceptual framework within which to understand the organisational logic of minimal living cells (protocells). The potential of autopoiesis to inform protocell research is dependent on a greater understanding of the organisational pathways that may lead to the formation of the most basic autopoietic systems. A computational study into the formation and persistence of proto-autopoietic organisations from simple, unstructured beginnings is reported here.

Computer simulations show that unstructured populations of interacting finite state automata self-organise under different environmental conditions to robust, self-producing structures called niches. The criteria for an autopoietic system remains a contested issue in the field and, as such, these niches could not be deemed to be fully autopoietic although they did routinely demonstrate the critical processes of self-production and adaptation. Competition at the individual, networked and niche level operated on such processes and was responsible for the continuous transformation of the population's structure in response to changes in the environment. Such structural coupling ensured the maintenance of the organisational identity of the proto-autopoietic system - the hallmark of autopoiesis - which was enabled by the emergence of hierarchical, strongly connected and dynamically stable networks that proved resilient to major environmental perturbations.

This work has tested the hypothesis that autopoietic systems can emerge from simple, unstructured beginnings. The research findings uphold this hypothesis and several important features and properties of proto-autopoietic systems have been reported. This research has shown that proto-autopoietic organisations are generated and maintained through competitive production processes and protocell researchers should consider this in the design of their experimental strategies.



## DEDICATION AND ACKNOWLEDGEMENTS

I dedicate this work to the memory of my grandfather John Wiltshire from whom I inherited my ceaseless curiosity and inquisitiveness about the world. My grandfather was a World War II army veteran who was one of the fortunate to be evacuated from the beaches of Dunkirk and less fortunate to be re-deployed to North Africa where he was captured and transferred as a prisoner of war to the Auschwitz camp in Poland. At the end of the war he undertook a so-called 'death march' to freedom where he experienced yet more unforgettable horrors of what humans can do to each other. Throughout such difficult trials his passion for knowledge and understanding continued and he would often raise his eyes to the night sky and wonder about where else life existed in the universe. For him there was no question if. To him I dedicate this work which, in its own small way, is a modest contribution to the conversation on the origin of life. Wherever and however it might arise.

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Thank you to you all.

## AUTHOR'S DECLARATION

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: ..... DATE: .....



## TABLE OF CONTENTS

	Page
<b>Abstract</b>	<b>i</b>
<b>Dedication and acknowledgements</b>	<b>iii</b>
<b>List of Tables</b>	<b>xiii</b>
<b>List of Figures</b>	<b>xvii</b>
<b>1 Introduction</b>	<b>1</b>
1.1 Context . . . . .	1
1.2 Research Aims . . . . .	6
1.3 Rationale . . . . .	7
1.4 Scope . . . . .	8
1.5 Outline of Chapters . . . . .	10
<b>2 Background and Literature Review</b>	<b>15</b>
2.1 A Minimal Living System . . . . .	15
2.2 Autopoiesis . . . . .	23
2.2.1 The boundary of an autopoietic system . . . . .	26
2.2.2 Maintenance of an autopoietic system . . . . .	34
2.2.3 Cognition . . . . .	42
2.2.4 Limitations of Autopoietic Theory . . . . .	45
2.3 Computational Models of Autopoiesis . . . . .	47
2.3.1 Substrate-Link Model . . . . .	47
2.3.2 Algorithmic Chemistry . . . . .	50
2.3.3 Finitary Process Soup . . . . .	54
2.4 Summary . . . . .	57

---

**TABLE OF CONTENTS**

---

<b>3 Models and Methods</b>	<b>59</b>
3.1 Introduction . . . . .	59
3.2 Automata . . . . .	61
3.3 The Information Niche - a model of a self-producing population . . . . .	66
3.3.1 Internal Environment . . . . .	66
3.3.2 Production Dynamics . . . . .	67
3.3.3 Environmental Perturbations . . . . .	69
3.3.4 Co-Evolution of Niches . . . . .	70
3.3.5 Inter-niche Transfer of Automata . . . . .	70
3.4 The Computation Niche - a model of a self-producing population with a membrane . . . . .	71
3.4.1 Internal Environment . . . . .	72
3.4.2 Membrane . . . . .	74
3.4.3 Environment . . . . .	86
3.4.4 Computation in the niche . . . . .	88
3.5 Information Measures . . . . .	89
3.5.1 Shannon Information and Shannon Entropy . . . . .	89
3.5.2 Interaction Network Complexity . . . . .	91
3.5.3 Information Content of a Population . . . . .	92
3.5.4 Structural Complexity . . . . .	92
3.5.5 Information Processing Capacity of Automata . . . . .	93
3.6 Network Measures . . . . .	93
3.6.1 Interaction Network . . . . .	93
3.6.2 Membrane Network . . . . .	94
3.6.3 Topology and Degree Distribution . . . . .	95
3.6.4 Identifying strongly connected networks . . . . .	95
3.6.5 Determining the dynamic stability of an interaction network . . . . .	96
3.6.6 Identifying and counting the unique states of the membrane network	97
3.7 Summary . . . . .	98
<b>4 Results I - One-State Information Niches</b>	<b>101</b>
4.1 Reproduction of published paper: Emergence and Dynamics of Self-Producing Information Niches as a Step Towards Pre-Evolutionary Organization . . .	101
<b>5 Results II - Two-State Information Niches</b>	<b>117</b>
5.1 Introduction . . . . .	117

---

TABLE OF CONTENTS

5.2	Emergence of a two-state automata niche under well-mixed conditions . . . . .	118
5.3	Emergence of a two-state automata niche under non-diffusivity conditions .	125
5.4	Emergence of a two-state automata niches under influx conditions . . . . .	128
5.5	Quantitative Analysis of Niche Structures . . . . .	130
5.6	Summary . . . . .	132
<b>6</b>	<b>Results III - Spatial Patterns</b>	<b>135</b>
6.1	Introduction . . . . .	135
6.2	Pattern formation on the lattice of a one-state information niche . . . . .	135
6.3	Pattern formation on the lattice of a two-state information niche . . . . .	139
6.4	Summary . . . . .	142
<b>7</b>	<b>Results IV - Interacting One-State and Two-State Information Niches</b>	<b>147</b>
7.1	Introduction . . . . .	147
7.2	Simulation Set-up . . . . .	148
7.3	The dynamics of a joint one-state/two-state population under well-mixed conditions . . . . .	150
7.4	The dynamics of a joint one-state/two-state population under low diffusivity conditions . . . . .	152
7.5	The dynamics of the automata of niche 1A combined with the automata of niche 2B under initial uniform conditions . . . . .	155
7.6	The dynamics of the automata from the one-state niche 1A combined with the two-state niche 2B automata initialised to their original structures . . .	156
7.7	Disturbance of the one-state niche 1A via. influx of two-state niche 2B automata . . . . .	160
7.8	Perturbation of a one-state population via. the influx of two-state automata	162
7.8.1	The effect of removing the perturbation . . . . .	163
7.9	Summary . . . . .	167
<b>8</b>	<b>Results V - One-State Computation Niche Simulations</b>	<b>171</b>
8.1	Introduction . . . . .	171
8.2	Set up of the Computation Niche membrane . . . . .	172
8.3	The effect of a membrane on a self-producing population . . . . .	175
8.3.1	The effect of a membrane on production dynamics in the absence of environmental noise . . . . .	177
8.3.2	The effect of constant random environmental noise on production dynamics . . . . .	179

---

**TABLE OF CONTENTS**

---

8.3.3	The effect of constant environmental noise of fixed value on production dynamics . . . . .	181
8.3.4	Examining the information processing capacity automata were more sensitive to environmental noise . . . . .	183
8.3.5	The effect of intermittent environmental noise on production dynamics	184
8.3.6	Examining the intensity of environmental noise on production dynamics . . . . .	186
8.3.7	The effect of modulating environmental noise with emissions from the computation niche . . . . .	186
8.4	Analysis of the activity of the membrane . . . . .	193
8.5	Cognition and the Computation Niche model . . . . .	195
8.6	Summary . . . . .	196
<b>9</b>	<b>Results VI - Novelty in a Multi-State Computation Niche</b>	<b>199</b>
9.1	Introduction . . . . .	199
9.2	Simulation Setup . . . . .	201
9.2.1	Generating and characterising the seeding population . . . . .	201
9.2.2	Setting up the simulation . . . . .	203
9.3	The generation and effect of novelty within a computation niche . . . . .	204
9.4	Analysis of the effect of novelty on population dynamics . . . . .	211
9.4.1	Properties of the population . . . . .	211
9.5	Summary . . . . .	212
<b>10</b>	<b>Discussion</b>	<b>215</b>
10.1	Summary of Simulation Results . . . . .	215
10.2	Evaluation of Results . . . . .	221
10.2.1	Can autopoietic systems form from simple, unstructured beginnings?	221
10.2.2	If they exist, what pathways emerged and what were their properties?	223
10.2.3	If they exist, why and how do these pathways form?	228
10.2.4	What contribution does this make to the theory of autopoiesis?	235
10.2.5	What contribution does this make to the origin of life?	236
10.2.6	Can autopoietic theory contribute more to evolutionary biology?	236
10.2.7	How can a better understanding of the pathways to autopoiesis assist with the design of protocell experiments?	239
10.3	Summary . . . . .	240
<b>11</b>	<b>Conclusion</b>	<b>241</b>

---

TABLE OF CONTENTS

11.1 Summary of Research Findings . . . . .	241
11.2 Concluding Statement . . . . .	244
11.3 Limitations of this research . . . . .	244
11.4 Recommendations for Future Work . . . . .	245
11.5 Final Thoughts . . . . .	247
<b>12 Appendix</b>	<b>249</b>
12.1 Handling multi-state automata interactions . . . . .	249
12.2 Handling open-ended novelty . . . . .	250
12.3 Software implementation in MATLAB . . . . .	250
12.4 Explanation of the difference between the Information Niche and Computation Niche results for a one-state well-mixed population . . . . .	251
<b>Bibliography</b>	<b>255</b>



## LIST OF TABLES

<b>TABLE</b>	<b>Page</b>
1.1 Research questions . . . . .	7
2.1 Varela's criteria for autopoiesis . . . . .	25
3.1 A comparison of the attributes of the Information Niche and Computation Niche models . . . . .	61
3.2 For illustration purposes and assuming no probabilistic threshold is being applied to the inputs to each membrane automaton: $M_1$ was spontaneously activated and emitted a '0' symbol over its outgoing edges. As a result it re-activated itself and $M_2$ which was the only other automaton that could process the binary symbol '0'. Once $M_2$ was activated it emitted a '1' which activated $M_4$ and $M_8$ . Those two automata then emitted a '0' and a '1' respectively which, in turn, activated all remaining membrane automata that were not already active. During this information processing in the membrane, productions in the internal population created $T_1$ (via. self-replication), and $T_2$ and after the third time-step all automata types in the population were being produced. NOTE: in practice the activation of a membrane automaton is subject to a randomly determined threshold being surpassed meaning that even if an automaton is receiving an input it may not activate. This is a necessary measure to prevent self-activating membrane automata such as $M_1$ and $M_8$ from being constantly active. . . . .	80

5.1	The competing niches in a two-state population consist of symmetrical automata e.g. the automaton $T_1$ in niche 2A with the transitions $\{0 \mid 1, 0 \mid 0\}$ has a symmetrical twin $T_2$ in niche 2B with the transitions $\{1 \mid 0, 0 \mid 0\}$ however they do not interact to produce other two-state automata. Under well-mixed conditions these competing pairs contribute to, and benefit from, the replicative performance of the automata that also constitute their respective niches. The automata from each niche were categorised according to the rate at which they were produced with respect to their initial $f$ which was 0.0005 for each automaton.	120
5.2	The histogram of the number of productions that occur in the interaction network and the number of automata that are produced in each bin. Analysis of the production of two-state automata showed that a very small number of automata (14 automata types representing 0.2% of the population) were produced considerably more often. . . . .	123
5.3	The automata in the niches 2A,2B behave differently under low-diffusivity conditions. Analysis of the dynamics that is driving such different behaviour is aided by categorising the automata into the five groups (A – E) as shown. . . . .	127
5.4	Comparison of (a) the average structural complexity ( $C_\mu(T)$ ) showing that the more highly structured niches consist of marginally more complex automata, (b) the information content ( $H(x)$ ) for each niche indicating an increase in the amount of information required to re-construct each niche as environmental disturbances are increased, and (c) the interaction network complexity $C_\mu(G)$ which is an overall measure of the complexity of the niche and, as can be seen, the complexity of the niches increase with changes in environmental conditions. All measures were generated using the final frequency distribution of the automata in each niche (i.e. the population structure). . . . .	131
5.5	The structural complexity measurements were compartmented into eight discrete and well-defined classes demonstrating the structural variation in the topology of the two-state automata population . . . . .	131
7.1	Comparison of key measurements between the joint population, niche 1B and niche 2C . . . . .	154

---

7.2 Comparison of the initial and final frequencies of each automaton type in the joint one-state niche (1A) and two-state niche (2B) population. The interaction network complexity $C_\mu(G_i)$ of each automaton type is also shown. NOTE: the indices for the niche 2B have been used to aid referencing back to the results of Chapter 5 and should not be confused with the niche 1A automata with the same index number. The simulation used the indices $i = 1 \dots 30$ for each automata with niche 1A automata indexed $i = 1 \text{to} 9$ and the niche 2B automata indexed as $i = 10 \text{to} 30$ . . . . .	158
8.1 The cumulative weightings of the incoming edges for each target membrane automaton ( $i$ ) comparing the initial weightings ( $t = 0$ ) with the final weightings ( $t = t_{max}$ ) with and without environmental noise present ( $E = \emptyset, E = [0.5, 0.5]$ respectively). The final cumulative weightings of each membrane automaton's incoming edges under those two environmental settings were different from each other and the initial values. This demonstrated how the membrane adapts to reflect the changing structure of the internal self-producing population. . . . .	172
8.2 The information processing behaviour of each membrane automaton showing the probability of the automaton emitting ( $P(Y)$ ) a symbol '0' or '1', the probability of the automaton receiving ( $P(X)$ ) a '0' or a '1' and the probability of the activation threshold ( $P_{max}^{\text{active}}$ ) being surpassed to activate the membrane automaton. . . . .	173
8.3 Examination of the activity within the membrane showed that seven membrane automata were active for 67% of the simulation and nine were active for 63% of the time. . . . .	177
8.4 Examination of the activity within the membrane showed that seven membrane automata were active for 67% of the simulation and nine were active for 63% of the time. Examining these groups separately showed that their activation only activates those parts of the interaction network that produce themselves in the internal population. . . . .	178
8.5 Comparison of the activity of membrane automata under isolated ( $\Phi = 0$ ) and random environmental noise ( $\Phi = 1$ and $E = [r, 1 - r]$ ) conditions showed a significant reduction in the activity of the group A membrane automata in the presence of environmental noise due to the limited processing of the mono-symbol input automata. The group B automata were also slightly inhibited however this did not significantly effect the production of those automata in the population. . . . .	180

8.6	The Shannon entropy of the environment ( $H_{env}$ ) for increasing rate of emissions from the computation niche ( $\Phi_{out}$ ) . . . . .	187
8.7	The different states that the membrane can occupy for various environmental settings . . . . .	194
9.1	The list of quantitative measurements that were used to characterise the effect of endogenous growth of novel automata on the seed population . . . . .	205
9.2	Comparison of the seed population at the end of 50 generations <i>in the absence</i> of the generation of novel automata vs. the seed population in the presence of novel automata. The structure of the seed population was disrupted leading to a significant reduction in the number of seed automata down to just 15.93% and the extinction of 82 of the 129 automata that were originally present at $t = 0$ . . .	207
9.3	Comparison of the Average Structural Complexity of the Population $C_\mu(T)$ and the automaton with the least number of states ( $Q_{min}$ ), the maximum number of states ( $Q_{max}$ ) and the mean number of states ( $Q_{mean}$ ) in the population for each of the four dynamic phases . . . . .	211
9.4	Comparison of the Interaction Network Complexity ( $C_\mu(G)$ ) and how much it changed (Rate of Change) across the four phases of the population . . . . .	211
9.5	Comparison of the composition of the population by the number of unique types and the rate at which new automata were being introduced within each dynamic phase. . . . .	211
12.1	Parallelising the task of constructing the interaction network for a two-state automata population . . . . .	249
12.2	The Hopcroft algorithm has a worst-case run time of $O(n.slogn)$ where $s$ is the size of the alphabet (4) and $n$ the number of states of the automaton . . . . .	250

## LIST OF FIGURES

<b>FIGURE</b>	<b>Page</b>
1.1 Luisi's schematic of a minimal autopoietic cell where a substrate entity ( <i>A</i> ) produces the product ( <i>S</i> ) which links to other <i>S</i> entities to form a boundary which encapsulates the $A \rightarrow S$ reaction. Over time <i>S</i> decays to the waste product ( <i>P</i> ) leaving a hole in the boundary. . . . .	3
2.1 The metabolic cycle is an autocatalytic chemical cycle consuming the nutrient 'X' and producing 'Y' as waste with intermediate 'A'; 'R' is a by-product of the replication process that is required to produce 'M' the membrane molecule . . .	20
2.2 Summary of the key papers contributing to or closely related to the field of autopoiesis . . . . .	22
2.3 Luisi's schematic of a minimal autopoietic cell where a substrate entity ( <i>A</i> ) produces the product ( <i>S</i> ) which links to other <i>S</i> entities to form a boundary which encapsulates the $A \rightarrow S$ reaction. Over time <i>S</i> decays to the waste product ( <i>P</i> ) leaving a hole in the boundary which is repaired by a newly produced <i>S</i> migrating to the cell boundary. The dynamic behaviour of the system is described by the two differential equations $v_{gen} = \frac{dP}{t}$ , $v_{dec} = -\frac{dP}{t}$ and the interplay of the two determines the present state of the autopoietic cell as growing, at homeostasis, or decaying. . . . .	24
2.4 Luisi's cyclic logic of cellular life as a depiction of autopoiesis as being 'the most general pattern of minimal life [that does not] specify the actual structures and their processes' . . . . .	25
2.5 An illustration of the operational limits of an autopoietic system as suggested by Virgo et al. . . . .	29
2.6 The concept of social autopoiesis retains the circularity of chemical autopoiesis except that people are the entities that enter and leave the autopoietic system and the interactions between them are in the form of communication. . . . .	32

2.7 The organisational logic of modern cellular systems as proposed by Stephen Mann [1] that is an adaptation of Luisi's cyclical model of cellular life. . . . .	33
2.8 An illustration of the causal flows in Rosen's (M,R) system model which is a minimal abstraction of an open, dissipative system that is able to transition to and maintain an organised state. The solid lines indicate a material cause and dashed lines indicate an efficient cause. Labelling is expressed in category-theoretic language where: A is the environment, B is the Repair function, f is the Metabolism function and $\Phi$ is the Replication function. . . . .	37
2.9 The reaction schema for Varela's computational model of an autopoietic system	47
2.10 The first computer simulation demonstrating the spontaneous emergence of an autopoietic system . . . . .	48
2.11 Demonstration of an autopoietic system repairing itself . . . . .	49
3.1 An automaton was an information processor that received an input, processed that information, and emitted an output . . . . .	62
3.2 Automata could only interact when the range (output) from the first automaton matched the domain (input) of the second automaton . . . . .	63
3.3 Example of the production of a new automaton where it was identical to one of its parents . . . . .	63
3.4 Example of self replication . . . . .	64

- 3.5 (a) Schematic representation showing a compositionally closed population of 15 types of single-state automata ( $T$ ). The population included four members that are capable of only one transition ( $T_1, T_2, T_4, T_8$ ), along with six ( $T_3, T_5, T_6, T_9, T_{10}, T_{12}$ ), four ( $T_7, T_{11}, T_{13}, T_{14}$ ) and one ( $T_{15}$ ) that exhibited two, three and four transitions, respectively. The binary numbers on the curved arrows on the top or bottom of the circles indicate the various possible transitions; for example,  $T_3$  operated only with an input signal of 0, transducing this to either 0 (non-switched output) or 1 (switched output) with 50% probability in each case. (b) Scheme showing an example of the functional composition of two machines (described by the non-commutative equation,  $T_2 \circ T_{13}$ , where  $\circ$  is the functional composition operator) to generate  $T_{10}$ . The three outputs from  $T_{13}$  were received with equal probability and transformed by  $T_2$  to produce  $T_{10}$ , which inherited the input domain from  $T_{13}$  and the output range of  $T_2$ . The number of possible unique binary interactions (207) was described by an interaction network ( $G$ ) in the form of a  $T \times T$  matrix; all functional compositions were members of the set of 15 types producing a compositionally closed population of interacting transducers. Unsuccessful interactions between transducers created the transitionless machine  $T_0$ , which was prohibited in the model . . . . . 65
- 3.6 Graphic illustrating the computational model for generating internal production dynamics in a square lattice of  $n \times n$  sites comprising single-state automata of type  $T$ . The lattice had periodic boundary conditions, i.e. a regular toroid topology, and, as such, an automaton in the top two rows of the lattice could interact with automata directly opposite it in the bottom two rows of the lattice and vice versa. The same condition applied to an automaton on the left edge and right edge of the lattice. Spatial mixing also occurred in the same manner. An automaton ( $T_d$ ) on lattice site  $G_{i,j}$  was chosen at random for replacement by functional composition involving types ( $T_a, T_b$ ) selected from the sites (1,2,3,4) adjacent to  $T_d$ . Only one pair of neighbours from the two possible pairwise combinations (1,3 or 2,4) was selected to interact according to the non-commutative equation  $T_b \circ T_a$ , where the order of the interacting pair was selected randomly according to an equal probability of 1/4. If the functional composition generated a new automaton ( $T_c$ ), this replaced  $T_d$  at lattice position  $G_{i,j}$ , which was subsequently removed from the population. If no interaction occurred, then a transitionless machine  $T_0$  was generated such that  $T_d$  was not replaced and remained on the lattice site. The new population was then subjected to different levels of spatial mixing. . . . . 67

## LIST OF FIGURES



3.11 The computation niche extended the concept of the information niche to model the relationship between three processes: a self-producing population that was operationally closed (blue), an environment that was continuously generating binary information (red), and a membrane that bisects the self-producing population of automata from the environment (green). The nexus of these processes was the membrane component which changed to reflect both the structure of the population (represented as changes in the weightings over the edges of the membrane network) and the binary information that was being received from the environment at time $t$ . Information from the environment was processed simultaneously by all membrane automata with the effect of inhibiting the production of automata in the population (flows labelled 'A'). Changes in the structure of the population affected the distribution of weights over the membrane network leading to a change in the information processing behaviour of the membrane (flow labelled 'B'). Information generated by emissions of membrane automata were transmitted into the environment subsequently modulating environmental information (labelled 'C') . . . . .	84
3.12 There were three types of information flow within the membrane and with its environment: (i) information generated by automata and received by other automata within the membrane, (ii) information generated from the environment and received by membrane automata, and (iii) information generated by all membrane automata that cumulatively is emitted into the environment. . . . .	87
3.13 A breakdown of one computational cycle in the computation niche that illustrates the type of information processing occurring: information transfer (orange), information storage (blue) and information modification/evaluation (green). The directed arrows show the procedural sequence in which each process was executed. . . . .	88
3.14 An example of the graphical representation of the interaction network ( $G$ ). The two nodes represent the $T_a$ and $T_c$ automata and the edge label represents the $T_b$ automaton in the functional composition equation $T_b \circ T_a = T_c$ . . . . .	94
3.15 An example of the graphical representation of the membrane network ( $G$ ). The two nodes represent the $T_a$ and $T_b$ automata in the functional composition operation $T_b \circ T_a = T_c$ and the edge label represents the binary symbol that was transmitted from $T_a$ to $T_b$ . . . . .	95

---

5.1	Simulation of a two-state population under well-mixed conditions shows an initial stage of competition between two different subsets of automata with one subset eventually dominating whilst the other decays rapidly. This <i>punctuated equilibrium</i> begins at the $10^5$ iteration. The result was a niche consisting of 21 automata (niche 2A). Repeated simulations revealed that occasionally the other competing subset of automata came to dominate the population to create a new niche (niche 2B) with a very similar steady-state structure. . . . .	118
5.2	The 21 two-state automata types that constitute niche 2A. . . . .	121
5.3	The 21 two-state automata types that constitute niche 2B. The topology of this niche's automata were identical to those in niche 2A whilst it processed a different domain and range of binary information. . . . .	122
5.4	The degree distribution of the two-state interaction network. The $x$ -axis are the $k$ (total incoming and outgoing edges of each vertex which represents an automaton type) values allocated into bins of width 100. The $y$ -axis are the log $P(k)$ values for each of the $k$ bins. As can be seen the large majority of vertices in the network have fewer than 200 edges whilst a very small number of vertices have a large number of edges ( $> 1,000$ ) indicating a heterogenous network structure with a small number of highly connected 'hubs'. . . . .	124
5.5	The competing interaction networks for niche 2A (blue) and 2B (black). Each network has an identical topology that is a fully connected network consisting of seven nodes and 49 edges. Neither network holds an intrinsic advantage and the 'punctuated equilibrium' that occurs is a result of chance. . . . .	125
5.6	The population dynamics of a two-state automata population under conditions that emulate no diffusion ( $c = 0, v = 0$ ) which leads to the emergence of a new niche (2C). The first $2.5 \times 10^5$ iterations follow the same trajectory as niches 2A and 2B however there is a sharp turning point thereafter with the Fast and Medium Growth groups of automata from those niches rapidly decaying. The 'No Growth' groups of automata from those niches instead experience rapid growth into two groups. . . . .	126
5.7	The emergence of niche 2D in the presence of an influx of external automata through random replacement at a rate $0.7 < \Phi \leq 0.9$ had the effect of neutralising the initial competition between the niche 2A and 2B automata leading to their co-existence in the population. The three clusters of automata that have undergone significant growth from $t = 0$ consist of equal numbers of automata from niches 2A and 2B e.g. $T_{411}, T_{712}$ from niche 2A and $T_{493}, T_{766}$ from niche 2B, and so on. $T'$ represents all other automaton types in the population. . . . .	129



- 6.3 Illustration of the *mutual maintenance* strategy that emerged for a small group of automata under conditions of low diffusivity on the lattice. The example automata here are  $T_{60}$  and  $T_{95}$  which self-replicate and produce each other in any interactions between them: (a) a small subsection of the lattice illustrating the  $T_{60}$  automaton type surrounding the  $T_{95}$  automaton, (b) two automatons are selected to interact  $T_{60} \circ T_{95} = T_{60}$ , (c) the interaction produces a new  $T_{60}$  automaton which replaces the  $T_{95}$  that was previously at that location, and (d) a sample of the same sub-section of the lattice at a later point in time indicates that the  $T_{95}$  has now successfully replicated itself in its interactions with the  $T_{60}$  automata according to  $T_{95} \circ T_{60} = T_{95}$  . . . . . 140
- 6.4 Illustration of the *replicate / lock-in* strategy that emerged during the simulation: (a) the  $T_{60}$  is a self-replicator and highly produced automaton that grew in number significantly in the earlier stages of the simulation and is highly concentrated on the lattice. Here it has surrounded the  $T_{47}$  which is a network replicator (i.e. it needs to interact with other automata apart from itself to produce replicants of itself), (b) in any interaction between these two automata the  $T_{47}$  automaton is produced and, as is seen here, replaces the  $T_{60}$  automaton, (c) this outward growth of the  $T_{47}$  automaton into the  $T_{60}$  rich lattice continues with the latter automaton acting as a foodset, and (d) this process continues until the  $T_{47}$  domain meets other domains consisting of automata that are also using the  $T_{60}$  type automata as a foodset. Where these domains meet the growth of the domain ceases as these automata do not interact with each other and, as such, these domains effectively become 'locked in' and no further growth of the domain occurs in the direction of the opposing domain. . . . . 141
- 6.5 The spatial patterns of the lattice for the niche  $2C$  at  $5 \times 10^6$  showing two areas of interest where the  $T_{766}$  automaton is surrounded by the  $T_{107}$  automaton indicating the presence of the 'mutual maintenance' survival mechanism. . . . 142



- 7.3 A graph showing the time-series frequency distribution of the joint one-state/two-state population over  $10^7$  iterations showing that: (i) the one-state niche (1A) was reproduced albeit with a different structure that accentuated the frequency gap between the four automata clusters 'Fast Growth' ( $T_{15}$ ), 'Slow Growth' ( $T_3, T_5, T_{10}, T_{12}$ ), 'No Growth' ( $T_1, T_2, T_4, T_8$ ) and 'Slow Decay' ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ) - see Chapter 4) - and, (ii) that the automata from both two-state niches (2A and 2B) were also present in the same proportions as the original niches albeit they were at a very low concentration representing just 3.3% of the population. All three niches were able to co-habit within the same space demonstrating a large degree of robustness of their respective organisations in maintaining their respective identities. . . . . 152
- 7.4 The time-series frequency distribution plot for the joint population of one-state and two-state automata under conditions of non-diffusivity ( $c = 0, v = 0, \Phi = 0$ ). As can be seen the one-state niche 1B formed readily (as indicated by the frequency distribution of automats  $T_1, T_2, T_4, T_8$  at  $t = 10^7$ ) and which came to dominate the population. The two-state population followed a similar trajectory to that which formed niche 2C however the 'mutual maintenance' automata that grew quickly early in the simulation (I and II) decayed rapidly after  $t = 0.5 \times 10^6$  and eventually went extinct leaving only the 'replicate & lock-in' automata (III) which were able to survive in the joint population albeit at a very low frequency. 153
- 7.5 The interaction networks for the set of automata from the one-state niche 1A ( $T_{1A}$ ), the two-state niche 2A ( $T_{2A}$ ) and the two-state niche 2B ( $T_{2B}$ ). This diagram captures the  $T_b \circ T_a = T_c$  relationship with the direction of the arrow indicating the  $T_a$  to  $T_c$  relationship which is transformed by the  $T_b$  automata as indicated on the edge label: (a) the one-state niche 1A and two-state niche 2B automata interaction network where 63 interactions ( $T_{1A} \circ T_{1A} = T_{1A}$ ) are the one-state automata reproducing each other, 147 interactions involving both  $T_{1A}$  and  $T_{2B}$  automata that generated all of the  $T_{2B}$  automata types according to  $T_{2B} \circ T_{1A} = T_{2B}$ , 315 interactions generated exclusively from two-state automata  $T_{2B} \circ T_{2B} = T_{2B}$  that only generated 2B automata and 189 interactions whereby the two-state automata interacted with one-state automata produced one-state automata ( $T_{2B} \circ T_{1A} = T_{1A}$ ; (b) the interaction network of the 1A niche and 2A niche automata showing a different structure to (a). Here the transformation of the output from  $T_{1A}$  automata by a  $T_{2A}$  automata produced more  $T_{1A}$  automata and, likewise, the transformation of the output from the  $T_{2A}$  automata by  $T_{1A}$  automata produced  $T_{2A}$  automata. . . . . 156

7.6	Population dynamics of the joint population of automata from niche 1A and 2B distributed evenly at $t = 1$ and evolved under well-mixed conditions ( $c, v = 0$ and $\Phi = 0$ ) for $10^7$ iterations. . . . .	157
7.7	Population dynamics of the joint population of automata from niche 1A and 2B distributed at $t = 1$ according to their proportions in their original niches. The population was evolved under well-mixed conditions ( $c, v = 0$ and $\Phi = 0$ ) for $10^7$ iterations. As can be seen the three 1A niche automata ( $T_5, T_{10}, T_{15}$ ) experienced rapid growth and came to dominate the population whilst six 2B niche automata went extinct leaving a reduced number of two-state automata (I).159	
7.8	Time-series frequency distribution for a simulation of the random replacement of incumbent niche 1A automata with two-state automata from niche 2B. Selection of automata from niche 2B was randomly determined with higher frequency automata in that niche more likely to be selected to replace an incumbent automata. The initial population is exclusively the one-state automata from niche 1B ordered in the proportions in which they persist in their original niche. As can be seen even with a very low rate of replacement of $\Phi = 0.05$ the two-state niche 2C is reproduced in this population to the detriment of the incumbent one-state automata. NB: I are the low frequency automata from niche 2B. . . . 161	
7.9	Time-series frequency distribution for four simulations of the random replacement of incumbent one-state automata population (15 types) with two-state automata population (1,873 types) for various values of $\Phi$ over $10^7$ iterations: (a) with $\Phi = 0.05$ the one-state automaton $T_{15}$ undergoes rapid and continued growth to dominate the population whilst the remaining one-state undergo a reduction in concentration whilst incoming two-state automata established . . . 163	



- 8.1 An illustrated example of the calculation of  $P_{max}^{active}$  for the membrane automaton  $M_1$ . Each membrane automaton  $M_j$  in the set  $M_J = \{M_1, M_3, \dots, M_{15}\}$  transmits information to  $M_1$  (it also transmitted to itself) in the form of a two-element probability distribution ( $P(M_j) = [P(y=0), P(y=1)] = 1$ ). The input function  $P(M_1)$  is the cumulative probability distribution of all inputs. In this example the weightings on each edge are assumed to be equal and therefore  $P_{max}^{active} = \max(P(M_1)) = 0.625$ . Under changing conditions the edge weightings modulate the information received by  $M_1$  that can lead to fluctuating values of  $P_{max}^{active}$  which subsequently effects the activation behaviour of the receiving automaton.  $Z$  is a normalising factor. . . . . 174
- 8.2 The topology of the membrane automata network where the directed edges indicate the flow of transfer of information between the source automaton ( $M_a$ ) to a target ( $M_b$ ) automaton from the interaction relationship  $T_b \circ T_a = T_c$  i.e. automaton  $M_a$  emitted information which was received by  $M_b$  that then subsequently processed that information according to its internal structure. This was a highly connected network with an average in-degree of 13.8 and an average out-degree of 13.8 giving a 1:1 ratio that indicated a highly symmetrical structure of 207 edges. As each membrane automaton was highly connected this created competition within the membrane network in the form of multiple source automata interfering in each others attempts to influence the activation of a target automaton. . . . . 175
- 8.3 The steady-state population structure of the computation niche model after  $1 \times 10^5$  iterations with and without environmental noise: (a) the steady-state population with no environmental noise ( $\Phi = 0$ ) was very similar to the one-state information niche 1D population structure; (b) a constant environmental noise that switches randomly from '0' and '1' led (where the randomly generated number  $r \leq 0.5$  indicated the generation of the '0' symbol and  $r > 0.5$  generated a '1' symbol) to a significant drop in the concentration of six automata (that were all mono-channel input) to generate a new steady-state structure; (c) a constant '0' was emitted as environmental noise and this led to the drop in concentration of all automata that could only process '1' symbols; (d) a constant '1' was emitted as environmental noise and this led to a reduction in those automata that could only process '0' symbols. For (b)-(d) the environmental aperture was set to  $\Phi = 1$  hence membrane automata were only processing environmental information. . 176

- 8.4 Comparison of the behaviour and structure of the internal population with (red) and without (blue) environmental noise effecting the membrane automata. Environmental noise had the most effect on the activity of membrane automata - in the absence of any environmental noise the activity range of membrane automata were tightly grouped in the range 63% to 67% of the time, compared to the range 50% to 100% of automata active over the duration of the simulation due to environmental noise. Such a difference in membrane behaviour resulted in a different population structure with the automata  $\{T_5, T_6, T_7, T_9, T_{10}, T_{11}, T_{13}, T_{14}, T_{15}\}$  increasing in concentration and the automata  $\{T_1, T_2, T_3, T_4, T_8, T_{12}\}$  decreasing in concentration. . . . . 180
- 8.5 Changes in the final frequency of each automaton type as a result of changes in environmental noise. The baseline (at zero) is the frequency distribution of the population in the complete absence of environmental noise. The +/- fractional change in frequency of each automaton is shown in the presence of random environmental noise (red), fixed '0' environmental noise (blue), and fixed '1' environmental noise (green). Those automata with minimal changes across all three environmental noise settings were deemed to be more robust to environmental noise. Group A automata (mono-symbol input) are  $T_1, T_2, T_3, T_4, T_8, T_{12}$  and the remainder are Group B automata (dual-symbol inputs). . . . . 182
- 8.6 Partition map showing the flow of production of new automata between the partitions. In general, production flows either downwards to partitions of lower information processing capacity ( $\varrho$ ) or horizontally within a partition. In only two cases -  $T_5 \circ T_3 = T_{15}$  and  $T_{12} \circ T_{10} = T_{15}$  from partition 2 - did production flow upwards to a higher partition due to the multiplicative effect of the functional composition of two automata. . . . . 183
- 8.7 The final frequency distribution of automata types for eleven different environmental settings incrementing from  $P(E) = (0, 1) \rightarrow P(E) = (1, 0)$  and with the environmental aperture set at  $\Phi = 0.5$ . The production of seven automata (indicated by \*) were more sensitive to changes in environmental information. The  $x$  axis indicates the environmental information setting used for that simulation run and the  $y$  axis indicates the final frequency distribution of the population automata after  $1^5$  iterations. The environmental setting of  $P(E) = (0.5, 0.5)$  was the closest match to the computation niche that forms in the absence of environmental noise. . . . . 185



- 8.10 The time-series plots of the frequency distribution of the computation niche population over  $1 \times 10^5$  iterations for various  $\Phi_{in,out}$  values: (a) the nominal population structure of the computation niche under endogenous information flow conditions with  $\Phi_{in} = 0, \Phi_{out} = 0$ ; (b) the population structure where a partial exchange of information between the environment and the niche was occurring with  $\Phi_{in} = 0.5, \Phi_{out} = 0.5$  leading to some separation of the  $T_3, T_5, T_{10}, T_{12}$  concentrations with the reduction in number of the  $T_3, T_{12}$  automata due to their only processing single symbols (e.g. '0' or '1' but not both); (c) the population structure where information flow within the computation niche membrane was solely from environmental noise ( $\Phi_{in} = 1$  and with the environmental noise itself mostly influenced by the emissions from the niche ( $\Phi_{out} = 0.75$ ). As can be seen there was a greater reduction in the production of  $T_3, T_{12}$ ; (d) the population structure where the 'information coupling' between the niche and the environment is total i.e. the membrane of the niche solely processed environmental noise ( $\Phi_{in} = 1$ ) and emissions from the niche completely determined environmental noise ( $\Phi_{out} = 1$ ) thus creating a closed cycle of information flow. As can be seen there was a reduction in the production of  $T_3, T_{12}$ . . . . . 190
- 8.11 Maps of the environment and niche entropy measurements over 121 simulations for various values of  $\Phi_{in}, \Phi_{out}$ : (a) the environmental entropy map showed a consistent decrease in entropy across all values of  $0 \leq \Phi_{in} \leq 1$  and with  $0 \leq \Phi_{out} \leq 0.75$ . However, there was a steady increase in environment entropy in the range  $0.75 < \Phi_{out} \leq 1$ . The mean environment entropy was  $\overline{H_E} = 6.18$  bits with a maximum of  $H_E^{max} = 6.6$  bits and a minimum of  $H_E^{min} = 5.67$  bits; (b) the niche entropy map showing a shallower profile where the entropy steadily increased as  $\Phi_{in} \rightarrow 1$ . There was a significant dip in entropy to its lowest point at  $\Phi_{in} = 1, \Phi_{out} = 0.75$  which corresponded exactly with the minimum entropy point of environmental entropy. The mean niche entropy was  $\overline{H_N} = 6.1$  bits with a maximum of  $H_N^{max} = 6.2$  bits and a minimum of  $H_N^{min} = 5.38$  bits. . . . . 192
- 8.12 A graph comparing the changes in the Shannon entropy of emissions from the niche and the environment over 21 simulations for increasing values for  $\Phi_{out}$ . At  $\Phi \approx 0.75$  there was a distinct drop in the Shannon entropy of both niche and environment. . . . . 193
- 9.1 The seed population was derived from all one-state and two-state self-replicating automata of which there were 10 one-state and 119 two-state automata for a total seed population of 129 automata types . . . . . 202

9.2	The interaction and production dynamics of the seed population over 200 generations where the production of novel automata was prohibited. The seed population had structured itself into four categories of automata: (A) Fast Growth - consisting of a single one-state automaton ( $S_{10}$ ) that accounted for 7.2% of the population, (B) Medium Growth - consisting of four two-state automata ( $S_{23}, S_{28}, S_{35}, S_{37}$ ) that collectively accounted for 11.2% of the population, (C) Slow Growth - consisting of 34 automata (four one-state and 30 two-state automata respectively) that accounted for 53.3% of the population, (D) No Growth - consisted of three two-state automata ( $S_{38}, S_{57}, S_{94}$ ) occupying 2.5% of the population, and (E) Slow Decay - consisted of the remainder of the seed population with five one-state automata and 82 two-state automata that occupied 25.8% of the population . . . . .	203
9.3	The results from simulating the population dynamics over 50 generations leading to the introduction of new (novel) automata that displaced the seed population: (a) the dynamics of the seed population only (the novel automata dynamics have been omitted) which should be compared to figure 9.2, (b) the dynamics of the novel automata only which appeared from generation 1, and (c) the combined results of (a) and (b) showing the effect of open-ended novelty generation on a seed population . . . . .	206
9.4	A graph comparing the relative concentration of the automata present at certain generations split into the generation in which the automata was introduced to the population. As can be seen the seed population (blue) decayed as the simulation proceeded. The novel automata that were introduced in Phase I (1-3 shown in red) actually increased in number over three generational phases and decayed at a slower rate than the seed population. Subsequent novel automata introduced in Phase II (orange) and Phase III (green) increased in concentration but at a much slower rate than the novel automata introduced in Phase I. . . .	207
9.5	Changes in the population over 50 generations could be classified into four distinct phases I - Diversification, II - Competition, III - Penetration and IV - Saturation : (a) the Interaction Network Complexity ( $C_\mu(G)$ ) vs. the Average Structural Complexity of the Population ( $C_\mu(T)$ ) over the 50 generations, (b) the Number of Automata Types in the population at the end of each generation, and (c) the Average Rate of Change in Automata Frequency in the population indicating that an initial and significant re-structuring of the population was followed by a drastic levelling off of the rate of novelty and the emergence of a steadier and more incremental introduction of novel automata . . . . .	210

9.6 Comparison of the mean, mode and the maximum structural complexity present in the automata population at each generation. Whilst the population is still generating increasingly complex automata the mean is only incrementally increasing whilst the overall mode of the population is locked in from the 8th generation. These estimates are consistent with what is expected from a 'passive evolution' process [3]. . . . .	212
10.1 The information niche served as a nexus as it was responsive to external factors such as changes in environmental conditions, information content and input dynamics, as well as to internal changes in structure . . . . .	233
12.1 Comparison of the number of times each automaton was produced in a simulation over $4 \times 10^5$ iterations under well-mixed conditions only. As can be seen in the 'Difference' column there is a significant increase in the production of the automata $T_2, T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ balanced against a significant decrease in the production of the automata $T_3, T_5, T_{10}, T_{12}, T_{15}$ . These changes were due to the partial sampling that occurs in the computation niche as a result of the membrane exciting or inhibiting different types of population automata. . . . .	254



## INTRODUCTION

Natural selection may explain the survival of the fittest, but it cannot explain the arrival of the fittest. -  
Hugo De Vries in *Species and Varieties: Their Origin by Mutation* (1904)

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### 1.1 Context

The theory of cellular life proposes that biological cells are the essential building blocks for living systems with the single cell subjected to Darwinian evolution being the primary unit for life. This raises the circular question of how the first living cells emerged in the absence of established biological evolution. The Russian chemist - Alexander Oparin - developed the concept of molecular evolution as the chemical progenitor of biological evolution [4] and this has come to be the basis for modern research into the origin of life. Specifically, Oparin proposed that initially simple abiotic molecules spontaneously formed more complex molecular chemistries. Current thinking [5] is that the integrated, co-emergence of the primitive processes of replication, metabolism and compartmentalisation would be a critical step on the pathway to the emergence of the first living cells. Such a primitive system would need to operate in a manner that maintains and increases its

viability in the presence of selective pressures. In this way it is envisaged that such a system would evolve as it endures under various environments. Such a system would be a form of autonomous chemical system which has been conceptualised as a protocell [6]. The need for a systems perspective on protocell formation has led to the emergence of the discipline of systems chemistry which focuses on the development of complex molecular systems that demonstrate emergent properties that are only possible through the collective behaviour of the interacting molecules that constitute the chemical system of interest.

"One of the grand challenges of Systems Chemistry, namely producing synthetic life, might be fulfilled through the design of a collection of molecules, a 'network', that is simple enough to self-organize, yet sufficiently complex to accommodate the essential properties of a living organism: compartmentalisation, replication and metabolism, all maintained out-of-equilibrium." [7]

As a discipline still in its infancy, systems chemists do not yet have a definitive body of knowledge of what design strategies will lead to achieving such outcomes: chemical affinities, reaction network structures, system dynamics, feedback loops, and so on. Nevertheless, attempts have been made to define the system architecture that are deemed to be most closely aligned to this aim and one of the more prominent and convincing models is based on the theory of autopoiesis [8].

The theory of autopoiesis [9] - from the Greek *auto-* meaning 'self' and *poiesis* meaning 'production' - was developed by two Chilean biologists Humberto Maturana and Francisco Varela who proposed that living systems are distinguished from non-living systems by the ability to continually reproduce and maintain themselves. An autopoietic system consists of entities that interact with each other to produce new entities which are identical to entities that participate in that process. In other words, an autopoietic system produces the components of which it is composed and this results in a system that can persist over time as it produces new entities as old entities decay. A key characteristic of an autopoietic system is that it creates an interface between its interior - containing the entities of the production process - and its environment. The characteristic model of an autopoietic system is a biological cell whereby the process of production creates the membrane that encapsulates the internal reaction network that produce the entities that constitute the membrane. This circularity gives rise to a self-contained system that is operationally closed. The relationships between the entities of such a system is called the *organisation* of the autopoietic system and the specific arrangement and configuration of those entities at any moment in time is its *structure*.

A conceptual example of an organisation is a chemistry consisting of three components [8] - a substrate, a product and a waste product - that collectively are sufficient to form

and maintain a boundary that encapsulates the reactions that are required to produce the boundary. A schematic of such a minimal autopoietic cell [8] is shown in figure 1.1. fl

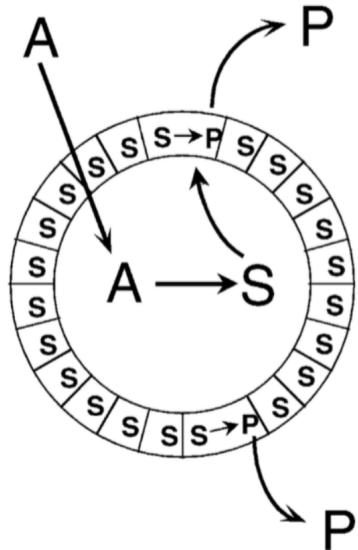


Figure 1.1: Luisi's schematic of a minimal autopoietic cell where a substrate entity ( $A$ ) produces the product ( $S$ ) which links to other  $S$  entities to form a boundary which encapsulates the  $A \rightarrow S$  reaction. Over time  $S$  decays to the waste product ( $P$ ) leaving a hole in the boundary.

This toy chemistry was first simulated by Francisco Varela in 1974 [9] and has since been examined in detail [10],[11] with more recent simulations emphasising the physical accuracy of the reactions and transport of artificial chemistries. The boundary of an autopoietic system does more than act as a compartment. It also acts as a mediating interface with the environment that through a sensorium [1] allows an exchange of matter and information between the interior and the exterior. This exchange can trigger changes to the structure of the autopoietic cell which, in turn, can lead to a change in the state of the system. Some of these changes may be transitory with no long term effect on the system whilst others may be persistent and that permanently change the structure (but not the organisation) of the system. This plasticity [12] is an important characteristic of an autopoietic system as it allows the system to adapt to its environment. Of course, a change in behaviour of an open system such as an autopoietic cell will lead to changes in the environment through altered emissions (as waste product or information) from the cell itself. Such structural coupling between cell and environment indicates a reflexive cycle i.e. the autopoietic system forms and is formed by its environment. This process of adaptation is called cognition and is the main mechanism by which an autopoietic system is claimed to evolve [13]. The process of cognition has been studied extensively [2],[14],[15],[1],[16],[17]

and combined with the process of autopoiesis (self-production) constitute and maintain the organisation of the system. The organisation of an autopoietic system is its invariant property and changes to it may constitute a new type of organisation that is no longer autopoietic.

The main strengths of the theory of autopoiesis are that (a) the concept is sufficiently abstract and agnostic to the chemical systems or molecules by which an autopoietic system can be realised and this has the desirable quality of minimality which, when seeking to model the formation of a basic living system, is to be favoured, and (b) it is a scalable concept that has explanatory power through all of the major evolutionary transitions [18] from the most basic living cell to human cognition to social systems and has generated interest outside of its field of origin (neurobiology) and applied to social systems [19], art [20], knowledge in institutions [21], computation theory [22], information systems [23], law [24] and architecture [25].

However, the adoption of autopoietic theory within biology has had a somewhat slow uptake primarily because it arrived at a time when a reductionist paradigm was prevalent with research efforts focused on the extrapolation of the genome to explain biological behaviour. However, towards the end of the twentieth century and with the increasing attention being given to system sciences - particularly systems biology and complexity science - autopoiesis began to be recognised as a concept that was somewhat ahead of its time [8]. Within the specialised field of neurobiology and cognitive sciences autopoiesis is now widely accepted as a central tenet of embodied cognition theory [26]. Within the relatively new field of synthetic biology autopoiesis has been adopted as a popular model of the system logic of a minimal living cell (the so-called protocell) [27]. However, within the broader field of biology autopoiesis has still not been recognised as part of the theoretical firmament alongside DNA and Darwinian evolution (the so-called modern synthesis) nor does it form part of the ongoing extended evolutionary synthesis movement. This has been investigated [28] with the conclusion that the lack of clarity and the under-developed nature of the relationship between autopoiesis and Darwinian evolution is the main issue. Attempts have been made to relate these two fields [13],[29],[30], [31] however a convincing explanation of a relationship remains inconclusive. Subsequently autopoiesis remains as an outlier in evolutionary biology research. As a case in point a recent review of the extended evolutionary synthesis [32] makes no mention or reference to autopoiesis or any related works even though the authors state the fundamental importance of 'constructive processes' to developing the field of biology. As will be discussed in more detail in Chapter 2 autopoiesis is intrinsically and fundamentally a constructive process and so its continued omission from the conversation on evolutionary biology warrants attention.

My view, which is introduced here but which unfolds throughout this thesis, is that the concept of autopoiesis does not directly address nor sufficiently explain *how* autopoietic systems may form from simple, unstructured beginnings. Or, in other words, given the innate power of autopoiesis theory to explain constructive processes it does not adequately explain the origin of itself. Maturana & Varela may describe the coming together of three concurrent processes (metabolism, compartmentation, ) but from where and how could these processes have emerged? The artificial chemistries used to demonstrate the formation of a minimal autopoietic cell [9] - and to prove the concept of autopoiesis - rely entirely on the presence of an ideal chemistry. Yet from where could such a chemistry have emerged? We could assume, no matter how improbable, that such a chemistry could occur spontaneously given a sufficiently diverse population of chemicals able to interact over very large timescales<sup>1</sup> but this dodges the question and effectively 'kicks the can down the road'. The hypothesis that needs to be tested is that autopoietic systems form from a pathway that originated from simple, undefined and unstructured beginnings. Such a system may become increasingly structured over time and such an organised chemical system may act as a resilient platform from which various candidate autopoietic organisations could be trialled and tested. Such platforms would themselves need to demonstrate a degree of self-maintenance and renewal simply to sustain themselves. As such, these platforms would need to exhibit autopoietic-like behaviour without actually being fully autopoietic. In this project I call these proto-autopoietic systems. With this simple distinction in mind we can now ask questions such as : what are the organisational pathways from very simple organisations to those that begin to exhibit autopoietic-like behaviour? What construction occurs *prior* to the formation of a fully autopoietic system? What are the properties of proto-autopoietic systems? How do such properties emerge from simple, undefined beginnings? Do such proto-autopoietic systems endure? Is it possible that fully autopoietic systems could form from these proto-autopoietic states? At what point does a proto-autopoietic system become a fully-fledged autopoietic system? Such proto-autopoietic states need to be understood if we are to explain how autopoietic systems may have formed on the early earth and before the arrival of the first living cell. An investigation into the possibly pathways to autopoiesis is the purpose of this project and the possible contribution that this research may make is a theoretical suggestion of the origin of autopoietic forms of organisation.

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<sup>1</sup>Stuart Kauffman's work on the emergence of autocatalytic sets answers this question more directly and this is discussed in Chapter 2

## 1.2 Research Aims

The research questions that this project is seeking to answer and the related aims of this project are:

Research Question	Research Aim
Can autopoietic systems form from simple, unstructured beginnings?	State the criteria and method for evaluating whether a system has achieved autopoiesis. Maturana & Varela originally proposed such criteria [13] which was subsequently refined [8]. The criteria for a physical boundary remains a contested issue [33] and this will be discussed in Chapter 2.
If they exist, what pathways emerge and what are their properties?	Develop a minimal computational model that supports an interacting population coupled to an environment. This will require a model that distinguishes an internal environment (i.e. the positions of the interacting entities in time and space) from an external environment (i.e. those global parameters that perturb the internal environment). It is important that the chosen model and methodology strikes the right balance between being minimal enough to avoid any claim of over-engineering the results and yet able to demonstrate non-trivial and interesting behaviours. Design a strategy for identifying and measuring any emergent properties of an evolving population of interacting entities. Both quantitative and qualitative approaches should be considered.

If they exist, why and how do these pathways form?	The model must have a temporal dimension from which a variety of time-series data can be generated e.g. changes in structure of a population over time, interaction networks, composition/diversity of the population. State their limitations and review the impact that this may have on supporting the formation of autopoietic systems. Review the results from simulations and define the characteristics for a 'resilient platform' from which autopoietic systems may emerge.
What contribution does this make to the theory of autopoiesis?	Identify and state clearly the current limitations of the theory of autopoiesis and its application. State which limitations this work addresses e.g. provide more insight into the origination of autopoietic systems.
What contribution does this make to the origin of life?	Review the state-of-the-art in theoretical approaches to the origin of life.
Can autopoietic theory contribute more than it has to evolutionary theory?	The project should support a comparison of proto-autopoietic system dynamics to extended evolutionary synthesis topics such as constructive processes, multi-level selection and niche construction
How can a better understanding of the formation of autopoietic structures benefit experimental work on protocells?	Suggest design principles for experimental researchers to fabricate proto-autopoietic structures.

Table 1.1: Research questions

### 1.3 Rationale

This project is examining how a simple, initial population of interacting entities may become more structured over time. The phenomena of self-organisation and emergence are

the two concepts from the field of complexity science - which is the study of the phenomena arising from large numbers of interacting entities [34] - that capture the behaviour that will need to be reproduced. As such this project is a complexity science centred approach to examining the formation of self-organising networks that may demonstrate autopoietic properties. A common method in complexity science is to reproduce the behaviour of a system of interest through simulating a computational model. Such an approach makes it possible for a large number of entities to interact concurrently under environmental conditions that are varying in 'real time'. Such variations are not plausible using analytical methods such as the numerical simulation of a system of differential equations.

Two of the main tools in the complexity scientist's toolbox that are valuable for this project are information theory and network theory. The former provides a way to quantitatively measure the complexity of a process, a structure or a collection of entities whilst the latter provides a concise mathematical approach to quantifying the relationships between large numbers of entities. Both approaches are required to capture the structure and processes that may emerge as a simple population self-organises and evolves.

Given that this project is simulating how minimal beginnings can generate complexity - inline with Oparin's suggestion of an increasingly complex autonomous chemical system - it will be important to maintain a degree of integrity to how entities interact and how they produce new entities. The basis for the model will need to be a minimal population where each entity in the system represents a unique behaviour of interaction. As will be discussed in Chapter 2 a pre-existing model developed by James Crutchfield & Olaf Gornerup called the Finitary Process Soup [35] provides a useful starting point with one of the advantages of this model being that the entities are a special class of finite state transducer called  $\epsilon$ -machines. These are minimal representations of unique physical processes that adhere to rigorous mathematical rules which makes them, and their collective behaviour, open to quantitative measures of complexity [36]. In the words of Crutchfield & Gornerup their model allows us to "state the question of whether or not complexity has genuinely emerged over time in pre-biotic and pre-chemical processes". However their model has severe limitations that needed to be overcome to allow this project's research aims to be pursued and this is discussed in the next chapter.

## 1.4 Scope

This research project is a computational study of the emergence and dynamics of proto-autopoietic systems as steady-state organisations that occur under various environmental conditions. The computer simulations focus on the nature of the interactions between

entities and the basis of their self-organisation. The intent was not to accurately model the physical and chemical processes that lead to the formation of a protocell [37],[38] as an example of a complete autopoietic unit that satisfies Maturana & Varela's criteria. Instead the focus is on examining the emergence of proto-autopoietic networks from an initially uniform and unstructured state. The formation of a membrane/boundary - which is commonly demonstrated in other computational work on autopoiesis - is not a specific aim of this project. As discussed in Chapter 2 the necessity of a physical boundary for a system to become autopoietic is a contested issue and pursuing it risked de-focusing the main aim of this project which is on understanding the structures and processes that emerge from undefined beginnings. Furthermore the number of assumptions that would need to be designed into the model would need to increase significantly to ensure that a credible process of physical boundary formation was being accurately simulated. This was deemed to be an unnecessary complication that would detract from a more elegant, minimal model of an interacting population subject to environmental perturbations where the primary aim is to investigate self-organisation, adaptation and persistence<sup>2</sup>.

Autocatalytic networks, and specifically autocatalysis, is not an explicit aim of this project. Autopoietic systems, even proto-autopoietic, are likely to consist of one or more autocatalytic cycles [33] and, in that context, they are examined. There is extensive literature on the formation and evolution of autocatalytic cycles [39] in origin of life scenarios but less so in the context of autopoietic systems. The key distinction in this project that distinguishes it from work on autocatalysis is the focus on the adaptive behaviour of the system in the presence of various forms of perturbation from the environment and neighbouring systems. This allows the important cognition process of autopoietic theory to be explicitly examined alongside the autopoietic process of production and maintenance.

Other models of living systems are considered - Tibor Ganti's chemoton [40], Eigen & Schuster's hypercycles [41] - however as is discussed in the next chapter they assume the presence of reasonably sophisticated biochemical machinery such as information-encoded molecules that can control replicative processes. As should now be clear this project is focused on examining the possible pathways to such biological capabilities and therefore, by definition, models that rely on templated replication are excluded as they do not support such research aims.

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<sup>2</sup>As it happened even a minimal model demonstrated the emergence of boundary-like spatial patterns (see Chapter 7)

## 1.5 Outline of Chapters

Chapter 2 examines in detail the theory of autopoiesis and related literature. The structure of the first part of this chapter is based on the three criteria of an autopoietic as proposed by Francisco Varela [42]: self-boundary, self-maintenance and self-generation. This proves to be a useful framework within which to examine not just the theory but also to unlock an exploration into the limitations and challenges to the underlying assumptions of the model. The main theoretical issue of whether or not an autopoietic system needs to have a physical boundary (i.e. an encapsulating membrane) or whether non-physical 'boundaries' are also allowed (e.g. a system is deemed to be maintaining a boundary if it is able to preserve its identity) is discussed. Whilst the issue is not resolved here it does prompt the need to appropriately define the forms of organisation that are generated from my simulations. This is subsequently discussed and I propose the term *proto-autopoietic system* to describe a system that consists of dynamically stable strongly connected networks of mutually producing entities that emerge under specific environmental conditions. Previous computational work that has directly demonstrated autopoiesis (Varela et al. [9], McMullin [43]) or that has demonstrated behaviour indicative of 'proto-autopoiesis' are discussed and compared and this gives particular attention to Fontana's algorithmic chemistry [44] and Crutchfield & Gornerup's Finitary Process Soup. Comparison of these models concludes with the recognition that the Finitary Process Soup - albeit with limitations that would need to be addressed - provides a rigorous and credible approach to examining self-organisation and to quantitatively measure structural and network complexities that may arise.

Chapter 3 explains how the research aims are to be addressed with the significant extension and enhancements to the Finitary Process Soup model and the associated measurement methods that would be required for simulating, analysing and characterising a population of interacting entities. Two models are described that both achieve the research aim of requiring the minimum number of assumptions whilst simultaneously having the potential to demonstrate complex behaviour within a quantifiable framework. The first model described builds on enhances the finitary process soup model [35] to examine the effect of environmental conditions and environmental perturbations on the dynamics of an interacting population. This model would subsequently come to be called the 'information niche' model to acknowledge the finding that the interacting population transforms itself to different structural configurations that 'fit' with specific environmental conditions and that the information content of these different states could be quantified. The second model is extends the information niche model to formally define a systems interface (analogous

to a membrane) that is positioned between the internal interacting population and the environment. This 'membrane' consists of the same automata types that are present in the internal population but with a different mode of operation. Whereas the automata in the internal population interact to produce new automata, the automata in the membrane ('membrane automata') process information that is generated by the internal population, within the membrane from other automata, and from the environment. This proved to be an important addition to the model as it allowed the autopoietic notions of structural coupling, cognition, and information processing to be examined. Subsequent analysis of this model revealed that the systems interface in conjunction with the environment and the internal population was computing the next state of the system. As such this model was called the 'computation niche' model. This chapter also describes the methods that were used for analysing the simulation results and includes: measures of information (i.e. Shannon entropy [45]), measures of complexity (i.e. Statistical Complexity [36] and Interaction Network Complexity [35]), and network analysis measures (i.e. Degree Distribution [46]). New methods for detecting strongly connected components in a complex network and testing those networks for dynamic stability were developed specifically for this project and these are also described.

Chapter 4 is a reproduction of the published paper, "Emergence and Dynamics of Self-Producing Information Niches as a Step Towards Pre-Evolutionary Organization" [47]. This paper describes the key properties of proto-autopoietic organisations that emerged from simulating a one-state automata population evolving under the influence of fixed and intermittent environmental conditions. The main contribution that this paper makes to the field of autopoiesis are twofold: (i) the proto-autopoietic organisations that emerge and that are analysed and quantified are formed from very simple conditions. As such, they represent a minimal beginning for an autopoietic system. The paper introduces the notion of an information niche as a particular instance of a proto-autopoietic system as a dynamically stable strongly connected network of mutually producing automata that form distinct organisational steady states under various environmental conditions. Critically it is noted that information can be lost or gained during a perturbation and, in some cases, this leaves the system unable to transform itself back to a prior configuration state. The environment can play the role of adding the necessary information back into the population in the form of a perturbation which proves sufficient for the population to transform to prior states. The paper is based on the information niche model and made use of most of the information and network measures described in the Methodology chapter.

Chapter 5 describes the results of simulating a more complex population of interacting two-state automata and examines the structure of the resultant steady-state populations.

Interactions between more complex automata can lead to open-ended novelty and this required the development of additional algorithms to handle those interactions to ensure that the integrity of the population was maintained i.e. that new automata met the strict criteria for an  $\epsilon$ -machine. This required the implementation of the Hopcroft algorithm [48] for minimising finite state automata and the detection of unreachable states. Simulation results reveal that competition between two niches (separate proto-autopoietic systems) occurs eventually leading to a punctuated equilibrium event that leads to the dominance of one niche at the demise of the other. New population behaviour is also demonstrated across the environmental landscape with the rise of the survival strategies of 'replicate and lock-in' and 'mutual maintenance' under very low diffusivity conditions and also, in the presence of some influx of automata from outside the population, the co-habitation of the same space by the previously competing niches. The characteristics and complexity of the underlying networks are examined and this reveals similar properties to those identified in the one-state information niche simulations. The main conclusion from simulating a two-state population is that an increase in the complexity of the constituent automata leads to an increased number of competitive mechanisms.

Chapter 6 examines the spatial patterns that emerge in one-state and two-state information niches under zero diffusivity conditions. In the one-state population the patterns that emerged under zero diffusivity conditions was characterised as two competing domains of automata separated by a dynamic and continually produced boundary consisting of two other types of automata. Competition between these domains proceeded under a 'protected outgrowth' mechanism determined by the expansion of the domain boundaries. The two-state niche resulted in a similar structure with domains consisting of a single type of automaton that had grown outwards until they met other domains. However, there was no evidence of boundary-type automata. Instead the domains were in direct contact with other domains and competition between them proceeded by two mechanisms: 'replicate and lock-in' and 'mutual maintenance' with the former proving to be the more effective. The emergence of these various competitive, or survival, strategies was entirely unexpected and were not evident from examination of the individual automata.

Chapter 7 is part one of a two part investigation into the cognitive process of an autopoietic system which is Maturana & Varela's concept for how an autopoietic system adapts to changes in its environment. Specifically, the ability of an information niche to assimilate and accommodate material that is generated from external processes is examined by allowing two niches (a one-state and a two-state niche) to interact and exchange material (i.e. automata). This led to two main findings: (i) information niches that consist of simpler entities tend to be more resilient in the presence of foreign automata, and

(ii) they are also more readily reproduced in neighbouring niches. These findings show that proto-autopoietic systems that contain the simplest of automata tend to be more resilient to structural changes due to an influx of foreign automata and, secondly, that simpler networks tend to be more easily reproduced. This has implications for understanding how proto-autopoietic systems may scale and evolve.

Chapter 8 is part two of the examination of the cognitive process. This chapter introduces the use of the computation niche model which explicitly defines the system interface of an autopoietic system with its environment. This allowed several features of autopoietic theory to be examined including: (a) structural coupling of the niche with its environment, (b) the relationship between a system interface (analogous to a membrane) and the production of new automata, and (c) the effect of 'noise' on system dynamics. The main findings are that the system dynamics are hierarchical with an interplay of top-down, bottom-up and same-level information processing yielding a proto-autopoietic system that demonstrates information closure i.e. it is able to retain the information required to re-generate all possible system states something which was not evident from simulating the information niche model. This has implications for understanding the causal structure of an emergent proto-autopoietic system. An important finding was that proto-autopoietic systems with a population of automata that are too simple cannot respond effectively to extreme environmental conditions (specifically, the simplest one-state automata effectively cease to participate in interactions with other automata). This observation is one of two key findings that led to the conclusion that proto-autopoietic systems must reside within a 'window of viability' to endure as resilient platforms from which more complex organisations may form.

Chapter 9 examines the endogenous diversification of a computation niche driven entirely from an initial 'seed' population. This seed population consists of all 129 self-replicating automata types from a one-state and two-state population. These self-replicators were chosen as they could interact with each other to produce novel types of automata whilst also reproducing themselves. As such this was deemed to create a degree of competition between self-replication and the diversification of the population which would reveal whether novelty could be regulated via a competitive, dynamic steady-state. The results were unequivocal: an explosion in the appearance of novel automata is noted followed by a rapid tailing off in the rate of production of novelty. After 50 generations the population transitioned through four phases characterised as: (a) Diversification, (b) Increased Competition, (c) Penetration and (d) Saturation. The main finding is that open-ended novelty - even in the presence of a competing dynamic in the form of self-replicating automata - remained unregulated. There was no emergent regulation on the production of novel

automata as a result of any competition from established automata. Subsequently, novelty dynamics dominate the population and this leads to a diverse, unstructured population. This leads to the conclusion that an ability to regulate the rate of novelty production must be a critical property of any autopoietic system. This is a new finding in the field of autopoiesis and is the second key finding that leads to the concept of a 'window of viability' which can now be summarised as a proto-autopoietic system must not be too simple nor too diverse but rather reside somewhere between those two extremes. Cognition is the process by which the system maintains itself within that window of viability in light of changes to its environment.

Chapter 10 discusses the above findings in more detail and evaluates them in light of the original research aims of the project. Several themes emerge in this chapter: the window of viability, information content, the general properties of proto-autopoietic systems, for example, which are all behaviours generated by a universal process of competition. It is therefore proposed that at the heart of the autopoietic dynamic is a process of competition. All other processes - such as cognition, information processing, and so on - are realised through a competitive process. Not only does this have implications for what types of processes should be sought (i.e. competitive) in producing an autopoietic system in the real-world but this also has implications for bridging the conceptual gap between autopoiesis and Darwinian evolution i.e. selection at multiple levels occurs even in the most simple of proto-autopoietic systems and therefore a competitive process is the continuum that joins these two theories. In addition, the general properties of an autopoietic system are proposed as: (i) a strongly connected networks driving the self-production process, (ii) redundancy within that network and the population, (iii) diversity as a mechanism to recover from environmental perturbations, (iv) modularity in the network architecture which equips the autopoietic system with the ability to completely reproduce itself. These properties equip the system with the qualities of robustness and resilience which would be critical to the survival and long-term persistence of a platform which can act as a substrate for more complex forms of organisation to emerge such as autopoiesis.

Chapter 11 concludes with a summary of the research findings, an assessment of the limitations of the research that must be borne in mind when interpreting the results and conclusions, recommendations for future work are put forward, and a final concluding section summarises with the observation that the hypothesis that autopoietic systems emerge from simple, unstructured beginnings holds and that the work undertaken in this project to identify and characterise the properties and dynamics of such pathways is a worthwhile contribution to the study and practice of autopoiesis.

## BACKGROUND AND LITERATURE REVIEW

This chapter provides the necessary background to understand autopoiesis as a model of a minimal living system. The three criteria for determining whether a system is autopoietic is examined in detail by reference to the current thinking and literature in the field. This leads into a review of computational models of autopoiesis (termed 'computational autopoiesis') that are based on simulated artificial chemistries as a way to demonstrate how autopoietic systems can self-organise and endure. Several limitations in the field are identified and, specifically, the lack of any convincing narrative for how autopoietic systems may form from simple, unstructured beginnings.

### 2.1 A Minimal Living System

A living system is distinguished from non-living matter by its ability to reproduce and maintain itself [9]. To achieve this a minimal living system must integrate three functions [6]: (i) it must maintain its identity through the localisation of its constituent parts (compartmentation), (ii) it must use free energy from its environment in order to maintain, grow and reproduce itself (metabolism), and (iii) it must be equipped with some form of heritable information that can be transferred to future reproductions of itself. Alexander Oparin proposed that the origin of the first living cell must have emerged from increasingly complex chemical reactions that were able to endure over extended periods of time [49]. Such a system would be a form of autonomous chemical system able to demonstrate sufficient functionality and behaviour to be determined as living.

A biological cell is the archetype of a living system and a minimally functional version is called a protocell [5]. Efforts to develop protocells has grown significantly in the past two decades [27] and experimental approaches have branched into [50]: (a) constructing a protocell from the top-down approach that takes a contemporary biological cell with the aim of isolating the minimal genetic requirements to maintain the cell as a living system by the progressive removal of non-essential genes up to the point at which biological function is retained [51], and (b) a bottom-up approach that aims to synthesise a living cell from simple chemical precursors [52] such as nucleic acids and peptides encapsulated in lipid or fatty-acid vesicles [53], peptide-nucleotide microdroplets as membrane-free protocells[54], or protein-polymer nano-conjugates [55]. Whilst the top-down approach efficiently makes use of the building blocks that already exist (DNA/RNA/proteins) it is not an approach that can directly explain how living systems may have emerged in the absence of such complex molecular machinery. By comparison, it is necessary with the bottom-up approach to consider more broadly the chemical pathways by which a protocell can be created.

A chemical pathway from random molecular assemblies to a minimal protocell, without the use of any genetic apparatus, has been hypothesized [56] as feasible through mutually catalytic metabolic networks that exhibit the transfer of chemical information. Such assemblies of molecules would be held together by non-covalent interactions [57]. Whilst this is a compelling argument there remains the issue of whether such ensembles have the capacity to store and transfer information and to undergo chemical selection and evolution in the absence of informational polymers [58]. Therefore, a major requirement is demonstrable proof that a complex of molecules can retain and transfer information over generations in the absence of informational polymers such as RNA and DNA. There have been some suggestions of how this informational step could be achieved with the suggestion that protein interactions were the first form of reproducing life and that nucleic acids evolved later as 'memory molecules' [59]. An alternative suggestion is that a protocell is the basic unit of prebiotic evolution [60] that increases in organisational complexity as it evolves. This implies that there are minimal cells (e.g. vesicles) that are sufficiently robust that they allow alternative phenotypes to be explored with successful variants representing a change in the functional capability of the protocell. Such successful phenotypes become the new basic unit of evolution from which more sophisticated phenotypes can be trialled.

This is very much aligned to Oparin's view of abiogenesis resulting from a long and increasingly complex system of chemical reactions. Shirtless et al. set out three challenges to experimental protocell research: (i) *coupling chemistry with vesicle dynamics*: discover simple reaction networks that can spontaneously absorb into existing vesicles to modify the properties of the vesicle to induce growth and reproduction. In turn, the

vesicle should be supportive of that chemistry. This has similarities to autopoiesis (see section 2.2); (ii) *finding conditions and mechanisms for minimal functional integration*: this requires a search for specific conditions and the set of interactions that lead to a minimally function system that, at the least, integrates spatial and kinetic mechanisms; and (iii) *characterising the evolutionary dynamics of pre-Darwinian protocells*: working with low molecular weight chemical species (i.e. simple chemical structures) explore how such chemical assemblies could operate far-from-equilibrium in a robust manner such that a range of alternate phenotypes can be explored. Coupled to simple chemistry that can also divide with regularity this provides a minimal platform from which alternate mechanisms that produce increasingly reliable operation and heredity can be examined. As will be discussed in section 2.2 Shirtless et al's third challenge resonates strongly with the notion of a proto-autopoietic system.

The investigative effort into exploring alternative chemical pathways to abiogenesis has given rise to a new discipline within the field of chemistry called systems chemistry that:

“seeks insight into complex networks of interacting molecules and their system-level properties. These properties emerge through the collective behaviour of the system’s components and cannot be attributed to the individual components acting in isolation. The way in which specific interactions between the components propagate through the system dictates these emergent properties”[61]

This definition incorporates language from complexity science [34] (collective behaviour, emergent properties) and has parallels with the work of Maturana & Varela’s theory of autopoiesis. Complexity science is the body of knowledge, tools and techniques for the study of complex systems which have been defined as:

“a system in which large networks of components with no central control and simple rules of operation give rise to complex collective behaviour, sophisticated information processing, and adaptation via. learning or evolution”[34].

Complexity science is therefore concerned with how large systems change over time as a result of the interactions between the entities of which the system is composed [62]. Such relationships tend to be nonlinear and interactions at the local level can lead to changes at the global level through a process of self-organisation. A common phenomenon of self-organisation is the emergence of behaviour that cannot be predicted from examination of the individual entities of the system. This is one of the hallmarks of complex behaviour and, due to the nonlinear relationships involved, favours the development of mathematical models implemented as agent-based and/or numerical computer simulations to reproduce such dynamics.

There are two classes of computer models in systems chemistry: computational systems chemistry that seeks to build highly detailed molecular simulations that attempt to accurately reproduce the physical and chemical kinetics that may be involved in the formation of a protocell [63]. Computational chemistry is a definable and active area of research that requires access to substantial computer resources to perform very complex calculations to model interatomic forces, electron density surrounding nuclei, and so on [64]. By contrast the more abstract (one could say that they are achemical) approaches emphasise the general processes and properties that could lead to the emergence of systems that could support protocell formation. These efforts are far more diverse and varied in their approaches, solutions and insights that is occurring across multiple disciplines. The common phenomenon of these approaches is their attempt to reproduce complex behaviour such as self-organisation, emergence and adaptation which are concepts that reside within the discipline of complexity science. This is not a new insight and the field of complexity science - with its depth and richness of tools, concepts and methods that have been tried and tested across multiple disciplines - has the potential to enrich the domain of chemistry and systems chemistry [65]. The maturity, and therefore the usefulness, of complexity science rather than systems chemistry in developing our theoretical understanding of pathways to autopoiesis is helpful. For example, the mention of networks and collective behaviour is similar to that used in the definition of systems chemistry. Whilst adaptation via. evolution is implicit to the protocell as a 'basic unit of evolution' [5] it is not covered at all in the definition of systems chemistry. Furthermore, whilst systems chemistry mentions 'propagation' this is a rather ambiguous term and it is not obvious what information processing may mean in the context of a protocell. This is a serious omission given that information processing in living systems and particularly biological cells is an active and important field of investigation [66]. The complexity science description of a complex system resonates more directly to the concept of a protocell. In general complexity science has much to offer the development of the systems chemistry field not least in bringing greater clarity and maturity of thinking to what constitutes a complex system. Whilst systems chemistry is fundamental to experimental protocell work it lacks the body of knowledge required to also examine the theoretical aspects of protocells. Therefore the main epistemological backdrop to this project is the language, concepts and tools of complexity science. This topic is returned to in chapter 10.

Theoretical models of a minimal living system have been proposed with the three more prominent models referenced in protocell experimental research being Ganti's chemoton [40], Maturana & Varela's autopoietic systems [9], and Eigen & Schuster's hypercycles [41] [63] - see [38] and [67] for a detailed review of the state-of-the-art. Such models have

guided and inspired the design of computer-based models [6],[12] to examine and explore the dynamics and formation of *in silico* (artificial) cells. Two other important theories of living systems are (a) the Metabolism-Repair (M-R systems) model developed by Robert Rosen [68] and that overlaps considerably with autopoietic theory however as it is not so well recognised in the protocell research field it is not discussed here. Rather M-R systems theory provides an important comparison to the adaptive nature of autopoietic systems and, as such, it is introduced and described in section 2.2.3; and (b) Stuart Kauffman's autocatalytic sets [69] which suggests how networks of reactions can become more complex over time. Whilst Kauffman's work isn't as complete a theory as the others mentioned here it does provide important concepts that are relevant to thinking about pathways to living systems from simple beginnings. His work is most related to the specific process of autopoiesis and, as such, is discussed where it is most relevant (see section 2.2).

Eigen & Schuster's hypercycle model is an abstract model of self-replicating entities that form autocatalytic networks. They defined self-replication as the ability of an entity to catalyse its own reproduction. When that same entity formed part of an autocatalytic cycle they referred to as network replication which was defined as the mutual dependency of an entity on other entities to reproduce itself. Self-replication is reminiscent of RNA whilst network replication is characteristic of a metabolism. The combination of self-replication and network replication processes organised into a system called a hypercycle. A hypercycle is a system of entities that replicate themselves through self-reinforcing loops (self-replication) and that catalyse the self-reproduction of other entities (network replication). In this way the production of entities are related such that each of them catalyses the creation of its successor, with the final entity in the system catalysing the first entity. As such a hypercycle reinforces itself. This process of continual reinforcement through a system of replications satisfies the notion of a living system. As a theory it is wholly dependent on replicative processes that use informational molecules and highly refined catalysts (e.g. RNA and proteins) and, as such, can aid in both top-down and bottom-up experimental research that seeks to harness and/or reproduce modern molecular machinery. However, given that my research is examining minimal, unstructured beginnings of a living system any theory that is dependent on the presence of complex molecular machinery is, by definition, outside of the scope of this project. As such, Eigen & Schuster's hypercycle theory whilst well-studied and supported is excluded from further consideration and is not discussed in any further detail. Ganti's chemoton and Maturana & Varela's autopoiesis are models that make fewer assumptions about the chemistry that is present.

Tibor Ganti proposed a particularly elegant model of a protocell which he termed a

chemoton [70]. The chemoton is a contained system consisting of three reaction cycles: an autocatalytic cycle that constitutes the protocell's metabolic system, a replication cycle consisting of the protocell's genetic system, and a membrane-forming system (see Figure 2.1). Nutrients enter the cell and waste is extracted from the cell and this is managed by the metabolic system. The creation, maintenance and reproduction of the cell is the result of a carefully orchestrated interplay of these three subsystems. This is an intricate and detailed explanation of the internal features of cellular life that continues to prove its worth as a general heuristic for experimental design [71].

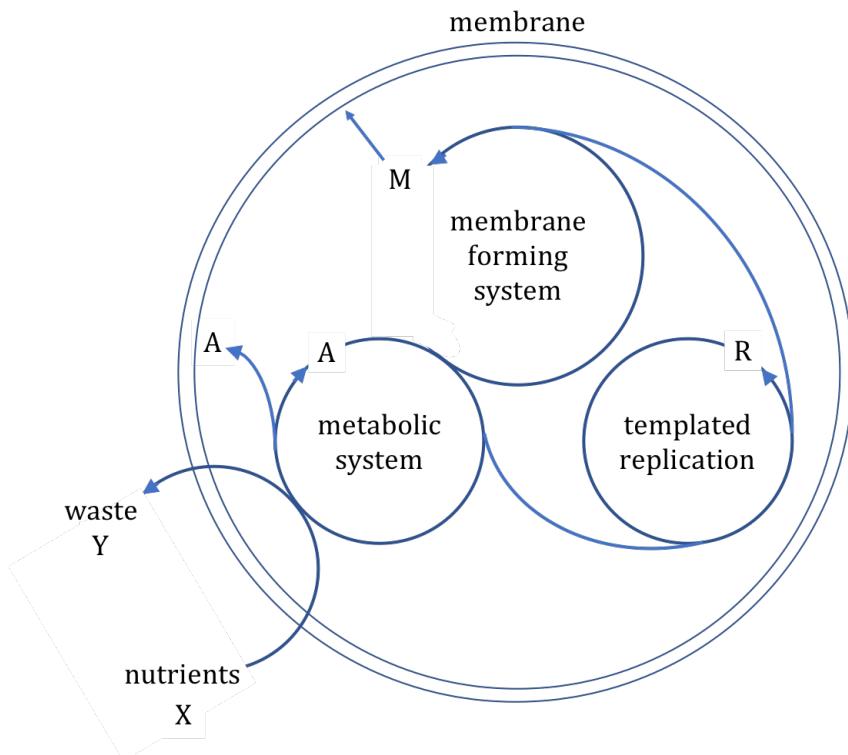


Figure 2.1: The metabolic cycle is an autocatalytic chemical cycle consuming the nutrient 'X' and producing 'Y' as waste with intermediate 'A'; 'R' is a by-product of the replication process that is required to produce 'M' the membrane molecule

Ganti's chemoton offers a simpler depiction of the necessary processes to generate and maintain a minimal living system that also includes a templated replication process albeit Ganti is less prescriptive over the use of informational molecules. His theory leans slightly more towards a bottom-up constructive approach. However, whilst this level of detail builds confidence in the model it has been argued that it is too prescriptive and, as such, this conceptual model is too narrow to expand to include higher notions of life centred around

concepts of epistemology, cognition and social behaviours [12]. By comparison the theory of autopoiesis does not have such profound limitations.

Maturana & Varela's theory of autopoiesis is a more general theory of a living system that does not require the explicit processes of templated replication nor informational molecules. It is also the chosen framework of bottom-up protocell researchers for understanding the system logic of a minimal living cell [27] with the openly cited reason for the continued popularity of autopoiesis the independence from nucleic acids thus providing experimental researchers with greater freedom to innovate [12].

## CHAPTER 2. BACKGROUND AND LITERATURE REVIEW

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	Theory of Autopoiesis	Computational Autopoiesis	Related Work
1950-1980	<p>Realization of the Living (Maturana &amp; Varela 1973)</p> <p>Formal model of autopoiesis (Zeleny 1977)</p>	<p>Computational model of autopoiesis (Varela et al. 1974)</p>	<p>Cybernetics (Ashby 1956)</p> <p>Viable System Model (Beer 1959)</p> <p>M-R Systems (Rosen 1970)</p> <p>Hypercycles (Eigen &amp; Schuster 1979)</p>
1980-2000	<p>Autopoiesis, reproduction, heredity &amp; evolution (Maturana 1980)</p> <p>Formal Model of Autopoiesis (Zeleny 1981)</p> <p>Autopoiesis – Implications &amp; Applications (Mingers)</p>	<p>Rediscovering computational autopoiesis (McMullin &amp; Varela 1997)</p> <p>Evolving Reaction-Diffusion Ecosystems with Self-Assembling Structures in Thin Films (Breyer et al. 1998)</p> <p>Lattice Artificial Chemistry (Ono &amp; Ikegami 2000)</p>	<p>Algorithmic Chemistry (Fontana 1981)</p> <p>Collective Autocatalysis (Kauffman 1984)</p> <p>Evolution of Individuality (Buss 1987)</p> <p>Arrival of the Fittest (Buss &amp; Fontana 1994)</p> <p>GARD model (Lancet 1996)</p> <p>Viable System Theory (Schwarz 1997)</p> <p>Matrix Chemistry (Banzhaf 1999)</p>
2000-2018	<p>Minimal Model of an Autopoietic Cell (Luisi 2003)</p> <p>Autopoietic and (M,R) Systems (Letelier 2003)</p> <p>Autopoiesis and Natural Drift (Etxeberria 2004)</p> <p>Autopoiesis With and Without Cognition (Bitbol &amp; Luisi 2004)</p> <p>Autopoiesis 40 years later (Razeto-Barry 2012)</p> <p>Systems of Creation (Mann 2012)</p>	<p>Towards evolving autopoietic artificial agents (McMullin &amp; Grob 2001)</p> <p>30 Years of Computational Autopoiesis (McMullin 2004)</p> <p>Autopoiesis and the Game of Life (Beer 2004)</p> <p>Autopoiesis and Cognition with Tesselation Algorithm (Bourgine &amp; Stewart 2004)</p> <p>Autopoietic Automata (Wiedermann 2007)</p> <p>Simulation of an Abstract Autopoietic Machine (De Loor et al. 2009)</p> <p>Simulation of an abstract autopoietic machine (De Loor et al. 2009)</p> <p>Anticipatory Artificial Autopoiesis (Dubois &amp; Holmberg 2010)</p> <p>Lattice Model of Emergence and Maintenance Autopoiesis (Wang et al. 2013)</p> <p>Evolutionary Simulations of Autopoietic Cells with Cognition (Matsufuji &amp; Narikiyo 2015)</p>	<p>Review of Artificial Chemistries (Diitrich 2001)</p> <p>Autonomy and Open-Ended Evolution (Ruiz-Marazo 2004)</p> <p>Chemical Organisation Theory (Diitrich 2006)</p> <p>Finitary Process Soup (Crutchfield &amp; Gornerup 2006)</p> <p>Autocatalytic Closure and Evolution of Cellular Networks (Decreane 2009)</p> <p>Characteristics of reflexive, autocatalytic networks (Hordijk et al. 2010)</p> <p>Autogenesis (Deacon et al. 2013)</p>

Figure 2.2: Summary of the key papers contributing to or closely related to the field of autopoiesis

There are a number of other related models of living systems including Beer's Model of Living Systems [72], Schwarz's Living System Model [73] and Dittrich & di Speroni's chemical organisation theory [74]. These models are only cited here for completeness;

conceptually they are more detailed and draw on a larger number of assumptions and as such are not minimal models of living systems. Figure 2.2 provides a summary of the core literature on autopoiesis and related works.

## 2.2 Autopoiesis

In 1974 two Chilean biologists, Humberto Maturana and Francisco Varela, announced their theory of how living systems are organised. They proposed that all living systems are *autopoietic* (*auto* - self and *poiesis* - producing) and that it is this unique behaviour that distinguishes living from non-living matter. Figure 2.3 illustrates the concept of an autopoietic system as a topological bounded structure maintained by the dynamic interplay between the boundary and internal reactions. As can be seen the semi-permeable boundary allows the substrate  $A$  to diffuse into the system where it participates in the internal reaction  $A \rightarrow S$  the product of which is a component of the boundary itself. Over time the component  $S$  decays to a waste product  $P$  in the reaction  $S \rightarrow P$  leaving a hole in the boundary. This hole is subsequently 'repaired' by the migration of the product  $S$  to the boundary thus completing a maintenance cycle. This minimal example is demonstrating that:

"a system can be said to be living if it is able to transform external matter/energy into an internal process of self-maintenance and production of its own components" [12]

A protocell - as the archetype of autopoiesis - is an open, dissipative system with a sequence of chemical processes occurring inside the cell to maintain a boundary and therefore its identity within its environment. The maintenance of its boundary and its identity is the defining behaviour of an autopoietic system.

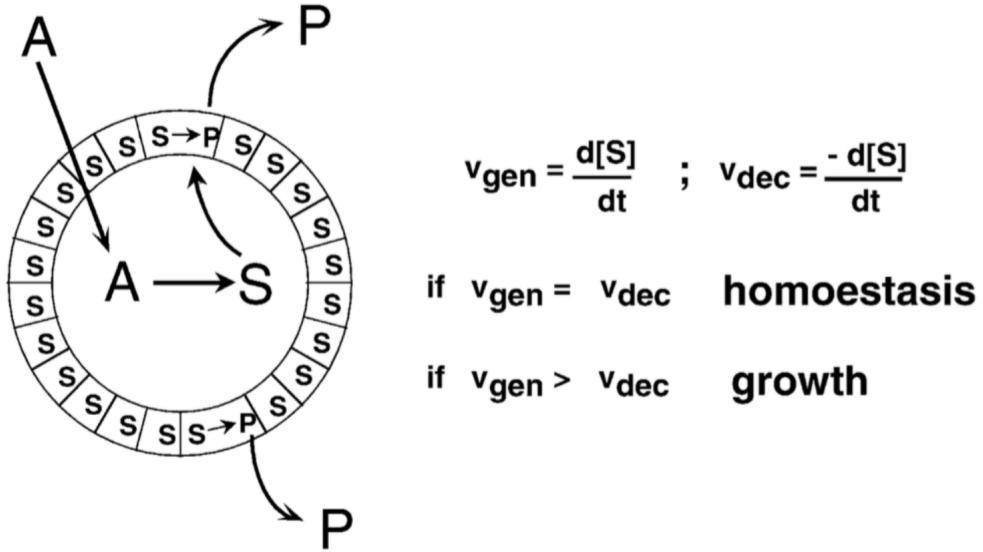


Figure 2.3: Luisi's schematic of a minimal autopoietic cell where a substrate entity ( $A$ ) produces the product ( $S$ ) which links to other  $S$  entities to form a boundary which encapsulates the  $A \rightarrow S$  reaction. Over time  $S$  decays to the waste product ( $P$ ) leaving a hole in the boundary which is repaired by a newly produced  $S$  migrating to the cell boundary. The dynamic behaviour of the system is described by the two differential equations  $v_{gen} = \frac{dP}{dt}$ ,  $v_{dec} = \frac{-dP}{dt}$  and the interplay of the two determines the present state of the autopoietic cell as growing, at homeostasis, or decaying.

An autopoietic system is able to maintain itself through its internal network of reactions that produce the components of which the system is composed. Therefore, autopoietic systems:

“(i) through their interactions and transformations continuously regenerate and realize the network of processes that produced them, (ii) constitute [the cell] as a concrete unity in space in which [the components] exist by specifying the topological domain of its realization as such a network” [9]

In other words the autopoietic system organises the production of its own components which allow it to maintain the network that is producing them. The self-referential nature of these systems is a signature characteristic of autopoiesis. Consider Maturana's own words on this matter:

“When you regard a living system you always find a network of processes or molecules that interact in such a way as to produce the very network that produced them and that determine its boundary. Such a network I call autopoietic. Whenever you encounter a network whose operations eventually produce itself as a result, you are facing an autopoietic system. It produces itself. The system is open to the input of matter but closed with regard

Self-boundary	Does the system have a boundary of its own making?
Self-maintenance	Is the system capable of maintaining its own identity via. dynamic processes, i.e. those components that are being used up are made anew by the system itself?
Self-generation	Does this happen throughout a network of reactions that are generated by the system itself?

Table 2.1: Varela's criteria for autopoesis

to the dynamics of the relations that generate it.” [75]

Luisi [12] offers a useful depiction of the ‘cyclic logic of cellular life’ (see Figure 2.4) <sup>1</sup>:

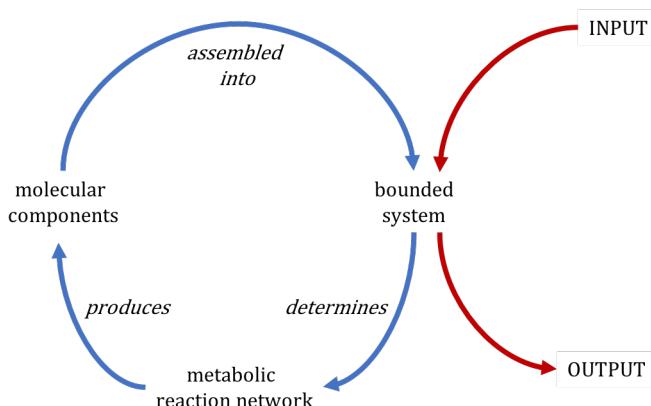


Figure 2.4: Luisi’s cyclic logic of cellular life as a depiction of autopoesis as being ‘the most general pattern of minimal life [that does not] specify the actual structures and their processes’

For me the most compelling aspect of autopoesis - and as illustrated in Luisi’s cyclic logic diagram - is that it does not require any assumptions over the specific molecules or chemistries that are required to construct a living system. The self-referential abstraction of a living system as one that produces components from which it is formed has a simplicity and minimality that it is hard to conceive of any other model or theory that could reduce such requirements any further. Varela [12] proposed three criteria for autopoesis:

Applying these criteria to the real world, Luisi gives the example of the following as not being autopoietic: ‘a virus.... as it does not produce the protein coat of its boundary or its nucleic acids (the host cell does this)’ [12]. Each of these criteria will now be described alongside any related literature.

<sup>1</sup>this became a useful framework within which to understand and organise my own results on simulating the formation of autopoietic systems from simple, unstructured beginnings (see, for example, Chapter 4)

### 2.2.1 The boundary of an autopoietic system

Applying the first criteria - the system has a boundary of its own making - is perhaps the most contentious issue. As explained by Barry McMullin [33], with molecular autopoiesis (i.e. as it pertains to a biological cell), 'the boundary performs at least the function of limiting or controlling the spatial diffusion of the molecules constituting the system' and 'in the absence of such control on diffusion, the reactant concentrations may dilute to the point where one or more of the defining reactions effectively ceases to operate, and the whole self-sustaining reaction network then breaks down'. In other words, molecular autopoiesis is wholly a physical manifestation of an autopoietic system and the criteria should apply to a physical system. However, and McMullin goes on to explain, a computer simulation of an autopoietic system (see section 2.3) demonstrates the compartmentation of a reaction network with the compartmental boundary maintained by that network. In this simulation the boundary is constantly decaying and that requires continuous maintenance which is a sufficient demonstration of one of the phenomena of autopoietic systems. Nevertheless, and as explained by McMullin, '... the fact that the spatial localization is regularly interrupted in this way makes it more difficult to be clear what exactly the 'topological' autopoietic requirement is' [33]. Here McMullin is referring to an older criterion of an autopoietic system as 'specifying the topological domain of its realization' [13] which Varela subsequently simplified to 'does the system have a boundary of its own making?'. The apparent quandary that McMullin identifies is born out of his investigation into what distinguishes an autopoietic system from an autocatalytic one. This is an important question as, it is generally assumed, that any reaction network that continually produces the components that regenerates the network is an autocatalytic one. An autopoietic system is highly likely to always consist of an autocatalytic reaction network. What, then, is the distinction? As McMullin states, 'the critical distinction is that autopoiesis specifically requires that this confinement should itself be in some sense a product of the confined reaction network, whereas collective autocatalysis is assumed to rely on some independent confinement mechanism' [33]. Dissatisfied with the lack of clarity of Maturana & Varela's criterion McMullin proposed the following informal heuristic test:

1. Consider two instances of the same collectively self-sustaining reaction network consisting of exactly the same set of molecular species
2. Each is constituted instantaneously by distinct collections of individual molecules occurring in separate reaction vessels

3. Mix the contents of the two vessels together into a single vessel assuming that any food set continues to be available
4. Are there still two separate reaction networks of just one?

The final question is only true if the networks themselves maintain their individuality in the absence of any spatial separation mechanism. If this can be meaningfully shown then the reaction networks can be reasonably believed to meet the criteria for 'specifying the topological domain of its realization'. If the reaction networks cannot be readily distinguished then the singular network that is the product of their amalgamation should be considered as collectively autocatalytic. I acknowledge what McMullin is attempting here - to generalise on the concept of a 'boundary' to extend the applicability of autopoietic theory outside of cellular life - however how does one use this in practice? How does one go about distinguishing the continued co-existence of two separate reaction networks that are constituted of an identical set of molecules? This requires an ability for the reaction networks to co-exist in a physical space that would, nevertheless, allow them to maintain themselves as separately identifiable entities. Indeed, McMullin goes on to use his heuristic test on contemporary state-of-the-art computer simulations that may demonstrate autopoiesis [33]: Walter Fontana's algorithmic chemistry which I discuss in section 2.3, John Holland's  $\alpha$ -universes, Tom Ray's Tierra model and the Substrate-Catalyst-Link (SCL) model which McMullin developed with Francisco Varela and which I present in section 2.3.1. Given that three of these models do not specifically set out to demonstrate autopoiesis - they allude to the existence of a relationship based on observations of self-organisation, renewal and persistence - it is of no great surprise that McMullin's "test" places them firmly as collectively autocatalytic systems and not autopoietic. However, what is surprising is that the SCL model, designed as it was to specifically demonstrate autopoiesis, does not in fact pass the McMullin heuristic either and therefore should not qualify as exhibiting *proper* autopoietic organisation. The emphasis here on proper is mine and in recognition of the contested status of what is deemed an irrevocable characteristic of autopoietic behaviour. It is interesting to note that the majority of discussion in the literature centres on the definition of what qualifies as an autopoietic system rather than on a deeper understanding of the underlying mechanics from which self-producing behaviour emerges. One of the contributions that my work makes here is to bring a quantitative dimension to the underlying processes and components that constitute a system-level behaviour that demonstrates how a system can maintain its identity within a changing environment and, it can be argued, is maintaining a non-physical boundary.

An attempt to illuminate the mechanics of an autopoietic system comes from the field of artificial life [76]<sup>2</sup> where Virgo et al [17] challenge the significance (or not) of the spatial boundary in an autopoietic system and, in doing so, deconstruct the continual renewal of such systems to processes and dynamics. They agree that boundary formation and maintenance is critical to the demarcation of the living system as a unity against its background environment, however, the boundary does not exclusively take on the role of containing the processes that constitute the autopoietic system. In separating out demarcation from containment the authors de-conflict two concepts which, they claim, are too often conflated: the physical boundary of an autopoietic system and the operational limits of the system itself. The former is produced by the system whilst the latter determines which processes are part of the system. Their aim is to bring precision to the definitions and meaning associated with autopoiesis. For example, they define a process as, 'something that happens repeatedly or which tends to happen whenever the right conditions are met' [17] and that within the physical/chemical realm that such processes share properties e.g. every process transforms something into something else. Processes have a causal effect. By comparison, the dynamics of a system are the way in which the variables of the system change over time and processes are the things that effect those changes. The essential point here is the co-dependence between processes (e.g. process B is wholly dependent on process A) and that this forms networks of dependent processes which have the property of operational closure. Operational limits therefore describe which processes are in scope to the correct functioning of an autopoietic system. Consider Figure 2.5, which illustrates an autopoietic system that consists of several inter-dependent processes one of which ('M') forms the boundary. One of the enabling processes on which process 'M' is indirectly dependent (process 'W' in the example) resides outside of the operational limits.

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<sup>2</sup>incidentally it has been suggested that autopoiesis is a founding concept for artificial life

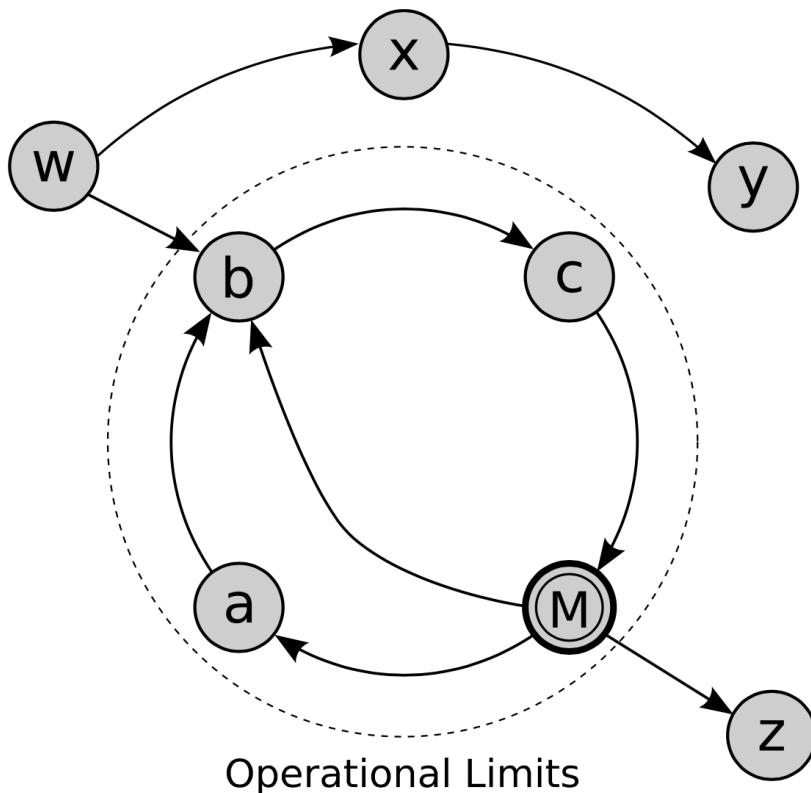


Figure 2.5: An illustration of the operational limits of an autopoietic system as suggested by Virgo et al.

From Figure 2.5 the processes 'w','x','y' and 'z' are not part of an operationally closed network i.e. there is an absence of cyclical dependence on their activity. By comparison, the processes 'a','b','c' and 'M' are in a strongly connected network that is cyclical i.e. operationally closed. One can assume, and Virgo et al's depiction does not dissuade us otherwise, that those processes which reside within the operational limits are also contained within the spatial boundary formed by process 'M'. As they state quite clearly the spatial boundary is not the same as the operational limits. This is an interesting claim as, apart from challenging the conceptual constraint that an autopoietic unit must have a physical boundary, it clarifies the embedded nature of an autopoietic system in its environment. For example, by accepting that the spatial boundary of an organism is not equivalent to the operational limits of the system this forces the acceptance that an autopoietic system may include processes that are not occurring within its spatial boundary. This is a pertinent point to bear in mind when considering the role of structural coupling in the process of cognition within an autopoietic system (see section 2.2.3). They then proceed to prove this statement by referring to the original works of Maturana & Varela where they state that

autopoietic systems are homeostatic. Virgo et al. test this statement by demonstrating that homeostatic machines can consist of processes and dependencies outside of the defined operational limits of the autopoietic unit e.g. a thermostat as a homeostatic machine has to take into account the heater, the air in the room, and so on.

This notion of dependent processes outside of the classically defined autopoietic unit they refer to as 'extended autopoiesis'. To illustrate this point they recite the example given by Wheeler [77] of an earthworm: the worm builds tunnels held open by its secretions which in turn helps it to digest its food. If the autopoietic boundary of the worm is considered as just consisting of its outer skin then this completely ignores the dependency that it - as an autopoietic system - has on the effects of its secretions. So what is the autopoietic system here? The worm or the worm and its secretions and tunnels? Maturana & Varela themselves provide the explanation, '... if one says that there is a machine  $M$ , in which there is a feedback loop through the environment so that the effects of its output affect its input, one is in fact talking about a larger machine  $M'$  which includes the environment and the feedback loop in its defining organization' [13]. Therefore the worm and its secretions form the autopoietic system even though the secretions reside outside of the physical spatial boundary of the worm itself. In conclusion, Virgo et al. have demonstrated a respectable argument for why defining the spatial boundary as a critical defining component of an autopoietic system is too limited and risks missing important structural dependencies. Their work also appears to highlight a contradiction in Maturana & Varela's original thinking between the necessity of a boundary to achieve operational closure whilst paradoxically also recognising that dependencies on processes external to that boundary should be considered part of the operational closure of the system. Virgo et al. set out to challenge the notion of the sacredness of a spatial boundary in identifying autopoietic systems and I believe it does this well through the notion of extended autopoiesis. This does, of course, raise the question of how to identify autopoietic systems if spatial boundaries are not a reliable guide. Surprisingly they do not explore this and yet they have laid out the necessary concepts - dependent processes and extended autopoiesis - from which a procedure could be developed to detect and trace the autopoietic forms in a complex system. My work progresses these concepts somewhat with an investigation into the processes and dynamics that lead to the formation of non-trivial self-producing populations of interacting entities. As will be discussed shortly I claim that such interacting populations that have evolved to a steady-state configuration under specific environmental conditions - what I call a niche - are proto-autopoietic i.e. they are critical processes that provide a resilient platform on the pathway to autopoietic systems.

Another challenge to Maturana & Varela's insistence that the boundary is a physical

one comes from the social sciences. Niklas Luhmann was the pioneer of social autopoiesis [19] and who quite successfully introduced the concept of autopoiesis into efforts to understand collective human behaviour. He stated his goal as, 'the application of the notion of autopoiesis to social systems [which] required the development of a more general "non-physical" notion of autopoiesis' [78]. Luhmann began to tackle this by proposing that the social processes of the autopoietic network were processes of communication between people rather than molecular reactions. In Luhmann's own words:

"For a theory of autopoietic systems, only communication is a serious candidate for the position of the elementary unit of the basic self-referential process of social systems" [19]

Luhmann's adaptation retains the main feature of autopoiesis - self-maintenance due to a process of self-generation from within - and that the 'boundary' in a social system are the rules that define the system. These social systems are open in that they interact with their immediate environment and other social systems and they do so without losing their identity. Consider a football team which occupies a location (the football ground), the team colours, the team emblem, the team's history and its supporters. These define the properties of the system and new players/new supporters are transformed into being team players and team supporters as they become integrated into the bounded structure which is the team's identity. Consider Figure 2.6 which is reproduced from [12] that illustrates the same cyclical logic that Luisi uses to define an autopoietic system (as per Figure 2.4) except that here human relationships substitute for chemical reactions and the rules of the social community substitute for the membrane boundary. The critical distinction that Luhmann made and that extricated autopoiesis from the biological realm - sadly without the support of its founders - was to re-define a boundary as non-physical. This was an important development in the field of autopoiesis that led to application of the theory into other non-biological areas such as art [20], knowledge in institutions [21], computation theory [22], information systems [23], law [24] and architecture [25]. As will be seen in later chapters of this thesis both types of boundary are evident in my work which suggests that Maturana & Varela's prescription for a physical, bounded domain may be too restrictive and that challenges to this have merit.

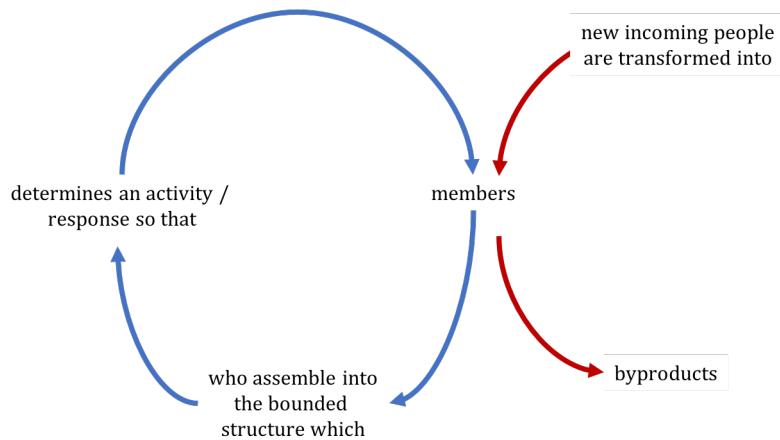


Figure 2.6: The concept of social autopoesis retains the circularity of chemical autopoiesis except that people are the entities that enter and leave the autopoietic system and the interactions between them are in the form of communication.

The final challenge to the physical boundary conjecture comes from the field of synthetic biology and protocell research. Whilst some high profile protocell researchers specifically denote the need for a membrane [52] there is a growing body of research focused on membraneless protocells [79],[80],[81]. These approaches employ complex coacervates formed from aqueous two-phase separation techniques (such as electrostatics) [79]. If you consider the two-phase separation that occurs when oil and water are mixed together then coacervate protocells employ the same principle but entirely in an aqueous solution by varying the pH, temperature and ionic strength of the two components with separation occurring when the polymer component exceeds a given threshold [82]. So does this mean that synthetic biologists are abandoning autopoiesis as a systematic framework? I believe the answer is no they are not and instead greater emphasis is being placed on the organisational logic of a cell as consisting of autopoietic processes [1] that does not explicitly demand the formation of a physical boundary (see Figure 2.7). Instead the protocell is considered as an organised chemical system that undergoes changes according to its own activity and the inputs that it receives from its environment. Of course, this requires some delineation of what is part of the system and what is external to it however that particular task is left to the individual researcher to define within the context of their own experiments.

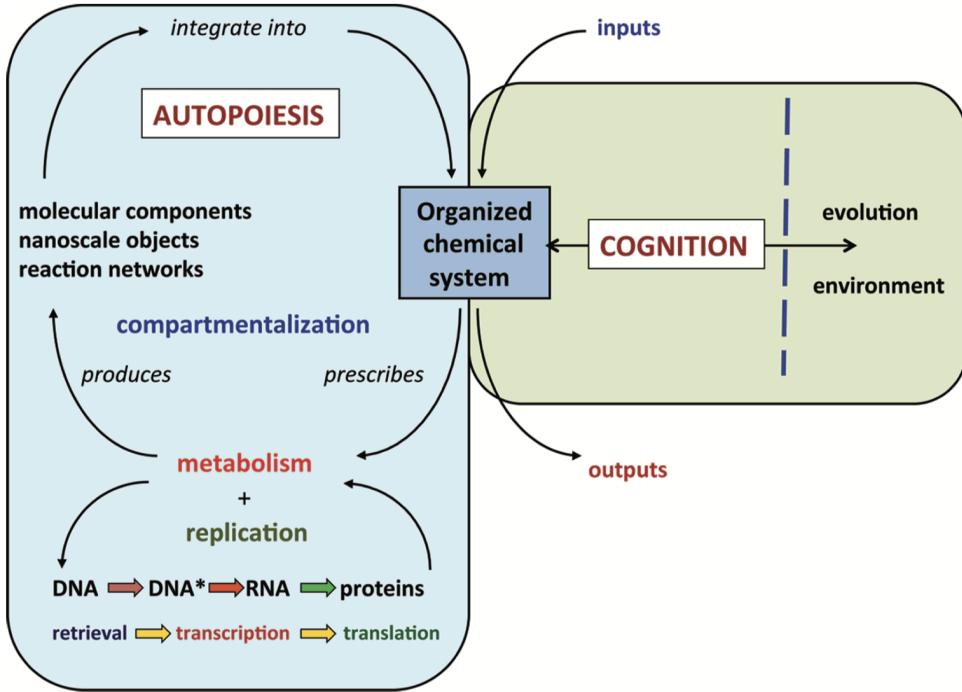


Figure 2.7: The organisational logic of modern cellular systems as proposed by Stephen Mann [1] that is an adaptation of Luisi's cyclical model of cellular life.

In summary, the boundary of an autopoietic system is considered critical criteria by the founders of the theory and yet it has become a contested issue. Two competing notions continue to exist in the literature: those who adhere to the strict physical meaning of a membrane-like boundary that only makes sense within biological systems, and those that promote a broader meaning of boundary to denote the existence of cyclical processes that are operationally closed with the effect of maintaining the identity of some system. The former advocate that only physical boundaries that encapsulate the reactions that create the boundary itself qualify as autopoietic systems. The latter advocate that the original physical meaning of a boundary is too restrictive and excludes a broader understanding of so-called extended autopoiesis where dependencies outside of any physical boundary are still critical to the functioning of that autopoietic system. The contribution that my research makes to this discussion is threefold: (i) I demonstrate that physical membrane-like boundaries can form spontaneously in very simple populations driven entirely by the chemical affinity between interacting entities, (ii) that the identity of a self-producing and self-sustaining population of interacting entities can persist even under significant environmental perturbations *in the absence of a physical boundary*, and (iii) given that I

observed the emergence of physical and non-physical boundaries in my simulations this suggests that the notion of 'extended autopoiesis' may well be correct. In general terms my work provides additional insight into the underlying dependent processes, structures and properties that lead to the retainment of a system identity. As discussed in Chapter 10 I outline the properties that I have observed in studying the proto-autopoietic networks that provide a resilient mechanism for maintaining system identities. I also offer the rule that a system is autopoietic if it can maintain sufficient information within its dynamic organisation to re-generate and maintain itself even after severe environmental shocks. The interesting observation that arises from this is that in some cases a system is wholly dependent on the environment to provide the necessary information required for it to re-generate itself. This strengthens the case for the extended autopoiesis argument. From my own research I find that I associate my understanding closer to that offered by [14] where 'an autopoietic system is a network of processes that produces the components that reproduce the network, and that also regulates the boundary conditions necessary for its ongoing existence as a network'.

### **2.2.2 Maintenance of an autopoietic system**

Maintenance - within the context of autopoietic theory - is the continued and enduring presence of the overall organisation of the system. Maturana & Varela give a very specific meaning to organisation as, '.. those relations that must be present in order for something to exist' (p. 42, [83]). The organisation of an autopoietic system is the relation between its components and the properties of those components that define the system as a single entity (a unity). For example, the organisation of a computer can be described as the necessary relations between components such as the central processing unit, memory, hard drives, power supply and so on. The unity of these components may be identified as a computer as this organisational form would produce the necessary properties expected of a computer. Organisation is the invariant property of an autopoietic system in that if the organisation changes then the identity of the system changes (e.g. removal of the central processing unit in our computer means that it is no longer identified as a computer) and may no longer be autopoietic. Maintenance is about the continued renewal of those components that are required to maintain the functional relations that permit the system to acquire and regenerate its own identity. Such maintenance represents organisational (or operational) closure whereby the product of the organisation of the system is the organisation itself. This is the essential and distinguishing behaviour of autopoietic systems from other autonomous systems. All possible states of the system must maintain this autopoietic organisation

otherwise the whole system falls apart.

Whilst the organisation of a system describes the invariant properties of the system its structure are those variable elements that actually constitute the system as a unity in space and time. Whilst the organisation of a protocell does not change between different manifestations of the cell (they are all of the same organisation which constitutes their autopoietic behaviour) their structures will be different. Structure describes the actual components and the actual relations of an autopoietic system. Structure is the real manifestation of an autopoietic system whilst its organisation is the more abstract generality that is common to all possible manifestations of such a system. An autopoietic system is structurally determined i.e. the structural changes that are possible within the system at a moment in time are determined by the current structure of the system itself. Structural changes arise through endogenous and exogenous sources as described by John Mingers [84]:

“[structural changes] will occur in response to both internal dynamics and environmental interactions.... perturbations in the environment trigger changes of state in the organism, but since all possible changes must maintain autopoiesis, the actual nature of these changes and the possible interactions which an organism can successfully undergo are determined by the organism’s physical structure”

The relevant point here is that the environment does not determine or specify the structural changes that occur in an autopoietic system. Only the present structure of the autopoietic system can determine what the possible state changes to the system are. Environmental perturbations can only act to trigger structural change and they do not determine the nature of that change. The interplay between environment and autopoietic unit, with the structure of the latter being influenced by the former, is known as structural coupling and this is discussed in section 2.2.3.

As such an autopoietic system - a unity - has both organisation and structure. Such a unity is realised at a moment in time as a particular structure and the changes in state of the system are structurally determined. There are many possible structures which can realise the same organisation in a many-to-one relationship. The structure will have properties and features not specified by the organisation e.g. the particular brand of CPU in the computer, the storage capacity of the hard disk, and so on. Hence, structural changes occur without altering the organisation e.g. as our hypothetical computer ages we upgrade the processor, add more memory, replace the power supply and yet its identity as a computer remains unchanged. However, organisation and structure are not independent of each other. An organisation of a living system can only exist (i.e. its identity) through the continued renewal of its components with the ability to do that, from moment to moment,

determined by the structure of the system. These are inextricably linked concepts. The operational limits of autopoietic systems are defined by its organisation and its relationship with its environment. The notion of extended autopoiesis that is implied here is relevant to the exploration of the possible pathways to autopoiesis and, more specifically, the types of organisation that may unfold from simple and uniform beginnings.

The notion of organisation and structure as two separate but linked entities is reinforced by Robert Rosen and his Metabolism-Repair (M,R) theory [68]. Rosen (who was a pioneer of studying biology as a complex adaptive system) claimed that the organisation of a system must be independent from the 'material particles'<sup>3</sup> that constitute the system. In a story told by his daughter Ms. Judith Rosen, he explains this quite beautifully as follows:

"The human body completely changes the matter it is made of roughly every 8 weeks, through metabolism, replication and repair. Yet, you're still you –with all your memories, your personality... If science insists on chasing particles, they will follow them right through an organism and miss the organism entirely." - Robert Rosen (as told to his daughter) [85]

Like Maturana & Varela, Rosen is emphasising the importance of understanding the organisation of a living thing rather than what it is made of. This is partly a statement that reductionism is not sufficient to understand biological phenomena and also an indication of what Rosen believed, namely, that understanding the relations between things in a living system is more important to explaining a living system than understanding the individual parts of that system.

Robert Rosen's Metabolism-Repair theory is based on the notion that biological systems are distinguished from non-living systems by their organisation which is a result of the complex interactions between the components of the organism the behaviour of which cannot be reduced to any one component in isolation. Specifically, 'when we break the system apart in order to study it, we destroy its organization and therefore cannot see how it functions' (p. 118 of [86]). His concept of organisation is that, 'a system is organised if it autonomously tends to an organized state' through a thermodynamic process of self-organisation [87]. The link to thermodynamics and, specifically the second law of thermodynamics, would therefore suggest that such organized states are out-of-equilibrium and that the underlying processes of the system are open and dissipative. Rosen suggests that the measure of a systems degree of organisation is equivalent to the improbability of its state (although he does not offer a method for determining this). From this he suggests that identifying and studying the properties of organisations that are able to 'autonomously' move to an organised state should be our primary focus in understanding

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<sup>3</sup>Rosen's 'material particles' are synonymous with Maturana & Varela's 'structure'.

biological systems. This motivation led to his development of the Metabolism-Repair (M,R) system theory that attempts to capture the minimal functionality of a living system.

An (M,R)-system consists of two functions: Metabolism (M) which is an abstraction of anabolic and catabolic functions, and Repair (R) which is an abstraction of a genetic function that provides the information necessary to construct the M-R system (including re-generation and replication). Unlike Maturana & Varela, Rosen does not specify the need for a boundary and in this sense it is a more general formalism of an autonomous, self-producing system. Consider Figure 2.8 which illustrates an (M,R) system as consisting of A an environment, B a Repair function,  $f$  a Metabolism function and  $\Phi$  a Replication function. The diagram can be understood as follows: A is transformed into B assisted by  $f$ , B is transformed into  $f$  assisted by  $\Phi$ ,  $f$  is transformed into  $\Phi$  assisted by B. Here the dashed and solid lines denote the efficient cause (the process which brings something about which, in chemical terms, would be a catalyst) and the material cause (the physical properties that are being changed in the formation of something i.e. chemical transformation) respectively with the directional arrows indicating the flow of causation. Metabolism is the set of chemical transformations  $A \rightarrow B$  catalysed by a set of catalysts  $f$ . Repair is the production of the set of catalysts  $f$  as instigated by the growth and decay of the system catalysed by the replication system  $\Phi$ . The organisational invariance (which Rosen calls 'replication') is realised through the maintenance of the repair system. In the (M,R)-system model all catalysts are produced internally.

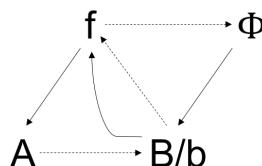


Figure 2.8: An illustration of the causal flows in Rosen's (M,R) system model which is a minimal abstraction of an open, dissipative system that is able to transition to and maintain an organised state. The solid lines indicate a material cause and dashed lines indicate an efficient cause. Labelling is expressed in category-theoretic language where: A is the environment, B is the Repair function,  $f$  is the Metabolism function and  $\Phi$  is the Replication function.

From this Rosen proposes that, 'a material system is an organism if, and only if, it is closed to efficient causation' (p. of [87]). That is, if  $f$  is any component of such a system, the question "why  $f$ " has an answer within the system, which corresponds to the category of efficient cause of  $f$  (p. 244 of [87]). In simpler terms, all information required about the system and its environment must be encoded into the organisation of the system itself. This information is 'capable of acting causally on the organism's present behaviour based

on relations projected to be applicable in the future' [88]. This insight gave rise to the notion of (M,R)-systems as anticipatory:

"An anticipatory system is a natural system that contains an internal predictive model of itself and of its environment, which allows it to change state at an instant in accord with the model's predictions pertaining to a later instant"[87]

This is not incompatible with autopoiesis and indeed Francisco Varela suggested the term 'intentionality' [42] to convey a similar notion. The effect of intentionality has been investigated using an artificial life simulation [89] with the result that an autopoietic system that embodies even the most basic form of anticipation improves its viability. In this work intentionality was manifested as self-repair of the membrane. Equivalently, the organisation of an autopoietic system is the internal predictive model encoded in the relations between its components that represent knowledge of how to self-produce; the ability to change state based on that model is structurally determined. An exploration of the properties of cellular self-organisation [90] reinforced the criticality of the notion of 'closure to efficient causation' in (M,R)-systems to the viability of an organism and that this is synonymous to the concept of 'organisational closure' in the theory of autopoiesis.

In general the (M,R) and autopoietic theories abstract out the specifics of components and instead emphasise a circular causation as the embodiment of a living system. The intersection of autopoiesis and (M,R)-systems theory has been investigated [88] with the conclusion that autopoietic systems are a subset of (M,R)-systems. If that should prove to be the case then an autopoietic system must inherit some of the characteristics of a (M,R)-system such as encoding all of the information required for self-production and self-maintenance. And yet, to the best knowledge of this author, there are no investigations into the information content of an autopoietic system. This unexplored aspect of autopoietic systems is directly investigated in this project and, as presented in Chapter 4 and discussed in more detail in Chapter 10, I discovered that the ability for a self-producing system to transition to different structural states can be quantified by the Shannon entropy of its current structure.

Whilst (M,R)-systems theory and autopoietic theory share a number of important concepts the former is based on category theory which is a rather specialist branch of mathematics. This is not without merit for a receptive audience - and, indeed, work has been published on distinguishing between the two theories from a category theoretic perspective [91] - however it was decided early on in this project that the technical nature of category theory risked making the model, and therefore the findings, too inaccessible to a wider non-mathematical audience. Hence, whilst (M,R)-systems would share a common conceptual home with autopoiesis it would not be central to this project.

Another closely related model to autopoiesis is autocatalysis [69] or, more precisely, collective autocatalysis [33]. Autocatalysis is a chemical dissipative system [92] that self-reproduces - it consists of a set of chemicals whose transformational interaction reproduces the chemicals in the set. Under conditions of dissipation and random decay autocatalytic sets have the potential to reconstruct their own lost components and if the energy input exceeds the energy output then the autocatalytic set grows in volume. If this autocatalytic set is within some form of cellular enclosure then osmotic pressure can cause the container to split (aka. cell fission). Stuart Kauffman [69] proposed and Doyne Farmer et al [93] developed in detail a computational model of polymers that were created through the reaction of smaller and simpler molecules and from which, over time and with a sufficiently diverse population of polymer species, an autocatalytic set formed. The idea is that polymers will emerge from the catalysed reactions of simpler molecules no matter how improbable those initial reactions may be. This assumption built on the results of experimental work by Cavadore [94] and Fox & Dose [95] that showed that small molecules (such as peptides) can catalyse the reactions of other peptides. Kauffman's hypothesis was simple: self-reproduction is a 'natural collective expression of polymer chemistry' [69] and the underlying physical mechanism that enables such behaviour is autocatalysis. To achieve catalytic closure in a set of catalytic polymers, Kauffman suggests four steps:

1. All possible polymers up to a critical length  $M$  should be available to participate in a reaction (either as a substrate or as an enzyme)
2. All possible combinations of legitimate reactions that can occur in this set and by which these polymers can be formed from one another should be considered
3. The capacities of polymers to catalyse reactions should be clearly defined i.e. all polymers have the capacity to catalyse a reaction (whilst there is a very small probability that a reaction can occur between two molecules in the absence of a catalyst these are not included in Kauffman's model)
4. The probability that a set of polymers contains a subset which is reflexively autocatalytic rises to 1 as a critical threshold is reached

In a system of just two molecules representing an initial food set there were  $\approx 2^{M+1}$  numbers of polymers that could be produced from the cumulative effect of increasingly complex molecules reacting and producing new molecules. Therefore as  $M$  increased the number of polymer species increased exponentially. The molecules that participated in the chemical reaction - the catalyst and the substrates - were chosen at random. As the process

iterates the proportion of new molecules in the population grow and, as such, were more likely to be randomly selected to be a catalyst in a future reaction. In this way a network of reactions grew over time with simple molecules reacting to create new molecules which themselves catalyse other reactions possibly those that create their own substrates. If a subset of this reaction network consists of molecules that catalyse and produce each other an autocatalytic set is deemed to have formed. Kauffman's autocatalytic sets in which every reaction in  $R$  is catalysed by at least one molecule involved in any of the reactions in  $R$  and (ii) if every reactant in  $R$  can be constructed from an initial food set  $F$  by successive applications of reactions from  $R$  then it is defined as a reflexively autocatalytic and  $F$ -generated (RAF) set [39]. A formal method for detecting and confirming such sets has been described in detail [96]. The emergence of an RAF set is the key mechanism by which more complex chemistry can arise and sustain itself from simple, random precursors. This is the cornerstone of Kauffman's theory.

There is a critical relationship between the probability  $P$  of a catalysed reaction occurring and the critical length of polymer  $M$  required to form an autocatalytic set. The critical length  $M$  is the threshold at which there is a sufficient diversity and number of polymer species  $2^{M+1}$  available to participate in reactions a subset of which form an autocatalytic set. The more improbable a reaction the greater the diversity and the longer the period of time required for a reaction network to begin to develop. The ratio of reactions to polymers is given by:

$$(2.1) \quad \sum_{i=1}^M \frac{M-i}{2^i} \approx M-2$$

The implication of equation 2.1 is that as  $M$  increases the number of polymer species increases. However, the number of reactions occurring increases faster than the number of new polymer species being created. Indeed the ratio of reactions to polymers increases linearly with  $M$ . As such this leads to more legitimate reactions in the system than there are polymers. The connectivity between polymers is therefore a key consideration in autocatalysis. Phase transitions in random graphs [97] can provide a succinct explanation of how the connectivity of a network reaches a critical point whereby all nodes are connected to at least one other node thus forming a complete path through the network. Kauffman refers to this connected graph as 'one gigantic component' and this characteristic of random graphs is another cornerstone in the theory of autocatalytic sets of proteins.

Kauffman ran a number of simulations to evaluate the model and a reflexively autocatalytic set successfully formed as a subset within a larger reaction graph. The conclusion of his work is that "... any sufficiently complex set of catalytic polymers can be expected

to be collectively autocatalytic" and, as such, ".. life may be more probable than we have supposed" [98].

A more recent development of the Kauffman model is the Graded Autocatalysis Replication Domain (GARD) model [99] which is a model of primordial chemical selection of mutually catalytic sets (mutual catalysis is equivalent to network replication as per Eigen & Schuster hypercycles [41]). The model describes how catalytic closure can sustain self-replication up to a critical dilution rate  $\lambda$  which is related to the extent of mutual catalysis involved. GARD simulations offer a rigorous kinetic analysis with which to model the behaviour of ensembles of molecules and the spontaneous formation and maintenance of autocatalytic sets. As popular as the GARD model has become it is not without its limitations. It is claimed that self-sustaining autocatalytic networks - as regularly generated by GARD simulations - do not evolve and, as such, constrain the prospect of metabolism as one of the main mechanisms of the origin of life [100]. A counter-argument [101] is that the GARD model does allow for and demonstrate how 'evolution-like' behaviour can emerge in molecular systems on the condition that excess mutual catalysis (network replication) is more present in the system than self-catalysis (self-replication). The evolvability of autocatalytic sets in the GARD model and the emergence of peripheries of molecules that were maintained by an autocatalytic core but that were not part of the core itself have also demonstrated [102]. These peripheries act as a form of phenotype and the rate at which they replicate is a measure of fitness compared to other peripheries and other autocatalytic cores thus demonstrating a degree of natural selection (and therefore evolution).

The relationship between autocatalysis and autopoiesis has been investigated [33] and this acknowledged that their formation and organisation are via similar processes with the critical distinction being that an autopoietic systems autocatalytic process generates a spatial boundary. Now, notwithstanding the contested nature of spatial boundaries in autopoietic theory, the distinction can be considered more generally as implying that autocatalytic systems are not autopoietic and yet autopoietic systems may consist of one or more autocatalytic cycles. A more fundamental difference - as argued in [103] - is that Kauffman's autocatalytic model of a living system is dependent on a large set of entities (polymers) numbered in the thousands. This is necessary because only large systems can have the statistical properties required for autocatalytic closure to occur as defined by Kauffman. This requirement is opposite to the model of a living system as devised by Maturana & Varela which implies that a much smaller system should be sufficient for a minimal autopoietic system. However, Kauffman's model is addressing impoverished and under-developed initial conditions i.e. the complete absence of highly efficient catalysts. For example, if any polymer in the system has a probability of  $10^{-9}$  of catalysing a reaction

then the probability of catalytic closure occurring is very low unless there are at least  $3 \times 10^8$  different species of polymer that are all available to interact with each other at any time. Clearly, more efficient catalysts would reduce the size and diversity of the population required to achieve catalytic closure. It may be the case that autocatalysis acts as the springboard from which more efficient forms of organisation can emerge and that these more optimal configurations are minimal, self-producing and self-maintaining systems that have the sufficient functionality and efficiency of operation to achieve not just catalytic closure but also efficient causation closure (i.e. as required by both autopoiesis and (M,R)-systems). These more efficient forms of organisation then provide the platform for the emergence of more sophisticated living systems. Autocatalytic cycles formed spontaneously in all of my simulations of a population of interacting automata and, in the context of autopoiesis, I propose that such networks - with properties of dynamically stable, strongly connected components - are a recurring feature of all systems that are developing towards an autopoietic state.

### 2.2.3 Cognition

Cognition<sup>4</sup> is a process that is, 'an *effective action*, an action that will enable a living being to continue its existence in a definitive environment' (page 29 of [83]). In simpler terms cognition is the process of bringing together the mutual interactions between an autopoietic system and its environment and the subsequent changes to both that occur as a result. More specifically, autopoietic systems are deemed to be structurally coupled to their immediate environment and, as such, undergo dynamic changes due to perturbations from the surrounding medium. 'Successful autopoiesis' [84] leads to the selection of a structure which is the most suited to the environment. An autopoietic system is realised by a particular structure and, as the system is structurally determined, this defines the future changes that may be possible. My own research confirms this and, specifically, quantifies the structural states that a given autopoietic system can transform itself to. John Mingers suggests that we think of structural coupling as:

"... changes may preserve the structure as it is or they may radically alter it (think of an acorn developing into an oak [tree]) so the structure is said to be plastic. This plastic structure exists within an environment which perturbs it and triggers changes. The environment does not determine the changes but it can be said to select the state from among those made possible at any instant by the system's structure" (p. 168 of [84])

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<sup>4</sup>it is an unfortunate choice of word which Varela himself admitted according to [12] given the anthropomorphic meaning usually attributed to it.

Two types of interactions between an autopoietic system and its environment have been suggested [14]: *type A* interactions that lead to changes in the internal state of the system, and *type B* interactions that lead to changes in the environment or that modify the relation of the system to the environment. Distinguishing the interactions in this manner allowed [14] to propose a more precise definition of cognition:

“A system is cognitive if and only if type A interactions serve to trigger type B interactions in a specific way, so as to satisfy a viability constraint”

Type A interactions are referred to as ‘sensations’ and type B interactions as ‘actions’. Type A interactions are mediated by specialised ‘sensory organs’ in the boundary of the system and type B interactions are mediated by specialised ‘effector organs’ also situated in the boundary. As such, they are defining the boundary as the systems interface between the internal organisation (which is maintained via. autopoiesis) and the environment. Hence, ‘the sensory input must not only be used to guide the actions in an intelligent way but that, conversely, the actions of an organism also have consequences for its subsequent sensory inputs’ (p. 339 of [14]). Whilst I am uncomfortable with the use of the word intelligent here (I prefer to use the word logical) the meaning is quite clear: sensory inputs have a causal effect on the internal structure of the autopoietic structure which, given that the system is structure-determined, will lead to a subsequent change in the sensory inputs in the systems interface.

Bitbol & Luisi [2] suggest that there are two meanings for cognition: (i) the metabolism of a living unit is the most direct form of cognition given the implied continual exchange with the environment both of which form and are formed by each other which they refer to as ‘a simultaneous coming to being for the organism and for the environment’ [2], and (ii) the adaptation of the system to novelty (the authors refer to ‘new foreign molecules’ however I prefer the more general notion of new entities) leading to a change in the metabolic pattern i.e. the underlying networks of production that are continually producing the critical components required to re-generate the autopoietic system. These two forms of cognition are equivalent to Piaget’s assimilation and accommodation with the latter arguably more useful in grasping the concepts here.

Piaget’s work is grounded in cognitive development from the field of psychology and the meaning of his two terms are best conveyed with the following example [104]:

“A child seeing a zebra for the first time and calling it a horse. The child assimilates this information into her schema for a horse. When the child accommodates information, she takes into consideration the different properties of a zebra compared to a horse, perhaps calling a zebra a horse with stripes. When she eventually learns the name of zebra, she has accommodated this information”

Hence, assimilation is the process of making sense of new information/entities by reference to the information/entities that are already present in the system and to attempt to fit the new entity into that model/schema/representation whereas accommodation requires the revision and change to the existing model/schema/representations so that the new information/entity can be incorporated. So, in the context of autopoiesis and Bitbol & Luisi's two forms of cognition assimilation is equivalent to the uptake and exchange of metabolites in the metabolic network, and accommodation is biological adaptation where the system's metabolic network is changed in a way that endures.

Bringing this together autopoiesis (self-production) and cognition (adaptation) are the two critical processes that generate and maintain a living system. Yet, which of these fundamental processes is the progenitor of an autopoietic system? Is there any primacy between these two processes: i.e. does a basic form of autopoiesis need to form before the system is able to perform any kind of cognition? What is the nature of their co-creation and co-dependency? Is one process sufficient for a system to be autopoietic? Bitbol & Luisi examined this [2] and concluded that 'autopoiesis alone is only a necessary, but not sufficient, condition for life'. In other words, some form of cognition is required for life. The claim that autopoietic systems require a basic form of cognition is worth exploring further as it may yield insight into the critical stages and properties of proto-autopoietic systems that equips the system with a sufficient capability to become fully autopoietic. I explicitly examine the assimilation/accommodation behaviour of a proto-autopoietic system with the development of the information niche model that emulates an influx of new entities (molecules) from the environment (see Chapter 7). To examine cognition in the type A/type B forms proposed by Bourgine & Stewart I developed the computation niche model (see section 3 and 8) which explicitly models a systems interface (boundary) as an information processing component that receives and transduces information from the environment (type A) that leads to internal changes in the structure of the system. Such changes lead to changes in the systems interface and also changes in the information emitted by the system into the environment. The emissions have the effect of modulating environmental information (type B interaction) which, in turn, is received by the systems interface thus completing an operationally closed cycle. The conclusion I draw from these studies is that a self-producing system that consists of hierarchical, dynamically stable and strongly connected networks are very robust to environmental perturbations. I also show that the underlying interaction network that drives the behaviour of the internal population adapts readily to new types of entities although this does not necessarily lead to a change in the structure of the system as a whole (i.e. the system is assimilating but not accommodating).

Evolution is the 'change in heritable characteristics of biological populations over

successive generations' [105] or, more generally, the gradual development of something. Darwinian evolution [106] states that organisms develop through natural selection of minor variations that occur over time and that may increase the organism's ability to compete and reproduce. As such, it is a theory of how biological evolution occurs. Humberto Maturana has proposed [13] that autopoietic systems evolve - in the general (non-Darwinian) sense of the word - by the continual interactions between environment and the system where the system regenerates and optimises its organisational states for maintaining its identity. The plasticity of the system - facilitated by the cognitive process of accommodation - in response to changes in the environment over time leads to natural drift. Natural drift is a dynamic process that affects the structure of an autopoietic system which over cumulative adaptations forms a historical product [30]. Bitbol & Luisi [2] declare that for an autopoietic system to evolve requires that as a minimum Piaget's accommodation is possible.

#### 2.2.4 Limitations of Autopoietic Theory

The three prevalent issues in the field of autopoiesis are:

*The conceptual gap between autopoiesis and Darwinian evolution.*

Autopoietic theory has been studied extensively [2],[14],[15],[1],[16],[17] (also see Figure 2.2) and yet it has not had a substantial impact within its field of origin which was biology. This has been investigated [28],[8] with the conclusion that (a) the lack of any emphasis on DNA at a time (in the early 1970's) when DNA/RNA dominated discourse of the behaviour of biological systems and the prevalent scientific worldview was almost entirely reductionist, and (b) the lack of any convincing explanation of evolution and, specifically, to Darwinian evolution. Addressing the former has been largely rectified [8] whilst several attempts to address the latter [13],[29],[30], [31] have remained inconclusive. Advocates of autopoietic theory can rightly demand greater clarification from Darwinism especially about the lack of serious questioning of the assumptions of natural selection as the primary mechanism (a largely philosophical issue given the phenomenological basis of Darwin's theory) whilst critics of autopoiesis may demand more evidence for evolution of such systems in the absence of genetic machinery [31]. Is there a possible contribution that the theory of autopoiesis can make to addressing the remaining theoretical issues of Darwinian evolution? As is discussed in Chapter 10 I believe that my research takes steps towards showing a unification of these two theories through the fundamental mechanism of competition. Clearly natural selection as a core mechanism of Darwinian evolution has

a competitive element. From my own research I have observed that the behaviour of proto-autopoietic systems can be explained by competition between interacting entities, networks and populations. Such multi-level selection - survival of the most competitive - was present where a selective pressure existed (e.g. a finite population size). Competition between automata - and the networks that they form - in my simulation model led to the growth and decay (and eventually extinction) of some automata types which led to the population structure reaching a steady-state within a given environment. The populations of automata transform via. a selection process with the emergent structure representing the best 'fit' to the environment. This is why I refer to these steady-state structures as niches. From what I am aware I am the first to explicitly claim that a fundamental mechanism of autopoietic operation is a competitive process that continues and persists throughout the Darwinian evolution of biological systems.

*Autopoietic systems are uncomputable.*

If we accept that an autopoietic system is a sub-class of (M,R)-systems then by association they are also closed to efficient causation and as such are non-computable [88]. This is a feature of (M,R)-systems that was proved by Robert Rosen but which remains a controversial and contested topic [103]. In essence, this non-computability claims that autopoietic systems cannot be modelled or simulated computationally. Specifically: 'The non-computability of autopoietic systems, as advanced here, apparently collides with the simulation results involving tessellation automatas (sic) [9]. But new versions of this simulation show that the original report of computational autopoiesis was flawed, as it used a non-documented feature involving chain-based bond inhibition [11]. Thus the closure exhibited by tessellation automatas is not a consequence of the "network" of simulated processes, but rather an artifact of coding procedures' [88]. However, this claim has been strongly refuted by McMullin who in collaboration with Varela identified and corrected the original model. In his own words, '...the overall thesis of Letelier et al. of the "non-computability" of autopoietic systems - should be taken as refuted, rather than corroborated, by the results of [11]' [107]. Hence, the non-computability of autopoiesis is a contested issue and the acceptance and weight given to any research findings generated from my simulation results will be interpreted with respect to the reader's own views on this matter.

*The criteria for a physical boundary remains contested and unresolved.*

As has already been discussed in this chapter the requirement for a self-producing system to have a physical boundary for it to be deemed to be autopoietic is a contested issue. There appears to be a trend in the field away from such a prescriptive requirement (e.g. Virgo et al's work on extended autopoiesis [17], Luhmann's work on social autopoiesis [19]) and towards acceptance of non-physical boundaries. This has important implications for how the findings that are generated from my own research are interpreted and basis of any claims that arise.

## 2.3 Computational Models of Autopoiesis

### 2.3.1 Substrate-Link Model

The first computer simulation that demonstrated an autopoietic system was Varela & Maturana's own computational model of autopoiesis [9] which remains the exemplar to this day. Their model consisted of a qualitative chemistry as shown in Figure 2.9.

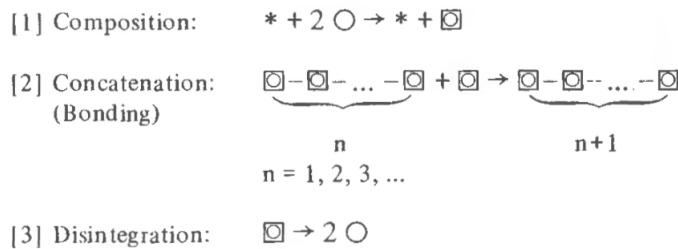


Figure 2.9: The reaction schema for Varela's computational model of an autopoietic system

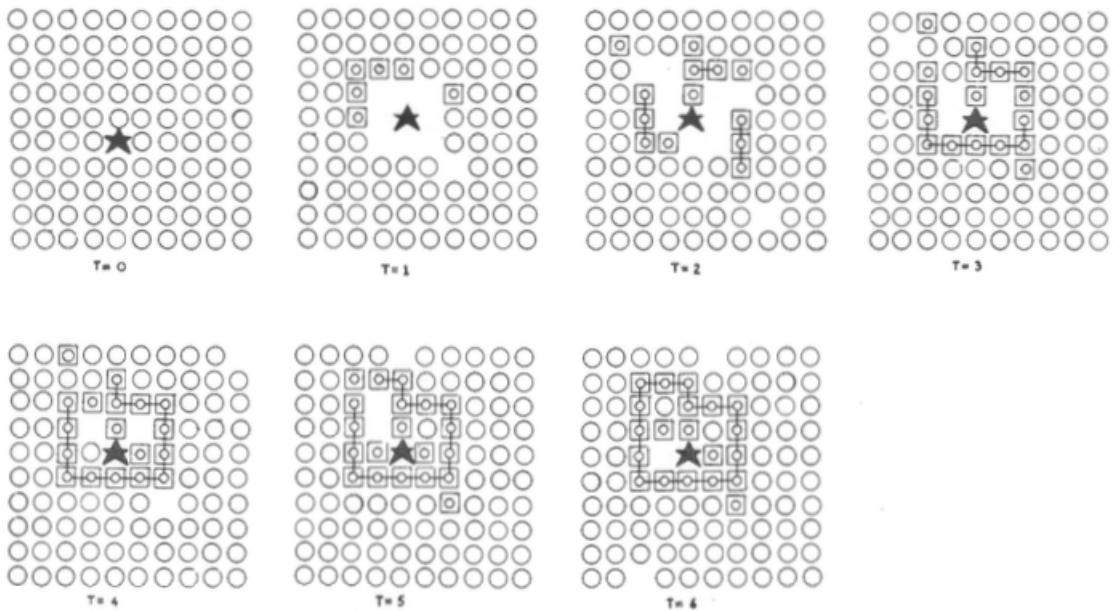


Figure 2.10: The first computer simulation demonstrating the spontaneous emergence of an autopoietic system

As can be seen in Figure 2.10 there are three reactions: composition via condensation of two substrate molecules catalysed by a single catalyst molecule to produce a linker molecule; bonding of two or more linker molecules into a chain; and the disintegration of linker molecules into two substrate molecules. Initially, the grid is composed of a single catalyst surrounded by substrate molecules. As the simulation proceeds substrate-catalyst reactions occur to create 'linker' entities which can bond to other 'linker' entities to form chains. Quite soon the production of linker molecules and chains have progressed sufficiently that the catalyst is now encapsulated within a boundary of a chain of linker molecules. These linker-chains are semi-permeable with substrate entities able to move freely into and out of the interior region. The catalyst entity cannot pass through. At each time step there is a probability of the chain of linker molecules that constitute the boundary to spontaneously decay into two substrate molecules thus leaving a hole. A 'repair' ensues if a linker molecule is next to the hole and hence the operational closure of the system is maintained (see Figure 2.11). This simulation successfully demonstrated the basic premise of an autopoietic system .

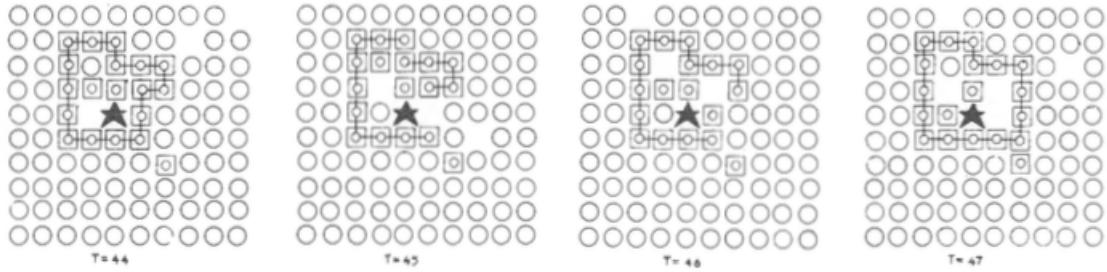


Figure 2.11: Demonstration of an autopoietic system repairing itself

Attempts to repeat Varela's simulation were not routinely successful [11] and a subsequent investigation led to the identification of 'chain bond inhibition' as a critical rule in the simulation. This rule only allows linker-linker formation at the terminal ends of the linker molecules or the terminal ends of linker-linker chains; a corrected version of the model was implemented and the simulation results confirmed Varela's earlier results [43].

A 3-D tessellation automaton was implemented to demonstrate a more complete and physically realistic demonstration of autopoiesis [14]. This minimal model of autopoiesis is based on a spherical membrane enclosing an internal volume. The semi-permeable membrane is a two-dimensional sheet that decays at a given rate to leave holes. Internal reactions generate the membrane product which diffuses from the interior to the outer boundary where they fill holes in the membrane. Conceptually their model is similar to the original model with the exception that it is implemented as a three dimensional entity. This more realistic model equipped Bourgine & Stewart to critically examine the definition of autopoiesis and cognition as they observed from their simulations and which led them to suggest the following clarifications to autopoietic theory, as follows:

- An autopoietic system is a network of processes that produces the components that reproduce the network and that also regulates the boundary conditions necessary for its ongoing existence as a network
- A system is cognitive if and only if sensory inputs serve to trigger actions in a specific way, so as to satisfy a viability constraint

They conclude that, "... a system can be autopoietic without being cognitive, and cognitive without being autopoietic". They theorise that: (i) an autopoietic system is a random dynamical system that is defined only within its organised autopoietic domain (that is, it is not dependent on any external source for constructing itself); and (ii) a system that is both autopoietic and cognitive is a living system. The first of these points does not

explicitly denounce 'extended autopoiesis' but rather simply states the possibility that an autopoietic system can form in the absence of any dependency on external processes. The authors conclude with the observation that more work is required to explore the increasing complexity of the simulation of autopoietic systems such that:

"a [network] of reactions so much richer... that the probability of it having emerged from an environment of the same level of complexity is close to unity"

This is consistent with Kauffman's hypothesis [98] that past a certain threshold of complexity and interconnectedness in a chemical reaction network, autocatalysis is likely to occur. However, whilst autocatalysis - more specifically, collective autocatalysis [33] - is a likely requirement for an autopoietic system it does not necessarily satisfy the criteria for an autopoietic system as has already been discussed.

These models - the original Varela computational model and the Bourgine & Stewart work - suffer from two serious limitations in addressing the research aims of this project: firstly, they are extremely limited in their ability to scale to consider other factors such as the effect of environmental perturbations, reproduction and heredity and interactions with other autopoietic systems; and secondly, and most critically, they are totally reliant on assuming the presence of an ideal qualitative chemistry which by design overcomes the need for their model to demonstrate how a 'network of reactions' would form in the first place. To explore autopoiesis and to further demonstrate its applicability to systems chemistry approaches to protolife it is therefore important to look to computational models that demonstrate how autopoiesis and cognition processes may form in the absence of any pre-determined selective chemistry. Such models will need to allow for a system to increase in complexity (the level of and diversity of its components and processes) from initially simple populations of randomly generated entities that, yet, have the potential to undertake preferential interactions, to self-organise and to generate self-producing behaviour. Such models exist and are known as artificial chemistries [86].

### 2.3.2 Algorithmic Chemistry

Algorithmic chemistry (AlChem) is an artificial chemistry whose molecules are represented as mathematical functions<sup>5</sup> that can interact with other mathematical functions [44]. The interaction between these functions generate a new function via. a process called functional composition whereby the new function inherits the domain (the input) of the first parent function and the range (the output) of the second parent function. Not all inter-

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<sup>5</sup>a mathematical function is simply a mapping from one domain to another and represents a transformation e.g. the  $\times$  function takes as input the numbers '2' and '8' and outputs the number '16'

actions yield a valid function and these are prohibited and essentially ignored. Algorithmic chemistry is based on the  $\lambda$  calculus which is a minimal language of computation.

More formally, functions are represented as  $\lambda$ -expressions. Each unique  $\lambda$ -expression has the possibility of operating on other  $\lambda$ -expressions and, by doing so, transforms that expression into a new  $\lambda$ -expression. However, unlike a normal chemical reaction, the reactants (the  $\lambda$ -expression that transformed the other  $\lambda$ -expression) do not get consumed in the process and continue to exist alongside their new child operator. Instead, as one new operator is created another one is randomly selected and removed from the simulation. As such, the overall population size is kept constant and creates a form of selective pressure between operators to replicate and/or to form mutually replicative networks of interactions with other operators.

Each function is a  $\lambda$ -expression which simply denotes the syntax and language used to describe a function. In simple terms: a function receives a variable, processes that variable in some manner determined by the internal structure of the function, and outputs a variable. Each  $\lambda$ -expression is a mini-algorithm that describes how to process the variable received by the function. As these molecules collide the collision can be reactive (a product molecule is produced) or elastic (no product molecule is produced). If two molecules react then the product molecule is the result of functional composition i.e. the input to one function  $f$  is the output from the other function  $g$  written as  $f(g)$ .

The algorithm that describes how these molecules react is as follows:

1. Select two functions from the population
2. Test whether their collision is reactive or elastic
3. If reactive then add the product molecule into the population; remove another - randomly selected molecule - from the population to maintain a constant population size
4. If elastic then no product molecule is produced
5. Repeat

This collection of functions - which are essentially interacting strings of characters in the language of  $\lambda$  calculus - that collide, react and create - is known as a 'Turing Gas'. Fontana simulated experiments in a Turing Gas as follows:

#### *Turing Gas without Perturbations*

An initial population of 1,000 randomly generated and unique functions evolved over  $10^5$  iterations involving 100,000 reactions that led to the creation of 18 new functions

that were not present initially. This lead to a quasi-stationary state of the system that self-organised from random initial conditions. This was cited as evidence that the AlChemey model can generate innovation. The relationship between the 18 functions that remained at the end of the simulation (all others were diluted out of the population) were described as an interaction graph that was autocatalytic, closed and that did not consist of any parasitic sets.

### *Turing Gas without Copiers*

The second type of experiment set the boundary condition that no copying functions were allowed. Some functions are identity functions - that is, when they react with another function the product is identical to the non-identity function - and they are universal copiers. Other copiers are 'partial copiers' meaning that they create a copy of themselves or the function they are reacting with but they only do this with a subset of functions in the population. In running simulations of this type Fontana identified three 'absorbing states' for the population:

- heterogenous mixture of elastic colliders (dead system)
- a single self-reproducing function
- a self-reproducing set in which every function is a seeding set (this absorbing state was described as a quasi steady-state)

This experiment also revealed that:

- innovation decays fast
- the trend towards closure of the population is based on the appearance of identity functions and partial copiers
- functions not linked to transformation pathways are eventually displaced by dilution (removed from the population)
- nesting of autocatalytic components is a frequently observed pattern

Fontana summarised his findings as:

- the only way for a function to survive is to become part of some transformation pathway

- a transformation pathway survives by becoming closed (self-maintaining)
- stability of self-reproducing sets (of functions) is strongly influenced by the number and size of the initial seeding sets (functions created under initial conditions)

The AlChem model demonstrated the formation of three hierarchical levels of organisation:

- Level 0. The operators (objects) in the system only perform one type of operation - an identity operation and thus self-replication. Within a Level 0 organisation it is possible that a hypercycle [41] emerges whereby operators mutually copy one another.
- Level 1. By prohibiting identity function a different organisation emerges. In the words of Fontana: "... at the syntactical level there exist common regularities that characterize the structures of all operators maintained in the system. These regularities define a grammar, i.e. lawful arrangements of identifiable substructures.... furthermore, when new operators are created from interactions within the system, their structure conforms with the grammar.... the subspace specified by the grammar is invariant as interactions proceed; closure has been attained". This invariant subspace bears similarities to the invariant frequency distribution of a single state finitary process soup (see Section 2.3.3). These laws specify the relationships between objects whose structure conforms with the specified grammar. Overall a system that attains such properties is behaving as a single object and this invariant entity is called an 'organization'. Indeed a Level 1 organisation is conceptually equivalent to a Crutchfield & Gornerup 'meta machine' in the finitary process soup (see section 2.3.3).
- Level 2. Self-maintaining organisations (Level 1) that are combined in some manner have the potential to create Level 2 organisations. Level 2 organisations are characterised as two or more Level 1 organisations that co-exist with cross-interactions producing new operators that do not belong to either organisation. These interstitial operators act as a glue (according to Fontana) that links, or integrates, the Level 1 organisations in a higher order unit. This is an interesting result as it is a demonstration of two autopoietic systems becoming structurally coupled which could be indicative of a pathway to multicellularity.

Although not mentioned by Fontana, there appears to be an association between Level 0 and Level 1 organisations with the autopoietic process, and Level 2 with the

cognition process. Furthermore, there is a close similarity between Fontana's operators and 'organizations' with Crutchfield's  $\epsilon$ -machines and meta machines (to be discussed shortly). Fontana's model succeeds in demonstrating an increase in the complexity of initially simple and unconnected unity's into hierarchical organisations from an initial achemical state and - through the mutual transformations that emerge - begins to exhibit chemical behaviour with the formation of sustained networks of interactions (i.e. autocatalysis).

However, the model has a number of limitations: (i) as networks become more complex the ability to detect and analyse the existence of separate organisations in the Turing Gas becomes problematic; (ii) there does not appear to be a natural extension of the model to a spatial dimension, and (iii) the model - based on  $\lambda$ -expressions does not allow for a straightforward estimation of the information content of the 'Turing Gas' or any organisations present within it. In a sense, the AlChemistry is too minimal (or abstract) to allow a more detailed pursuit of the research goals of this project.

Such limitations - particularly the difficulty with which to identify organisations in an increasingly complex Turing Gas - were partly addressed by Peter Dittrich and Pietro Speroni di Fenizio with their theory of chemical organisation [74]. Their approach consisted of two parts: (i) they defined a chemical organisation as a closed and self-maintaining set of components which explicitly linked an interaction network with the set of possible organisations that could be generated by those interactions; and (ii) mapped the set of organisations to a state space. This two step process was represented as a differential equation that describes the chemical dynamics of the network and, as such, every stationary state that could be found was an instance of an organisation. This was an elegant solution to the first of the limitations of the AlChemistry model as described above. However, it did not address the remaining issues and for that we have to turn to Crutchfield & Gornerup's Finitary Process Soup model.

### 2.3.3 Finitary Process Soup

The Finitary Process Soup (FPS) model was adopted as the underlying model that was subsequently enhanced and extended during this project. As such, a detailed explanation of the model is contained in Chapter 3. In what follows the FPS is introduced in general terms followed by a brief discussion on its limitations.

The Finitary Process Soup (FPS) [35] is an abstract approach to studying prebiotic mechanisms that, in a similar way to the AlChemistry model, makes no assumptions about a pre-existing chemistry. Crutchfield & Gornerup define a population of entities that can interact. Each entity represents a function, specifically, an information processing function

i.e. they process binary information (bits). Functions receive binary information, process that information in some way, and then emit binary information and they can do so in increasingly complex and well-defined ways. Hence, as was the case with the AlChemey model, functions can interact with each other and their product is a new function via. the process of functional composition. However, where Fontana chose  $\lambda$ -expressions to represent these functions Crutchfield & Gornerup chose to represent functions as a special class of finite state transducer called  $\epsilon$ -machines.  $\epsilon$ -machines are minimal representations of unique stochastic processes and the manner in which they are defined, and the basis for their interaction with other  $\epsilon$ -machines, follow explicit rules for evaluating functional compositions and to retain only valid  $\epsilon$ -machines in the population.

As  $\epsilon$ -machines interact with other  $\epsilon$ -machines over extended periods of time ( $10^6$  are normal) the overall structure of the population reaches a steady-state where the frequencies of each object become invariant. These invariant distributions are called 'meta machines' and are deemed to be analogous to an autocatalytic set. Each  $\epsilon$ -machine's internal structure can be quantified precisely by estimating its structural complexity [36]. Furthermore, the structure of the population can also be measured by estimating the interaction network complexity [35]. The ability to quantitatively measure the structure of individual entities and their collective organisation directly addresses the first and third limitations of the AlChemey model.

Simulations of the FPS model revealed that an initially uniform population of  $\epsilon$ -machines self-organise to a steady-state distribution that persists over time - what the authors called a 'meta machine'. This meta machine represented a 'global complexity [that was] due to the emergence of higher level structures and this in turn is facilitated by the discovery and maintenance of relatively non-complex, but general objects' [35]. 'General objects' refers to the most simple  $\epsilon$ -machines (i.e. one-state finite state automata) and 'higher level structures' is referring to the underlying network of production that emerged as the population evolved. Whilst Crutchfield & Gornerup intimation that such meta machines are autopoietic is questionable - they are not as their work does not demonstrate any kind of perturbation that may disrupt the identity of the meta machine - the self-producing and persistent nature of the organisation of automata is indicative of, at least, the process of self-production and as such their work demonstrates the emergence of some but not all of the fundamental processes of autopoeisis.

The FPS model has a number of distinct advantages over the AlChemey and the Substrate-Linker model:

1. The emergence of a self-producing system from simple, undefined beginnings is

demonstrated by the FPS model.

2. The emergence of a steady-state structure that persists through the formation of self-producing networks is a clear example of proto-autopoietic behaviour. However the FPS model does not demonstrate autopoiesis as the process of cognition is not demonstrated (a limitation which is addressed by this project).
3. The structure of  $\epsilon$ -machines can be quantified using structural complexity which is derived from algorithmic information theory. This presents an objective measurement for the complexity of individuals within a population, and how the complexity of the population changes over time. Such a measurement is not feasible with either the AlChem or Substrate-Linker models.
4. The model is grounded in information theory and computation theory which are two well defined and researched fields.
5. Unpublished work on a spatial dimension added to the FPS model shows the emergence of spatial patterns that are reminiscent of boundary formation [108] and this is discussed in the next chapter.

However, the FPS model has a number of limitations:

1. The role of the environment in the population dynamics is limited to an influx of  $\epsilon$ -machines. The effect of short-range vs. long-range interactions is therefore excluded. Later unpublished work [108] adds a spatial dimension which partly addresses this issue (see Chapter 3) and yet this model was also too limited in that it did not allow for environmental perturbations. The information niche model addresses all of these issues and is described in Chapter 3 and the results of simulating the model are presented in Chapters 4 - 7.
2. There is no mechanism for examining emissions or outflow from the population into the environment and the effect that this may have on the subsequent feedback from the environment on population dynamics. This is required for examining structural coupling. Addressing this issue required the extension of the FPS model to specifically model a systems interface between the interacting population and the environment. The model that was developed to address this is called the computation niche model and this is described in Chapter 3 and the results of simulating the model are presented in Chapter 8.

3.  $\epsilon$ -machines are information processing objects and yet their functional behaviour is not examined in any of the models developed by Crutchfield & Gornerup [35] or Piantadosi & Crutchfield [108]. For example, each  $\epsilon$ -machine represents a unique stochastic process and its intrinsic information processing properties are only used to determine the information processing properties of potential offspring. This omits the interesting possibility of examining the behaviour of the process that it represents. In other words there is a duality to  $\epsilon$ -machines in the FPS model: (i) they are interacting entities that produce other entities via functional composition, and (ii) they are information processing objects that receive, process and transmit information. The former is the only aspect of an  $\epsilon$ -machine that is considered in the FPS model. This is not necessarily an issue but rather a missed opportunity. The computation niche model that I have developed makes full use of the dual nature of an  $\epsilon$ -machine by modelling interactions between them as per the FPS model but also by modelling their information processing behaviour in an explicitly defined systems interface (a membrane) between the internal interacting population and the environment.
4. interactions between steady-state populations are not supported by the FPS model. As such, important concepts of autopoiesis such as reproduction and heredity cannot be examined. This is addressed by the information niche model and the results of simulating such inter-population exchanges are reported in Chapter 7.

These limitations are specifically addressed in this project with the development of the information niche and computation niche models which are discussed in the next chapter.

## 2.4 Summary

This chapter has introduced the theory of autopoiesis as a minimal model of a living system that whilst minimal and simple in concept provides a theoretical continuum from the formation of the most basic living system (a protocell) to systems of almost unfathomable complexity such as human cognition and social systems. A comparison to other models of living systems highlighted the general and universal nature of the theory and therefore its attraction as a framework for understanding the system logic of a basic living system.

The latest thinking and research on autopoiesis was presented and the current limitations in the field were discussed. Throughout I have indicated where my own research is addressing gaps in the field.

The second half of this chapter examined computational models of autopoiesis from Varela et al's original algorithm [9] (the Substrate-Link model) and related tessellation

models [14] that were reliant on the pre-existence of an ideal and well-defined chemistry to more abstract and 'bottom-up' models that emphasised the emergence of organisational forms from undefined and simple beginnings such as Fontana's algorhithmic chemistry [44] and Crutchfield & Gornerup's Finitary Process Soup [35].

This chapter concludes with an explanation on the benefits and limitations of the Finitary Process Soup model and this leads naturally into the next chapter where the enhancements and extensions that are made to the model are described in detail.

CHAPTER



3

## MODELS AND METHODS

### 3.1 Introduction

This Chapter describes the methodology, models and methods that were adopted, developed and implemented in addressing the Research Aims (as described in Chapter 1). Two computational models are described, the information niche model (see section 3.3) and the computation niche model (see section 3.4). The quantitative methods that were used to analyse and characterise the simulation results were drawn from information theory [109] and network theory [46] and the specific methods used and their application are described in section 3.6 and 3.6 respectively. A significant number of simulations of both models were run with various simulation set-ups that makes it impractical to discuss them in this chapter. Instead, the introduction to each of the Results chapters (Chapters 4 - 9) explains the specific set-up of the information niche or computation niche model relevant to the results that are presented in that chapter. All models and methods were developed in MATLAB and a description of the software implementation is described in Appendix 12.3.

The Finitary Process Soup (FPS) model [35] is a model of a population of interacting finite state automata that produce new automata via. those interactions. Simulations of the model revealed that a population would self-organise to a persistent steady-state thus demonstrating a basic process of autopoiesis (i.e. self-production). The rationale for selecting the Finitary Process Soup (FPS) [35],[108] as the starting point for the development of my own computational models was explained in Chapter 2. The FPS model

has the following limitations: (a) no provision for altering environmental conditions during the simulation to emulate perturbations and therefore no way to examine the robustness of the system nor the degree to which it can maintain its identity, and (b) the inability of the model to support any kind of detailed investigation into the cognitive process such as how an interacting population can adapt. To address these limitations three major developments to the FPS model were made: (i) modelling environmental perturbations by allowing abrupt or incremental changes to environmental parameters to create a 'fitness landscape' through which the population can evolve to different steady-state niches and from which the relative robustness of these self-organising populations can be assessed (see Chapter 4), (ii) transfer of entities between populations to model and simulate the 'accommodation' form of the cognition process (section 3.3.4, and (iii) the development of a model of a membrane that acts as the system interface between the interacting population and its environment (see section 3.4). These additional developments were necessary to generate a sufficient level of data - both in terms of variety and volume - to allow the research aims to be investigated. Developments (i) and (ii) were implemented in the 'information niche' model (see section 3.3) and development (iii) was implemented in the 'computation niche' model (see section 3.4.2).

The information niche model was an enhancement to the FPS model<sup>1</sup> [35],[108] that allowed the nature and dynamics of the production processes that generated and maintained a self-producing population to be examined under a wide range of environmental conditions. Information niche was the label given to a steady-state population of automata that were generated and maintained through dynamically stable, strongly connected networks of mutually producing automata.

A computation niche was an extension to the FPS model that explicitly defined a systems interface (a membrane) between an internal population of interacting automata operating under well-mixed conditions and an environment that was generating information. The membrane was a network of finite state automata (belonging to the  $\epsilon$ -machine class) each of which simultaneously processed information received from other 'membrane' automata and from the environment. The internal structure of the population dictated the weightings given to the edges of the membrane network. A computation niche was a steady-state population of automata that was generated and maintained through the continuous transfer, storage and modification of information that was an intrinsic property of the production and computation processes occurring between the interacting population,

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<sup>1</sup>A description of the FPS model has been subsumed into the description of the information niche model (section 3.2 and section 3.3) with the enhancements that were developed during this project identified where appropriate.

the membrane and the environment.

The following table compares the main attributes of each model:

model attribute	information niche	computation niche
units of production	one-state & two-state automata	one-state & multi-state automata
internal environment	cellular automata lattice	well-mixed reactor
selective pressure	random replacement	random replacement
membrane	parameter	multi-state automata network
environmental perturbation	rate of influx of new automata ( $\Phi_{in}$ )	environmental information magnitude ( $\Phi_{env}$ )
perturbation effect	global	local
population mobility (diffusion)	variable (zero diffusivity to well-mixed)	fixed (well-mixed)
material influx	random generation of new automata	none
information influx	none	environment information aperture ( $\Phi_{env}$ )
adaptation	accommodation / assimilation	structural coupling via modulation of the environment
reproduction	inter-niche exchange of automata	N/A
novelty	N/A	open-ended evolution

Table 3.1: A comparison of the attributes of the Information Niche and Computation Niche models

Analysis of the simulation results from both models used methods from information theory [45] and network theory [46]. From information theory Shannon's entropy [45] was used to measure the information content of steady-state populations and the complexity of the population (i.e. the Interaction Network Complexity measure) [35] and the structural complexity of individual automata (i.e. the Statistical Complexity measure [36]). From network science the use of graph theory to represent the relationships between automata in the interacting population (e.g. topology) and the structure of such a network (e.g. degree distribution) proved invaluable in revealing the underlying dynamics of the interacting population. These information-theoretic and network-theoretic methods and how they were applied to the information niche and computation niche models are described in section 3.5 and section 3.6 respectively.

## 3.2 Automata

Automata were a special class of finite state transducers ( $\epsilon$ -machines) that could read a binary alphabet i.e. accept an input  $x$ , process that information according to the internal

structure of the automaton  $f(x)$ , and emit an output  $y$  (Figure 3.1). As these automata belonged to the  $\epsilon$ -machine class they had to adhere to the following properties: (i) all of their states form a single strongly connected component, (ii) all transitions are deterministic whereby the current state and the next input symbol was sufficient to determine the next state <sup>2</sup>, and (iii) the automaton was minimal in that it was the smallest causal representation of the transformation that it implements.

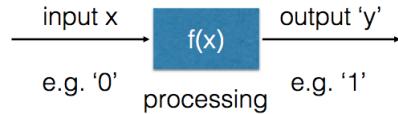


Figure 3.1: An automaton was an information processor that received an input, processed that information, and emitted an output

Formally, an automaton was the tuple:

- $Q$  was the finite set of causal states of the automaton labelled as  $Q = \{A, B, C..\}$
- $A$  was the finite set called the alphabet of the automaton where  $A = \{0, 1\}$
- $\delta$  was the state transition function  $Q_i \times A \rightarrow Q_j$
- $S$  was the symbol set  $S = \{x, y\}$  consisting of strings over the alphabet  $A$  where  $x$  was the input symbol and  $y$  was the output symbol

The state transition function ( $\delta$ ) was represented as a  $Q \times Q$  matrix, for example for a two-state automaton:

$$(3.1) \quad G = \begin{matrix} & \begin{matrix} A & B \end{matrix} \\ \begin{matrix} A \\ B \end{matrix} & \begin{pmatrix} 0|1 & 1|1 \\ 0|0 & 1|0 \end{pmatrix} \end{matrix}$$

Which indicated that if the automaton was in state  $A$  and received a '0' input symbol then there was an equal chance of it taking transition  $01\$$  or  $\$00$ . In the former case it emitted a '1' symbol and stayed in state  $A$  and in the latter case it emitted a '0' and moved

<sup>2</sup>this is in the strict sense that the next transition of an  $\epsilon$ -machine wasn't determined probabilistically and it was entirely acceptable for there to be two transitions leaving the current state triggered by the same input symbol and, in such cases, the transition that was taken was determined with equal probability

to state  $B$ . In the case of two possible transitions for a given input symbol the transition that was taken was determined with equal probability.

The interaction of two automatons (labelled  $T_a$  and  $T_b$ ) was calculated as the functional composition  $T_b \circ T_a = T_c$  whereby the new automaton ( $T_c$ ) inherited the domain of the first automaton ( $T_a$ ) and the range of the second automaton ( $T_b$ ) - see Figure 3.5. This was a non-commutative relationship where  $T_b \circ T_a \neq T_a \circ T_b$ . An interaction was only successful when the range of automaton  $T_a$  overlapped with the domain of automaton  $T_b$ :

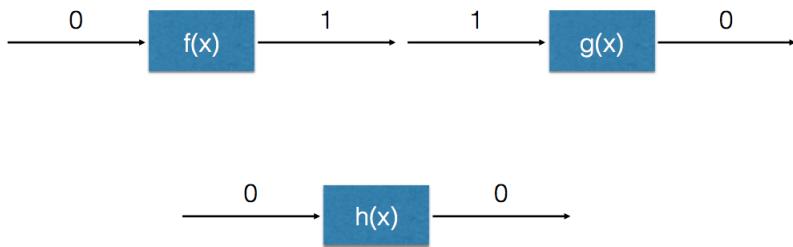


Figure 3.2: Automata could only interact when the range (output) from the first automaton matched the domain (input) of the second automaton

In this example, the new automaton  $T_c$  ( $h(x)$ ) was different to its parents and as such the production process had generated a new type of automaton in the population. In other cases the new automaton was a replica of one of its parents, for example:

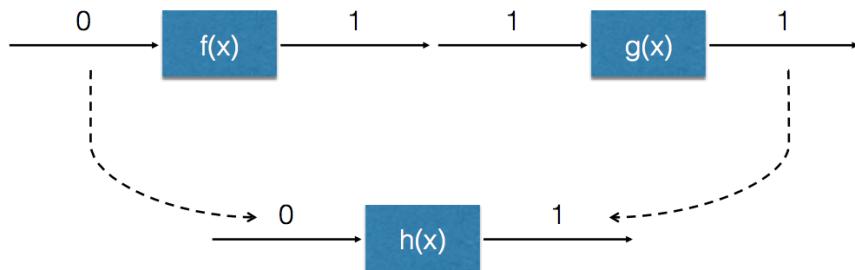


Figure 3.3: Example of the production of a new automaton where it was identical to one of its parents

Automatons could also interact with automatons of their own type and, for some automatons, this led to self-replication:

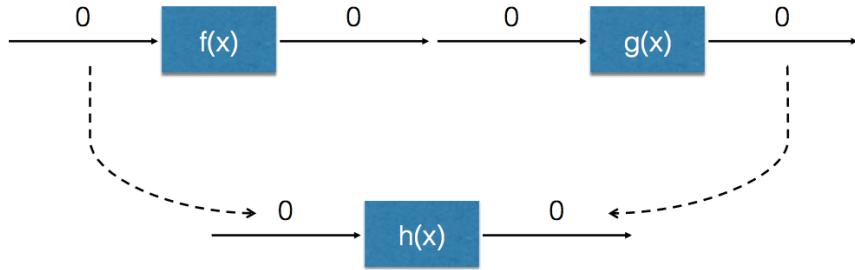


Figure 3.4: Example of self replication

As such there were four outcomes from automaton interactions:

- No production - the parent automata could not interact resulting in the creation of the transitionless automaton  $T_0$  which was forbidden in the population as in any interaction with other automata (including itself) it would always produce itself
- Type 1 - a new automaton type was generated from the networked interaction of two other automata and was different from both parents
- Type 2 - a new automaton was generated from the networked interaction of two other automata and was identical to one of its parents
- Self-replication - a new automaton was generated that was identical to both of its parents

Automata were categorised based on their number of states e.g. one-state, two-state, and so on. The library of one-state automata used in the information niche and computation niche models are shown in their graphical representation in Figure 3.5.

Interactions between automata with multiple states ( $Q > 1$ ) produced new automata with  $Q_{new} = Q \times Q$  states. Given that all automata were required to satisfy the criteria for the class of finite state transducers known as  $\epsilon$ -machines - thus maintaining the integrity of the automata types in the population as representing unique, non-duplicated functions - the product automaton ( $T_c$ ) was further processed in the following sequence [110]:

1. all unreachable states of the product automaton were removed

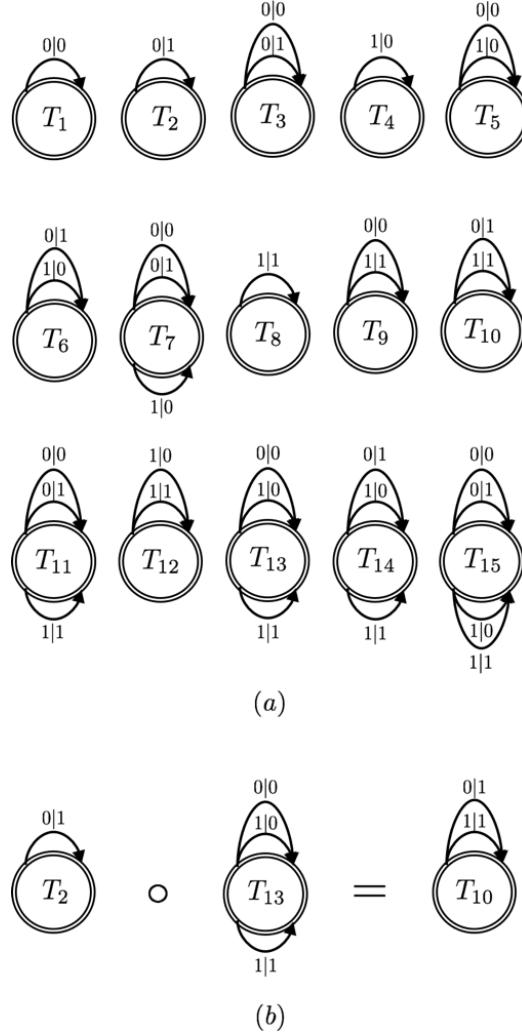


Figure 3.5: (a) Schematic representation showing a compositionally closed population of 15 types of single-state automata ( $T$ ). The population included four members that are capable of only one transition ( $T_1, T_2, T_4, T_8$ ), along with six ( $T_3, T_5, T_6, T_9, T_{10}, T_{12}$ ), four ( $T_7, T_{11}, T_{13}, T_{14}$ ) and one ( $T_{15}$ ) that exhibited two, three and four transitions, respectively. The binary numbers on the curved arrows on the top or bottom of the circles indicate the various possible transitions; for example,  $T_3$  operated only with an input signal of 0, transducing this to either 0 (non-switched output) or 1 (switched output) with 50% probability in each case. (b) Scheme showing an example of the functional composition of two machines (described by the non-commutative equation,  $T_2 \circ T_{13}$ , where  $\circ$  is the functional composition operator) to generate  $T_{10}$ . The three outputs from  $T_{13}$  were received with equal probability and transformed by  $T_2$  to produce  $T_{10}$ , which inherited the input domain from  $T_{13}$  and the output range of  $T_2$ . The number of possible unique binary interactions (207) was described by an interaction network ( $G$ ) in the form of a  $T \times T$  matrix; all functional compositions were members of the set of 15 types producing a compositionally closed population of interacting transducers. Unsuccessful interactions between transducers created the transitionless machine  $T_0$ , which was prohibited in the model

2. the automaton was minimised using the Hopcroft algorithm [48] which identified equivalent states and replaced them with a single state leaving an automaton with

$Q_{min}$  states where  $Q_{min} \leq Q_{new}$

3. validation that the topology of the minimised automaton had at least  $Q_{min}$  transitions. Where there are  $Q_{min} - 1$  transitions then at least one state did not have an outgoing transition and, as such, the automaton was *not* a strongly connected topology and hence failed the  $\epsilon$ -machine criteria

Not all interactions generated a valid automaton after the above processing had occurred and these were considered unsuccessful and the product automaton was discarded and no changes were made to the population. Successful productions were deemed to meet the criteria of an  $\epsilon$ -machine consisting of  $1 \leq Q_{min} \leq Q_{new}$  states. Sometimes new automata introduced new unique functionality into the population. These 'novel' automata were important in examining the dynamics of an open-ended population (see the results of simulations of generating novel automata in Chapter 9). Implementation of the above procedure for minimising and validating new multi-state automata as valid  $\epsilon$ -machines was computationally expensive and required a parallel processing strategy using the University of Bristol supercomputer 'BlueCrystal' (see Appendix 12.1 for further information).

In summary, interacting finite state automata produced new automata and the rules governing their interactions were implemented consistently in the information niche and computation niche models.

### **3.3 The Information Niche - a model of a self-producing population**

#### **3.3.1 Internal Environment**

An environmental context was imposed on the interacting automata by initially distributing equal numbers of the 15 types randomly across a square lattice  $\Gamma$  of  $n \times n$  sites with each site occupied by an individual single-state automaton to give a population size of  $N = n^2 = 90,000$ , which was then replicated iteratively using functional composition (see Figure 3.5b). The production of automata proceeded by randomly selecting a lattice site  $G_{i,j}$  whose occupying automaton ( $T_d$ ) may or may not be replaced by a new type  $T_c$  depending on the competition between the environmental influx and internal production dynamics (see Figure 3.6. The probability that  $T_c$  was a randomly generated automaton entering from the external environment or alternatively derived from the functional composition of two neighbouring automata was given by  $\Phi$  and  $1 - \Phi$ , respectively. Production of  $T_c$  by either option replaced  $T_d$ , which was subsequently removed from the population to maintain

a constant value for  $N$ . This constraint generated a survival selective pressure between different types of automata, which must be continually produced to prevent depletion from the population.

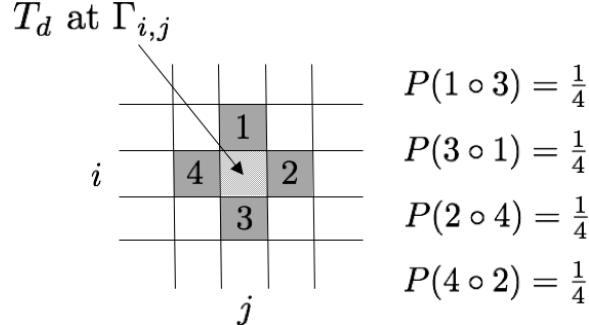


Figure 3.6: Graphic illustrating the computational model for generating internal production dynamics in a square lattice of  $n \times n$  sites comprising single-state automata of type  $T$ . The lattice had periodic boundary conditions, i.e. a regular toroid topology, and, as such, an automaton in the top two rows of the lattice could interact with automata directly opposite it in the bottom two rows of the lattice and vice versa. The same condition applied to an automaton on the left edge and right edge of the lattice. Spatial mixing also occurred in the same manner. An automaton ( $T_d$ ) on lattice site  $G_{i,j}$  was chosen at random for replacement by functional composition involving types ( $T_a, T_b$ ) selected from the sites (1,2,3,4) adjacent to  $T_d$ . Only one pair of neighbours from the two possible pairwise combinations (1,3 or 2,4) was selected to interact according to the non-commutative equation  $T_b \circ T_a$ , where the order of the interacting pair was selected randomly according to an equal probability of 1/4. If the functional composition generated a new automaton ( $T_c$ ), this replaced  $T_d$  at lattice position  $G_{i,j}$ , which was subsequently removed from the population. If no interaction occurred, then a transitionless machine  $T_0$  was generated such that  $T_d$  was not replaced and remained on the lattice site. The new population was then subjected to different levels of spatial mixing.

### 3.3.2 Production Dynamics

The production process was iterated for up to  $10^7$  time steps to simulate the emergence of a number of distinct information niches. Changes in the structure and composition of the population were observed with increasing numbers of iterations, and this was captured at each time step by updating the frequency distribution ( $f$ ) of the information processing types present in the emerging community. The following differential equation described the changes in  $f$  on each time step [108]:

$$(3.2) \quad \frac{df_c}{dt} = (1 - f_c) \sum_{T_a \circ T_b = T_c} f_a f_b - f_c \sum_{\substack{T_a \circ T_b \neq T_c \\ T_a \circ T_b \neq T_0}} f_a f_b$$

Where  $T_a, T_b$  were the interacting machines,  $T_c$  was the new automaton produced from that interaction and  $f_a, f_b, f_c$  were their normalised frequencies of occurrence in the population.  $T_0$  was the transitionless automaton that represented an unsuccessful

interaction and was prohibited in the population. Equation 3.2 determined two factors: (i) the probability of adding the automaton  $T_c$  was equal to the probability of selecting two neighbours  $T_a$  and  $T_b$  that produced  $T_c$  multiplied by the probability that the automaton that was being replaced ( $T_d$ ) was not the same as  $T_c$  and (ii) the probability of neither  $T_c$  nor  $T_0$  being produced. The invariant frequency distribution of machine types could therefore be determined by solving  $df/dt = 0$ . Here, discrete time was a good approximation for continuous time as only one lattice location was updated on each time step and so for large  $N$  (our minimum value for  $N$  was 90, 000 automata) this led to a small change in the overall frequency distribution of all automata. This equation assumed that all interactions were possible on each time step, which was consistent with a well-mixed environment with no influx of automata.

#### Asynchronous and Synchronous Update of the Population

A cellular automata (CA) is a collection of cells usually arrayed on a grid that can be one of a number of finite states. Each cell 'updates' its state based on a rule that depends on the states of the neighbouring cells. The dynamics of the CA are generated by repeated application of this local rule by all cells. There are two approaches to updating the CA: synchronous whereby all cells are evaluated as per the local rule and the state of each cell is updated accordingly, and asynchronously where all cells are evaluated successively one after the other. The appropriate update process to use for modelling a biological process has been investigated and evaluated in terms of 'model stability' [111]. In summary, model stability consists of three considerations: (i) stability of the dynamic system that reaches stable stationary points, (ii) the qualitative behaviour of the model (and its results) do not change significantly if parameters are varied within a certain range, (iii) that the qualitative results of the model are only dependent on the assumptions made about a real biological system i.e. the results are not dependent on how the model has been implemented, for example, whether as a numerical solution of a differential equation or as a cellular automata. Schonfisch & de Roos identified that the two approaches can lead to qualitatively and quantitatively different results in both transient and long-term behaviours of the model with asynchronous updating offering a better approximation of real continuous time. Synchronous updating assumes that all events occur in parallel and, as pointed out by the authors, '... at most points in time and at most places nothing happens' and, as such, a model whereby at most only one event can happen more accurately captures a biological process.

The information niche model uses the asynchronous update approach.

### 3.3.3 Environmental Perturbations

Spatial mixing occurred within the population during replication by randomly selecting a lattice site and exchanging the residing automaton with another type positioned on a different lattice site along one of the cardinal directions at a distance  $d$  selected from a one-dimensional Gaussian distribution with variance  $v$  and  $mean = 0$  and rounding  $d$  to the nearest corresponding lattice site. This was repeated for  $c$  numbers of different sites per production time step. The combination of  $c$  and  $v$  approximated diffusion within the replicating population such that when  $c \rightarrow N$  and  $v \rightarrow n$  the population was well mixed, while for  $c = 0$  and  $v = 0$  the population of automata had very low mobility [108]. To simulate the coupling of the replicating population to changes in an external environment, randomly generated automaton types replaced randomly selected automata in the population at time  $t$  with a probability given by  $\Phi$ , where  $0 \leq \Phi \leq 1$ . With  $\Phi = 0$ , no random replacement occurred and population dynamics were driven entirely by the composition of existing automata. In contrast, with  $\Phi = 1$ , the population dynamics were determined entirely by randomly generated automata entering the lattice from the external environment [35]. The combinations of the spatial mixing ( $c, v$ ) and influx dynamics ( $\Phi$ ) parameters that were used for one-state and two-state simulations were varied to simulate a range of fixed environmental conditions to assess the impact on the production dynamics of the automaton population. The effect of fixed environmental conditions on automata populations were investigated with a one-state automata population (see Chapters 4 and 6) and a two-state automata population (see Chapter 5).

The effect of intermittent changes in the environmental parameters on the robustness of the population was investigated in a one-state automata population. For this, the following modifications in environmental conditions were imposed once a steady-state population was attained: (i) inversion of the spatial mixing parameter such that conditions contrary to those in which the steady-state population was produced are imposed, e.g. if a niche was formed in a well-mixed environment then the environmental conditions were reset to simulate a highly restricted movement of the automata ( $c, v = 0$ ); (ii) inversion of the influx setting of new machines into the lattice, e.g. if a niche was produced in the absence of any influx of automata ( $\Phi = 0$ ) then this parameter was reset to  $0 \leq \Phi \leq 1$ ; (iii) simultaneous perturbations associated with modifications (i) and (ii). Perturbations on the initially produced steady-state population were undertaken for a minimum of  $10^6$  iterations, which was usually sufficient for the population to reconfigure into a new steady-state conformation. The perturbations were then removed by resetting the environmental parameters back to their original values, and changes to the population structure recorded. Consequently, the

original population structure was re-created or a new population structure was established. Examination of intermittent changes in environmental parameters was investigated with a one-state automata population (see Chapter 4).

### 3.3.4 Co-Evolution of Niches

A one-state automata population and a two-state automata population were combined into a joint population located on a  $n \times n$  lattice. The effect of different initial proportions of each population were investigated:

1. all automata types from a one-state and two-state population ( $F_{all}$ ), consisting of 15 and 1,873 types respectively for a total of 1,888 types, were uniformly distributed across the lattice according to  $f_{joint} = f_i \in F_{all} : 1/f_i$
2. initial proportions were calculated from the normalised sum of both automata populations at steady-state ( $F_{ss} = \{f_{1state}, f_{2state}\}$ ) such that  $f_{joint} = f_j \in F_{ss} : f_j/Z$  where  $Z$  is a normalising factor and  $|f_{joint}| = |f_{1state}| + |f_{2state}|$
3. initial proportions were uniform across all one-state and two-state automata types in steady-state populations such that  $f_{joint} = f_k \in F_{ss} : 1/F_{ss}$ .

In all cases  $|f_{joint}| = |f_{1state}| + |f_{2state}|$  for the related population set  $F_{all}$  or  $F_{ss}$ . The evolution of the joint population was recorded for a minimum of  $10^6$  time-steps and the population structure was analysed. The results of simulating the co-evolution of niches is presented in Chapter 7.

### 3.3.5 Inter-niche Transfer of Automata

A two-state automata population donated an automata to a separate one-state automata population at a rate given by  $0 \leq \Phi \leq 1$  which was also the probability of a two-state automata replacing an existing automata in the one-state population at that time step. Each population was allowed to evolve to a steady-state and then the influx rate was increased  $0 \leq \Phi \leq 1$ . The structure of the host population adjusted to the presence of additional automata and over time the structure of the donating population was reproduced in the host population. The changes in the structure of both populations was recorded throughout the simulation and the results are presented in Chapter 7.

### 3.4 The Computation Niche - a model of a self-producing population with a membrane

The conceptual motivation for the computation niche model was Luisi's minimal autopoietic cell [8] - see Figure 3.7.

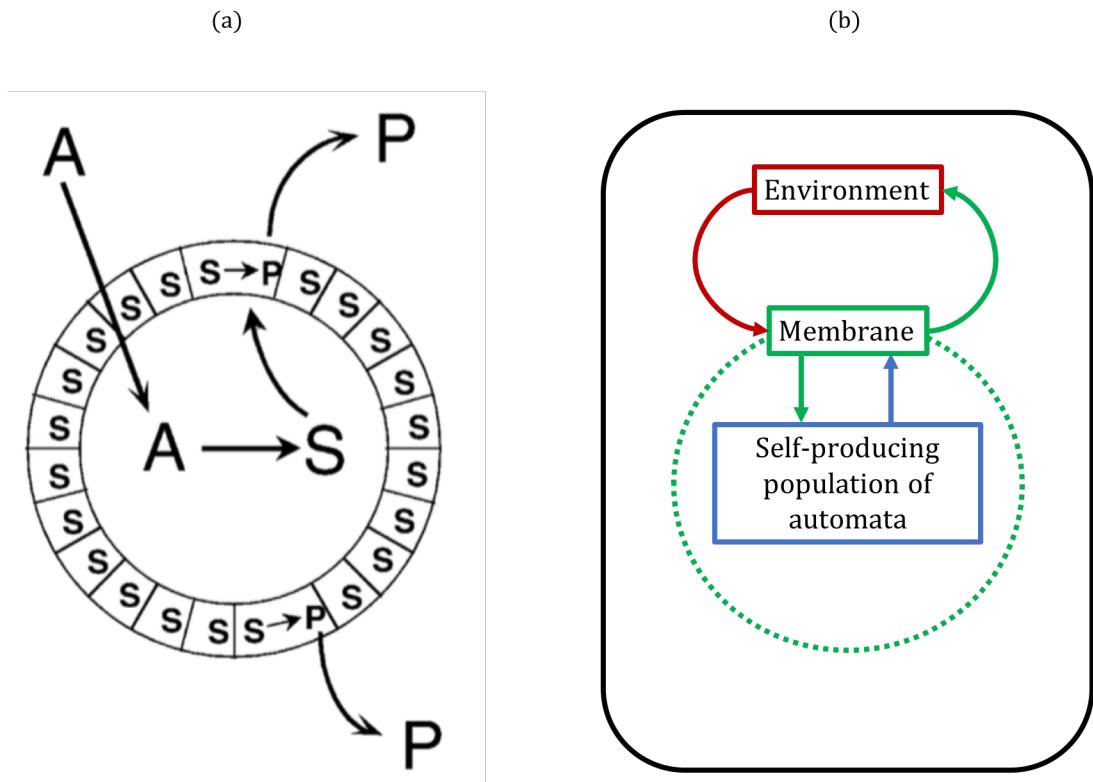


Figure 3.7: The computational model was partly inspired by Luisi's model of a minimal autopoietic unit (a) in that the membrane  $S$  is determined by the internal reaction  $A \rightarrow S$ . Furthermore, the decay of the membrane  $S \rightarrow P$  indicates the requirement for continuous renewal of the membrane via continual production of  $S$ . By analogy, the high level concept of the computation niche (b) is that the membrane reflected the productions that occurred in the interior. Furthermore, the membrane acted as the interface between the internal population of interacting automata and the environment. Luisi's model shows the migration of a substrate molecule  $A$  through the membrane but does not show the effect of the membrane on the internal reactions beyond simply acting as a container. The functionality of the membrane in the computation niche is more comprehensive whereby the behaviour of the membrane influences the productions that occur within the interior (green arrow). This is a limitation of the Luisi model and one that the computation niche addresses

The computation niche model explicitly models each of the three components: environment, membrane and the internal self-producing population each of which is now described in more detail.

### 3.4.1 Internal Environment

The internal population of the computation niche was based on a simplified version of the information niche model under well-mixed conditions. As global environmental conditions, such as spatial mixing and an influx of material (automata) were not examined in the computation niche model, there was no requirement for a cellular automata implementation of the population. Instead the interactions in the internal population was as a well-mixed chemical reactor (the same as the model that was implemented in the Finitary Process Soup [35]). All possible interactions at time  $t$  were determined by the activity of the membrane (see section 3.4.2) with excited automata interacting with all other excited automata to produce new automata<sup>3</sup>. Interactions proceeded on the assumption that in a well-mixed population all automata were available to each other to interact. For each new automata produced an existing automata was randomly selected and removed from the population thus maintaining a constant population size. All possible interactions that could occur were performed and hence this was, technically, a synchronous update of the population on each time-step. As has been previously explained an asynchronous update method is preferred for emulating biological behaviour in a cellular automaton model however this was deemed less relevant in the computation niche model for two reasons: (a) the well-stirred chemical reactor model used in the internal population of the computation niche is not a cellular automata, and (b) repeated simulation runs to test the computation niche model with a one-state population clearly demonstrated very similar results to a one-state information niche model under well-mixed conditions (see Chapter 8).

The internal population was defined by two variables: the interaction matrix  $G$  and the frequency distribution of the population  $f$ . On each time step the currently active membrane automata (represented by the binary vector  $\Psi$ ) operated on  $G$  to temporarily remove parts of the interaction matrix which corresponded with the inactive membrane automata. This led to the inhibition of the interactions involving automata of the same type as the inactive membrane automata and subsequently suppressed the production of the automata that would have been produced from interactions of those automata. The interactions that occur at time  $t$  were therefore determined by element-wise multiplication ( $\bullet$ ) of the interaction matrix  $G$  with the membrane automata status vector  $\Psi$  (and where  $\Psi'$  was the transpose of that vector):

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<sup>3</sup>An investigation into the effect of making this production step a stochastic process (i.e. possible interactions were subject to a failure rate) demonstrated a delay in the formation of the computation niche but qualitatively produced the same result. As such, a probabilistic aspect to the production of automata in the computation niche model was deemed to be unnecessary

$$(3.3) \quad G_\Psi = \Psi \bullet G \bullet \Psi'$$

Where two automata that can interact were (i) active ( $\Psi_i = 1$ ), and (ii) present in the population ( $f_i > 0$ ) a new automaton was produced. The automaton produced was indicated by the element of the interaction matrix at  $G_{ij}$  where  $i, j$  were the indices of the two interacting automata ( $T_a, T_b$ ) respectively. The increase in the frequency of automata of type  $i$  in the population was determined by:

$$(3.4) \quad \Delta f_i = \sum \sum f_t \bullet A_i \bullet f'_t$$

Where:

$f_t$  was the current frequency distribution of the population (as a row vector)

$A_i$  was the adjacency matrix of  $G_\Psi^i$  that describes all possible interactions that can produce automaton type  $i$

$f'_t$  was the transpose of the frequency distribution vector

Subsequently, the overall change in the frequency distribution of the population was:

$$(3.5) \quad f_{t+1} = \frac{F_t + \Delta F}{\sum F_t + \Delta F}$$

Where:

$F_t$  was the absolute frequency count of each automata type in the population (as an integer row vector)

$\Delta F$  was an integer row vector indicating the absolute change in the frequency of each automata type due to being produced or removed from the population

$f_{t+1}$  is the normalised frequency distribution of the population

The population's normalised frequency distribution was used to set the weightings of the edges in the membrane network (this is discussed in more detail in the next section).

When an automaton ( $T_i$ ) was no longer present then its frequency was set to zero ( $f_i = 0$ ) and all interactions involving it were removed from the interaction network ( $G(\Psi)$ ).

Because this particular type of automaton was no longer present in the population it was also removed from the membrane. An automaton type that was currently extinct could only be re-introduced into the population and the membrane by being produced by other automata that remained present in the population. Activating a membrane automaton therefore potentially benefited its equivalent population automata by increasing the probability of it being produced.

### 3.4.2 Membrane

The function of the membrane is to process information from three sources: the environment, from other automata within the membrane, and from the internal population.

#### Luisi's minimal autopoietic cell and the computation niche membrane

The concept of a membrane is inspired by Luisi's model of a minimal autopoietic cell [8] whereby the membrane is 'maintained' by internal reactions. In this case, the membrane promotes certain interactions in the interior which leads to the growth and decay of automata; simultaneously holes appear in the membrane at a rate consistent with the growth/decay dynamics in the interior. As such, the composition of the membrane should reflect the composition (or structure) of the internal population of automata. This relationship is represented in the membrane as a network with weighted edges between membrane automata. These weightings are directly calculated from the population structure. Subsequently, the membrane evolves to become a network representation of its internal population and its environment.

The principles and assumptions behind the design of the membrane were:

1. The membrane model is emulating cell signalling i.e. a membrane-bound protein  $M_i$  is activated in some manner and either allows small molecules into the interior or transduces information from a membrane-based activity with either event leading to the excitation of a particular molecular species in the interior. It is assumed that this excitation is of a high fidelity with an extremely low probability of activating non-target automata in the interior. Hence, excited automata in the interior population interact - under well-mixed conditions - with other excited automata to produce new automata. Within the computation niche model the automata in the membrane automata are assumed to be dormant by default and therefore need to be triggered in some manner before they excite/inhibit their counterpart in the internal population.

### 3.4. THE COMPUTATION NICHE - A MODEL OF A SELF-PRODUCING POPULATION WITH A MEMBRANE

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2. To model the maintenance of a membrane from the products of an internal population the membrane itself needs to reflect the composition of the internal population. One option that was considered was that the most populous automata formed the membrane. However this would lead to a homogenous membrane with very limited information processing capacity (i.e. the membrane would only ever represent the behaviour of one automaton type) and, as such, this was dismissed. The decision was therefore made that the structure of the internal population (i.e. the types of automata present and their relative concentrations) would be represented in the membrane as a network with each automaton type that was present in the internal population represented as a node in this network, the interactive relationship  $T_a \rightarrow T_b$  would determine the edges between the nodes, and the relative concentration of each automaton type in the population would be represented as a weighting over those network edges.
3. The membrane is only a representation of the structure of the internal population. It does not require the removal of any population automata into the membrane.
4. Conceptually it is assumed that the membrane consists of an inert medium that prevents automata in the membrane network from directly interacting with each other to produce new automata. The membrane automata are assumed to be fixed in position and only able to communicate with other membrane automata via. some mode of transferring binary information over their outgoing edges.
5. Changes in composition of the internal population directly effect the behaviour of the membrane due to the change in weightings on the network edges (we assume that automata in the membrane need to be replaced however there are limited positions in the membrane and therefore there is competition within the membrane for available slots; we directly relate the composition of the internal frequency distribution of automata to the composition of the membrane. To reiterate, the number of each automata type in the membrane is proportional to the composition of the population i.e. an increase in the frequency of an automata being produced in the population will increase the weighting given to that automaton's emissions in the membrane).
6. To clarify, the duality of a finite state automata as both function and replicator was represented in the computation niche model. Processing of information that led to a state change in the automata was a behaviour performed by the membrane automata. The functional composition of two automata to generate a new automata - which

was a function of the information processing capacity of each automaton - was a behaviour performed by the population automata.

The membrane was therefore a network of unique and distinct finite state automata that transmitted and received binary information from/to each other over the network edges. The network was derived from the interaction network (as described in section 3.6.1) and represented the interaction  $T_a \circ T_b$  where  $T_a$  was the source automaton whose emissions were transformed by the target automaton  $T_b$ . The automaton  $T_c$  which was produced from such an interaction was not represented in the membrane automata as it was already represented in the internal population (see section 3.4.1). An edge represented a communication channel between two automaton where the output from the source automaton ( $T_a$ ) was received by the target automaton ( $T_b$ ). Each membrane automaton processed the information it received according to its own unique function which was a property of its internal structure ( $\tau$ ).

The membrane model of the computation niche model has a number of conceptual similarities to random boolean networks but also important differences. Clarification of such similarities and differences is provided in Box 3.4.2.

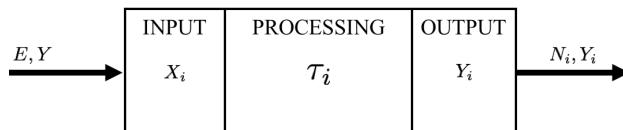


Figure 3.8: Each membrane automaton (node) in the network acts as an information processing unit transducing from one set of communications channel ( $X$ ) to another ( $Y$ ). Information was received at the membrane automaton's input ( $X$ ) from the environment ( $E$ ) and connected automata ( $Y$ ). The normalisation of that information was then processed by the automaton according to its intrinsic structure ( $\tau$ ) to determine if a threshold was surpassed that triggered an emission from the automaton ( $Y$ ) which was transmitted to the target membrane automata ( $Y$ ) on its outgoing edges. The activation status of the automaton is captured by the variable  $\Psi_i$  where  $\Psi_i = 0$  and  $\Psi_i = 1$  represented an inactive or activated automaton respectively. Cumulatively the emissions from all activated membrane automata were emitted to the environment as a probability distribution ( $N$ ) of two events occurring (the probability of the binary symbol '0' and '1' being emitted respectively).

### 3.4. THE COMPUTATION NICHE - A MODEL OF A SELF-PRODUCING POPULATION WITH A MEMBRANE

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#### Random Boolean Network compared to the Computation Niche membrane model

Random boolean networks are a certain type of discrete, dynamical network that was developed by Stuart Kauffman [112] to model gene regulatory networks. A random boolean network has  $N$  nodes in a directed graph where each node is either ON or OFF state (boolean 1 or 0). Each node in a RBN updates its state based on the state values of the nodes which it is connected to on its incoming links. By comparison, the membrane automata in the computation niche model update their state based on the information that is received over their incoming links. This is an important distinction as there are three possible values that are transmitted over incoming links ( $\emptyset, 0, 1$ ) whereas in the random boolean network model there are two values (0,1).

This information processing either led to the membrane automaton ( $M_i$ ) activating if a certain probabilistic threshold was reached ( $\Psi_i = 1$ ) otherwise the automaton remained inactive ( $\Psi_i = 0$ ). An activated membrane automaton: (a) emitted information corresponding to the processing that it had performed and this was transmitted over its outgoing edges to other automata in the membrane network, and (b) excited its equivalent automata types in the internal population so that they were available for interacting with other excited population automata (see 3.4.1). The membrane automata that were receiving emissions from activated automata treated the incoming information as one of a number of simultaneous information sources. As such the behaviour of each membrane automaton was a function of the cumulative information it received from all sources. If a membrane automaton wasn't activated then it did not transmit information to other membrane automata nor did it excite its equivalent automata types in the internal population. The effect of this on/off switching of membrane automata was to excite/inhibit internal interactions (top-down information flow) and to increase/decrease the activation threshold of other membrane automata (same-level information flow). The cumulative emissions from all activated automata was also emitted into the environment as a two-element probability distribution where it modulated environmental information (bottom-up information flow). Hence, the computation niche was modelling hierarchical information flows between three levels of abstraction.

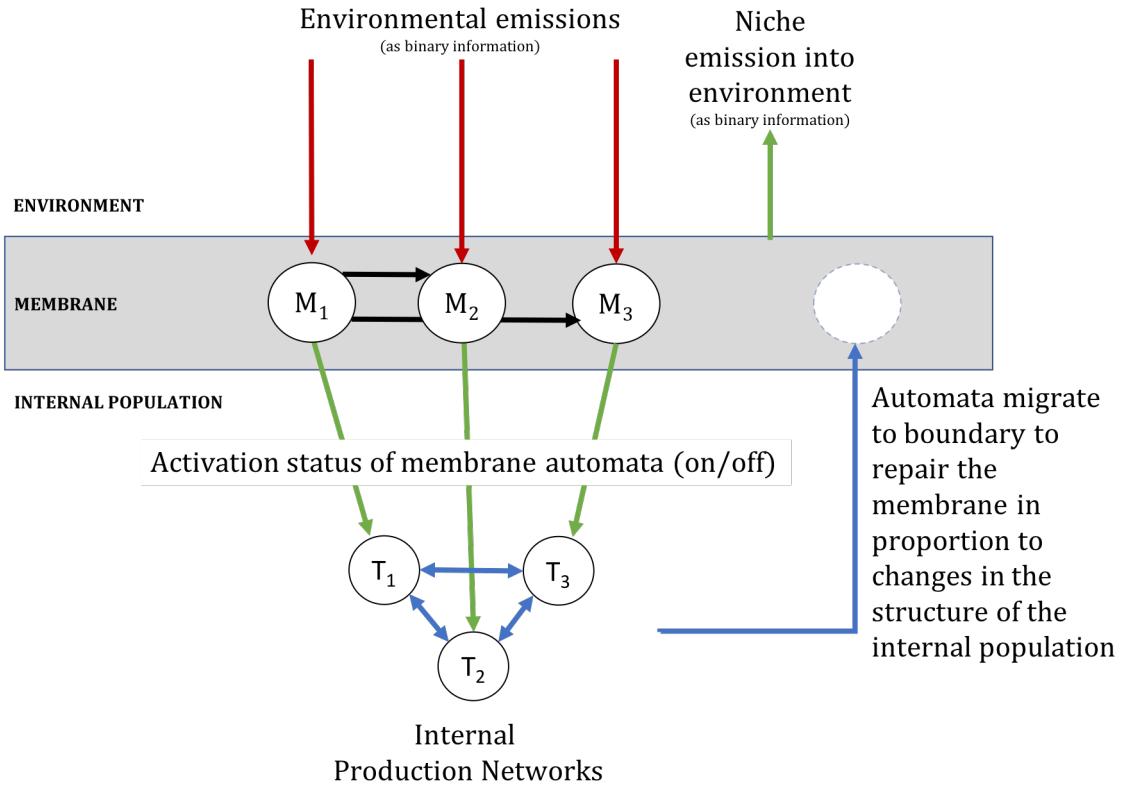


Figure 3.9: The membrane can be visualised as a continuous structure encapsulating the interacting population of automata that is embedded with different membrane automata ( $M$ ) each of which has a unique function and reflects the automata types ( $T$ ) in the population. Each membrane automata transduces information from the environment and other membrane automata and this sometimes led to emissions that signals to the internal population which automata are 'on' or 'off' and able to participate in an interaction to produce a new automaton (top-down information flow). This influences the production of new automata which, in turn, changes the internal composition of the population which is reflected in the composition of the membrane (bottom-up information flow).

Figure 3.10a is an illustrative example of a membrane. The information processing functions of four one-state automata are shown ( $M_1, M_2, M_4, M_8$ ) with  $M_1$  and  $M_8$  repeating the information they received whilst  $M_2$  and  $M_4$  modify the information by 'bit flipping'. Where the output from a membrane automaton can be received by another automaton a directed edge captures the relationship (see figure 3.10b). The membrane network matrix describing the networked automata membrane is shown in figure 3.10c with the corresponding topology shown in figure 3.10d. An example of the operation of this membrane is described in table 3.2.

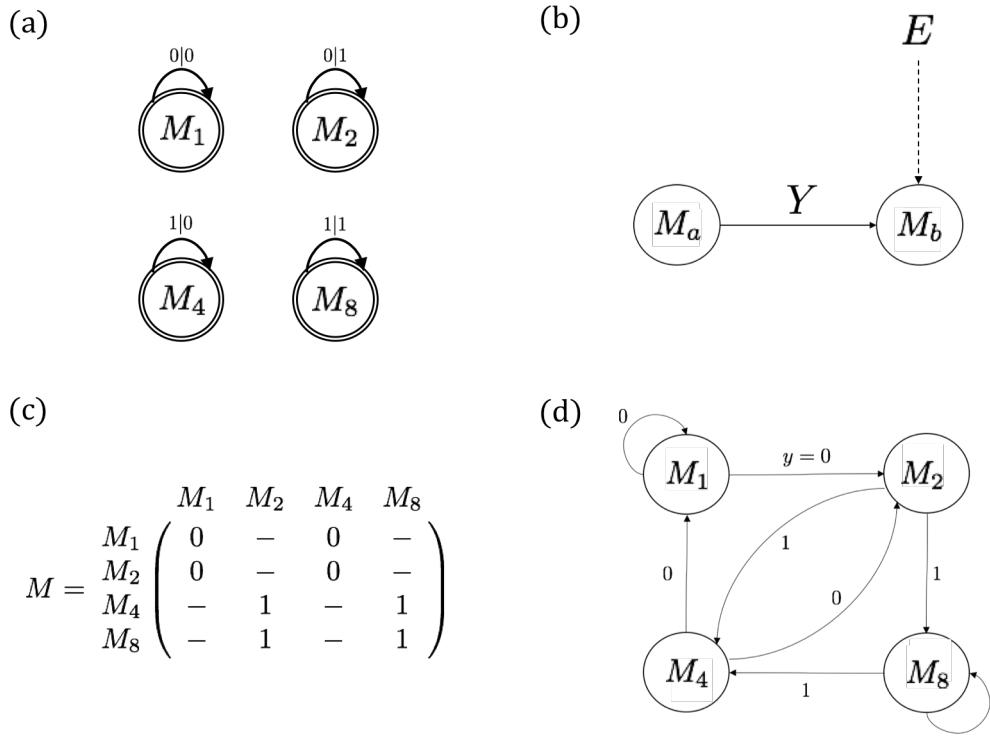


Figure 3.10: Illustrated example of a small membrane network consisting of four automata. The automata are of the same type as used in the information niche model however they are labelled as  $M_i$  rather than  $T_i$  to distinguish their function in the membrane as processing information rather than interacting to produce new automata: (a) the four membrane automata each of which is a single state information processing transducer that receives a single binary symbol and emits a single binary symbol; (b) the syntax of the membrane network where each node in the network represents an automaton type ( $M_i$ ). Directed edges between nodes indicate the flow of information e.g. information is emitted from an automaton that occupies the  $T_a$  role in the interaction equation  $T_a \circ T_b = T_c$  and which is received by an automaton occupying the  $T_b$  role. As such, all directed edges indicate that the connected automaton types interact to produce a new automaton. The automaton  $T_c$  produced by the interaction of  $T_a$  with  $T_b$  is not represented in the membrane network (this would duplicate information already contained in the interaction matrix  $G$ ); (c) the membrane connection network ( $M$ ) that describes the  $T_a \rightarrow T_b$  relationships that constitute the membrane network structure where the column headings ( $j$ ) signify the automaton type acting as  $T_a$  and the row headings ( $i$ ) signify the automaton type acting as  $T_b$  in the interaction equation  $T_b \circ T_a = T_c$ ; (d) the topology of the membrane automata network with an average degree distribution of 2 with the transmitted symbol labelled on each edge.

<i>t</i>	active	inactive	transmissions	productions
$t_0$	-	$M_1, M_2, M_4, M_8$	-	-
$t_1$	$M_1$	$M_2, M_4, M_8$	$M_1 \rightarrow 0$	$T_1$
$t_2$	$M_1, M_2$	$M_3, M_4$	$M_1 \rightarrow 0, M_2 \rightarrow 1$	$T_1, T_2$
$t_3$	$M_1, M_2, M_4, M_8$	-	$M_1 \rightarrow 0, M_2 \rightarrow 1, M_4 \rightarrow 0, M_8 \rightarrow 1$	$2 \times T_1, 2 \times T_2, 2 \times T_4, 2 \times T_8$

Table 3.2: For illustration purposes and assuming no probabilistic threshold is being applied to the inputs to each membrane automaton:  $M_1$  was spontaneously activated and emitted a '0' symbol over its outgoing edges. As a result it re-activated itself and  $M_2$  which was the only other automaton that could process the binary symbol '0'. Once  $M_2$  was activated it emitted a '1' which activated  $M_4$  and  $M_8$ . Those two automata then emitted a '0' and a '1' respectively which, in turn, activated all remaining membrane automata that were not already active. During this information processing in the membrane, productions in the internal population created  $T_1$  (via. self-replication), and  $T_2$  and after the third time-step all automata types in the population were being produced. NOTE: in practice the activation of a membrane automaton is subject to a randomly determined threshold being surpassed meaning that even if an automaton is receiving an input it may not activate. This is a necessary measure to prevent self-activating membrane automata such as  $M_1$  and  $M_8$  from being constantly active.

As the membrane is a reflection of the internal population the concentration of automata were represented as weightings ( $\lambda$ ) on the directed edges in the network. The weighting on each outgoing edge from an automaton is equal to the normalised frequency of its equivalent population automaton type ( $\lambda_i = f_i$ ). Therefore, the cumulative weighting of all outgoing edges from a membrane automaton ( $M_i$ ) is given by:

$$(3.6) \quad \lambda_Y = \left[ \sum_{y \in Y} f_i \right]$$

, where  $Y$  is the set of all outgoing edges from membrane automata  $M_i$ . Hence, each outgoing edge has the identical weighting  $f_i$ .

For all incoming communication channels ( $X$ ) to a given membrane automaton ( $M_i$ ) the cumulative weighting of all incoming edges is given by:

$$(3.7) \quad \lambda_X = \left[ \sum_{x \in X} \lambda_x \right] \cdot \frac{1}{Z}$$

, where  $X$  is the set of all incoming edges to  $M_i$ ,  $\lambda_x$  is the edge weighting of a particular edge and  $Z = \sum \lambda_X$ .

The higher the concentration of the equivalent population automaton the higher the magnitude of that membrane automaton's emissions are on the receiving automaton due to the edge weighting. Specifically, received transmissions of a higher magnitude have a greater effect on whether the target automaton activates. This weighting of edges allows for

### 3.4. THE COMPUTATION NICHE - A MODEL OF A SELF-PRODUCING POPULATION WITH A MEMBRANE

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population dynamics to influence information flow in the membrane (bottom-up causation) and, given that information activates/deactivates membrane automata, also indirectly affects the production dynamics in the internal population (top-down causation).

The information received ( $X_i$ ) by the target membrane automaton was given by:

$$(3.8) \quad X_i(t) = \left( \sum_{x \in X} \lambda_x \right) \cdot \frac{1}{Z}$$

Where:

$X$  is the set of all incoming edges from one or more source automata connected to the target automaton  $M_i$

$x$  is the information transmitted over each edge from source node to the target node in the form of a 2-element probability distribution where  $P(x) = P[x = 0, x = 1]$ . The absolute values of this distribution represent the emission of either a '0' or a '1' symbol given that only one symbol can be transmitted over a communication channel at each time step therefore if  $P(x = 0) = 1$  then  $P(x = 1) = 0$  and vice versa. If no information is transmitted - that is, the source membrane automaton is inactive - then  $P(x) = [0, 0]$ .

$\lambda_x$  is the weighting of the incoming edge  $x$

$Z$  is a normalisation factor applied to the sum of all the received information  $X$  to ensure that  $\sum X_i = 1$

Some membrane automaton could emit a '0' or '1' depending on the information processing that had been performed on the information that they had received. Hence, such automata would emit information over their outgoing edges that could not be received by receiving automata. For example, the membrane automaton  $M_{15}$  (functionally identical to the population automaton  $T_{15}$  - see Figure 3.5) can transmit a '0' or a '1' and it was connected to the membrane automaton  $T_1$  which can only receive a '0' symbol. As such, it was necessary to filter the incoming information ( $X_i$ ) by the functional domain of the receiving automaton ( $M_i$ ) according to:

$$(3.9) \quad X'_i = X_i \cdot \tau_i$$

Where  $X'_i$  sets the activation threshold of the automaton and was represented as a two-element probability distribution and  $\tau_i$  is the proportion of the target automaton's *input channels* (of its current state) that are able to accept a '0' or a '1' according to the syntax:  $T_i = \frac{|x=0|}{|x=0+x=1|}, \frac{|x=1|}{|x=0|+|x=1|}$ . For example, the input for each of the four automaton types shown in figure 3.10a were:  $\tau_1 = [1, 0]$ ,  $\tau_2 = [1, 0]$ ,  $\tau_4 = [0, 1]$ ,  $\tau_8 = [0, 1]$ .

To determine whether the automaton was activated, a random number  $r$  was generated and a conditional tested:

$$\alpha_i = \begin{cases} 0 & \text{where } x_0 || x_1 < r \\ 1 & \text{where } x_0 || x_1 > r \end{cases}$$

Where  $\alpha$  was a binary vector of length  $|T|$  where each element represented whether the membrane automaton  $M_i$  was now active ( $\Psi = 1$ ) or remained inactive ( $\Psi = 0$ ) at  $t$ . Hence,  $\alpha_i$  was '1' if either  $x_0$  or  $x_1$  surpassed the random threshold  $r_1$ . Where  $\alpha_i = 1$  the value for  $x$  that exceeded the threshold was taken as the activated transition of the automaton. If either value of  $x$  surpassed the threshold then the value of  $x$  to use was determined randomly with equal probability. When there was more than one possible transition that satisfied the condition (i.e. the current state of an automaton had two transitions  $0|0$  and  $0|1$  for  $x_0$  or  $1|0$  and  $1|1$  for  $x_1$ ) the transition that was taken was determined with equal probability. A random real number  $0 \leq r' \leq 1$  was generated and the following cases examined e.g. in the case where  $x_0$  activated the automaton:

$$r' = \begin{cases} \leq 0.5, & \text{transition } \{0|0\} \text{ was taken} \\ > 0.5, & \text{transition } \{0|1\} \text{ was taken} \end{cases}$$

The same conditions applied where  $x_1$  activated the automaton. For example,  $T_7$  has three transitions two of which accepted a '0' and the other a '1'. After determining the cumulative information received at  $T_7$ 's input, the input probability distribution was  $P(X_{T_7} = \{0.67, 0.33\})$ . Hence, where  $r = 0.5$  the '0' symbol has surpassed the activation threshold and triggered an emission from the automaton. The symbol that is transmitted is determined by the transition taken by the automaton on being activated. Given that there are two possible transitions for the input symbol '0' the transition that is taken is determined randomly with equal probability. The output symbol associated with the transition that was randomly selected was transmitted over the automaton's outgoing edges.

To recap an activated membrane automaton triggered two events: (i) the activated membrane emitted information associated with the output symbol of the transition that

### 3.4. THE COMPUTATION NICHE - A MODEL OF A SELF-PRODUCING POPULATION WITH A MEMBRANE

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was executed, (ii) the equivalent production automata in the internal population are activated and available to interact. Activated population automata could only interact with other activated population automata within that time step (as per the procedure described in section 3.4.1). If the membrane automaton was not activated then this had the effect of inhibiting all interactions of the associated population automaton in the internal population. Hence, the behaviour of the membrane directly effected the productions that took place in the population for that time step. This was a form of top-down causation on the population automata. Changes in the population structure occurred through the creation of new population automata that replaced existing automata. This led to changes in the structure of the internal population which led to changes in the edge weightings in the membrane automata network. This subsequently affected the flow of information in the membrane and the activation of membrane automata at  $t + 1$ . Changes in population structure therefore acted as a form of bottom-up causation on membrane behaviour (the circular relationships between membrane, internal population and the environment is illustrated in figure 3.11).

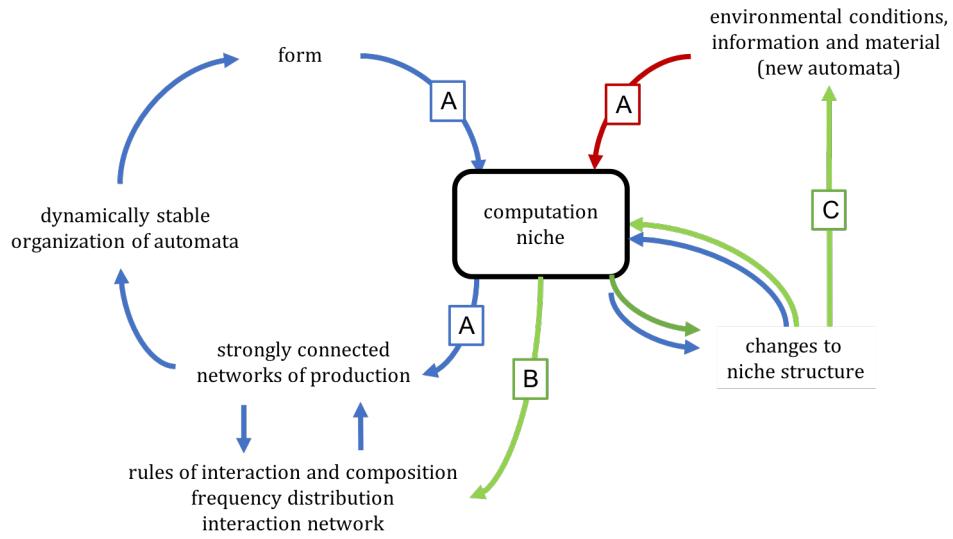


Figure 3.11: The computation niche extended the concept of the information niche to model the relationship between three processes: a self-producing population that was operationally closed (blue), an environment that was continuously generating binary information (red), and a membrane that bisects the self-producing population of automata from the environment (green). The nexus of these processes was the membrane component which changed to reflect both the structure of the population (represented as changes in the weightings over the edges of the membrane network) and the binary information that was being received from the environment at time  $t$ . Information from the environment was processed simultaneously by all membrane automata with the effect of inhibiting the production of automata in the population (flows labelled 'A'). Changes in the structure of the population affected the distribution of weights over the membrane network leading to a change in the information processing behaviour of the membrane (flow labelled 'B'). Information generated by emissions of membrane automata were transmitted into the environment subsequently modulating environmental information (labelled 'C')

The following pseudocode defines the algorithm for the operation of the membrane:

### 3.4. THE COMPUTATION NICHE - A MODEL OF A SELF-PRODUCING POPULATION WITH A MEMBRANE

Pseudocode for updating the membrane in the computation niche model

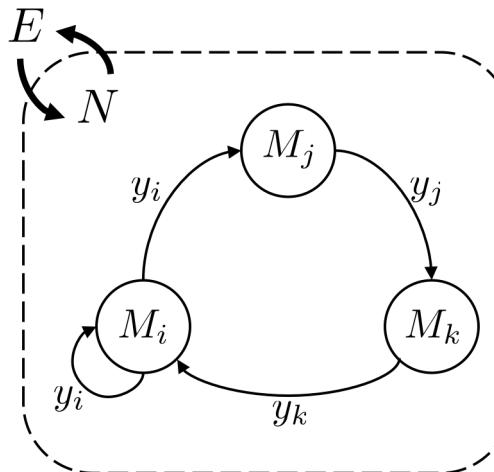
```
begin
    INPUTS:
         $M$  : the set of membrane network nodes
         $f$  : frequency distribution of current population
         $G$  : the interaction matrix of the internal population
         $X$  : the set of incoming edges to each target membrane automaton
         $\lambda$  : edge weightings over the membrane network
    OUTPUTS:
        updated  $f, \lambda$ 
    UPDATE PROCEDURE:
        for each  $i$  in  $M$ 
            comment: Determine input  $X_i$  to membrane automaton  $M_i$ 
            for  $x$  in  $X$ 
                 $R = x \bullet \lambda_x$ 
                comment: Filter input based on automaton's processing behaviour
                 $R = R \bullet \tau_i$ 
                comment: Determine if membrane automaton is activated
                 $r$  : randomly generated real number ( $0 \leq r \leq 1$ )
                if  $R > r$ 
                    comment: Membrane automaton has been activated
                     $\Psi_i = 1$ 
                fi
            end
            comment: Produce new automata in the internal population
            for each  $i$  in  $\Psi > 0$ 
                 $G_\Psi = \Psi \bullet G_i \bullet \Psi'$ 
                 $G_\Psi \rightarrow A$ 
                for all in  $G_\Psi$ 
                    comment: Create new population automaton of type  $i$ 
                     $f_i = f_i + 1$ 
                    comment: Replace existing population automaton of type  $d$ 
                     $f_d = f_d - 1$ 
                    comment: Update membrane to reflect changes in population structure
                     $M_\lambda = f$ 
                end
            end
        end
    end
```

### 3.4.3 Environment

The computation niche exists within an environment and the relationship between the two is modelled as an exchange of binary information. The information emitted by the environment is represented as a two-point Bernoulli probability distribution  $E = \{P(X = 0), P(X = 1)\}$  where  $P(X = 0) = p$  and  $P(X = 1) = 1 - p$ . For example,  $P(E) = (0.5, 0.5)$  represents an environment that is producing 0's and 1's with equal probability. By comparison,  $P(E) = (1, 0)$  is an environment that constantly produces a 0 symbol and  $P(E) = (0, 1)$  is an environment that constantly produces a 1 symbol. To consider the most general case of the effect of environmental information on the behaviour of the membrane the probability distribution  $P(E)$  was randomly generated on each iteration i.e.  $P(E) = (r_e, 1 - r_e)$  where  $r_e$  is a real number  $0 <= r_e <= 1$ . Every membrane automaton has an incoming edge which represents the information being received from the environment. Each automaton was receiving information from at least two sources - the environment and other membrane automata - and, as such, there was competition between these information sources that influenced whether the receiving automaton would activate or not. As such, the calculation for  $X'_i$  was extended to incorporate environmental information:

$$(3.10) \quad X'_i = (X_i + E) \bullet \tau_i$$

Where the environmental information ( $E$ ) was a two-point probability distribution that could be set to various generating modes e.g.  $E$  could be set to randomly emit '0' or '1' or  $E$  was set to emit a constant symbol (e.g. a '0' or a '1'). Sudden changes to the mode of generation of environmental information acted as a form of perturbation on the computation niche. Each node in the membrane receives the same information from the environment simultaneously and, from the perspective of a node, was simply another incoming edge ( $x_e$ ). Similarly, a weighting was given to environmental information which signified the level of influence of environmental information on the activation threshold of a membrane automaton. This parameter was given by  $\Phi_{env}$  and can be thought of as the size of the opening (aperture), or the permeability, of the membrane that determines the amount of influx of environmental information. As such as  $\Phi_{env} \rightarrow 1$  the aperture was completely open and the activation of membrane automata was completely determined by information flowing from the environment. Conversely, as  $\Phi_{env} \rightarrow 0$  the activation of automata was driven by the flow of information entirely from within the membrane itself.



$$E = (E_t + N) \cdot \frac{1}{Z}$$

$$N = \left( \sum_{y \in Y} y \right) \cdot \frac{1}{Z}$$

Figure 3.12: There were three types of information flow within the membrane and with its environment: (i) information generated by automata and received by other automata within the membrane, (ii) information generated from the environment and received by membrane automata, and (iii) information generated by all membrane automata that cumulatively is emitted into the environment.

To examine the effect of structural coupling between the computation niche and the environment two additional attributes were introduced: (a) the cumulative emissions from all active membrane automata at time  $t$  were emitted from the niche into the environment, and (b) the parameter  $\Phi_{out}$  which represented the magnitude of the effect of the niche emissions on the environmental. The niche emission  $N$  was the normalised output from all nodes at time  $t$  according to:

$$(3.11) \quad N = \left[ \sum_{y \in Y} y \right] \cdot \frac{1}{Z}$$

Where  $N$  was a two-point probability distribution of the niche emitting a '0' or a '1',  $y$  is the information emitted from a single active membrane automaton and  $Y_t$  is the set of all active membrane automata and  $Z$  is a normalising factor.

When  $\Phi_{out} > 0$  environmental information was modulated by  $N$ :

$$(3.12) \quad E_t = [(1 - \Phi_{out})E_B + \Phi_{out}N] \cdot \frac{1}{Z}$$

The term  $E_B$  is a two-point Bernoulli probability distribution that was introduced to represent a constant background noise being generated in the environment (the exact nature of  $E_B$  was set by whatever mode of generation of environmental information was being examined e.g. a randomly generated stream of binary digits or a constant value)

and this noise was being modulated by information flowing from the niche. As  $\Phi_{out} \rightarrow 0$  environmental information was dominated by this background information source and, conversely, as  $\Phi_{out} \rightarrow 1$  environmental information was dominated by the information being produced by the niche ( $N$ ). In practice, and as discussed in Chapter 8 a range of settings for  $Phi_{out}$  were examined.

### 3.4.4 Computation in the niche

The three main elements of the computation niche - the membrane, the internal population and the environment - and the relationships and exchange of information between them have been described. The computation niche model was so-called because it represented the core elements of computation: information transfer, information storage and information processing. Figure 3.13 illustrates how these three properties were manifested in the model.

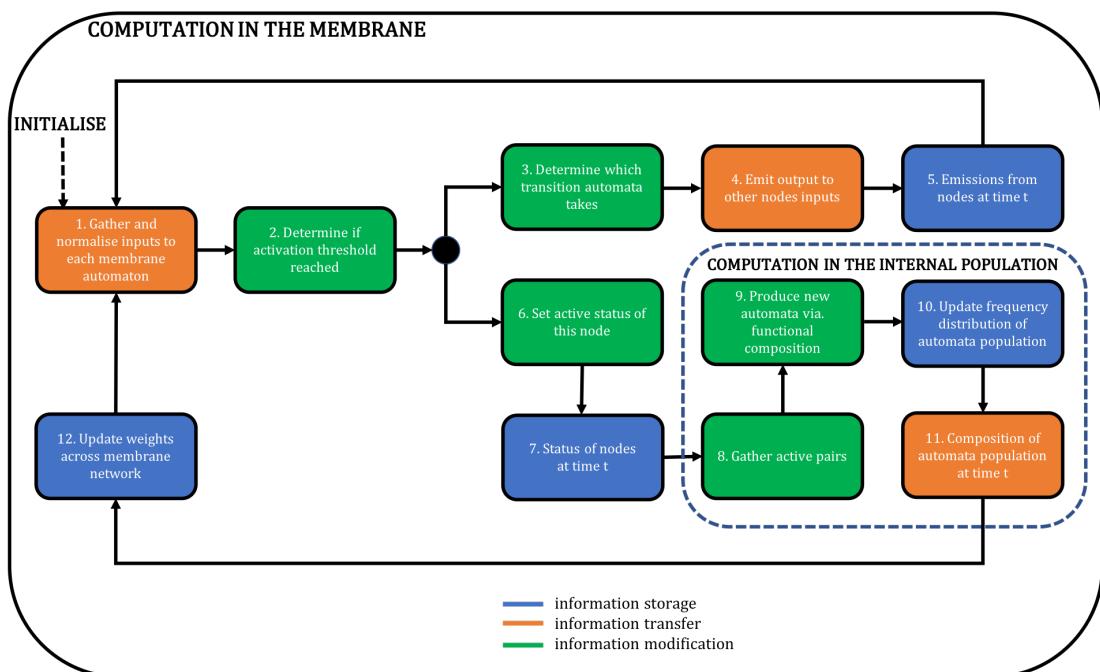


Figure 3.13: A breakdown of one computational cycle in the computation niche that illustrates the type of information processing occurring: information transfer (orange), information storage (blue) and information modification/evaluation (green). The directed arrows show the procedural sequence in which each process was executed.

## 3.5 Information Measures

This section describes the information measures and methods used to characterise and analyse the results of simulating the information niche and computation niche models. All of the methods described are derived from Claude Shannon's information theory [45] which is the field of study into measuring, storing and transmitting information.

### 3.5.1 Shannon Information and Shannon Entropy

One of the key measures in information theory is Shannon entropy which is given by:

Each event contains a certain amount of Shannon information, given by  $I(x) = -\log_2 p(x)$ , measured in binary digits (bits). Shannon information can be understood as the amount of information that is yielded on that event occurring. The less probable an event the more information it yields when it does occur. For example, the event of not winning the lottery jackpot yields very little information. By comparison, the event that you win the jackpot is a big surprise and conveys more information. As such, Shannon's Information is a measure of the degree of surprise - or the amount of uncertainty - we have about an event occurring.

The Shannon information can be calculated for each possible event occurring in a system. For example, on each time step in the information niche model one existing automaton is randomly selected and replaced with a new automaton. In a one-state population there are 15 automaton types. At the beginning of a simulation each automaton type is equally distributed and therefore there is a  $P(x) = 1/15$  chance of an automaton of type  $x$  to be selected to be replaced. Hence, if we did indeed select automaton type  $x$  then the Shannon Information that is yielded from this event occurring is  $I(x) = -\log_2 P(x) = -\log_2 1/15 = 3.9$  bits.

Shannon entropy is the average information of all possible events:

$$(3.13) \quad H(X) = - \sum p(x) \cdot \log_2 p(x)$$

, where  $p(x)$  is the probability of event  $x$  occurring from the set of all possible events  $X$ . Continuing with the example of the random selection and replacement of an automaton in a one-state population the Shannon entropy is 3.9 bits which is the same as the Shannon information of a single event. This is to be expected where each event is equiprobable. Indeed, a system state that is characterised by an equiprobable distribution of all events represents the maximum Shannon entropy of the system. When all events are equally probable we have the greatest uncertainty about which event will occur next. By comparison, and this is universally the case in all of the simulations of the information niche and

type	$T_1$	$T_2$	$T_3$	$T_4$	$T_5$	$T_6$	$T_7$	$T_8$	$T_9$	$T_{10}$	$T_{11}$	$T_{12}$	$T_{13}$	$T_{14}$	$T_{15}$
Frequency distribution of automaton types at $t = 0$															
$p(x)$	0.067	0.067	0.067	0.067	0.067	0.067	0.067	0.067	0.067	0.067	0.067	0.067	0.067	0.067	0.067
$I(x)$	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9
$p(x).I(x)$	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26
$\sum p(x).I(x) \quad H(X) = 3.9 \text{ bits}$															
Frequency distribution of automaton types at $t = 10^6$															
$p(x)$	0.069	0.069	0.125	0.069	0.125	0	0	0.069	0	0.125	0	0.125	0	0.225	
$I(x)$	3.85	3.85	3	3.85	3	0	0	3.85	0	3	0	3	0	0	2.15
$p(x).I(x)$	0.26	0.26	0.37	0.26	0.37	0	0	0.26	0	0.37	0	0.37	0	0	0.48
$\sum p(x).I(x) \quad H(X) = 3 \text{ bits}$															

computation niche model, as the production of new automata and the removal of existing automata proceeds then this uniformity is broken with some automaton types growing in number whilst others decay. Therefore, the probability distribution of all possible events in the system becomes non-uniform. The Shannon entropy of non-uniform probability distributions will always be less than the maximum Shannon entropy as our uncertainty about the next event to occur has been reduced i.e. given the higher concentration of automata of type  $x$  in the population there is an increased likelihood that one of those types will be randomly selected to be removed and replaced with a new automaton. Hence, as the information niche and computation niche simulations progress the initial uniform state of the population becomes less uniform. Our uncertainty about the system has been decreased as there is increasing structure within the system. Measuring the Shannon entropy of the normalised frequency distribution of each automaton type in the population provides a quantitative estimate of structure of the population.

For example, compare the normalised frequency distribution, Shannon information and Shannon entropy calculated for a one-state automata population in the information niche model once at  $t = 1$  where all automata types are equally distributed and again at  $t = 10^6$ :

Hence the Shannon entropy of the initial population and the final population was 3.9 bits and 3 bits respectively indicating a reduction in our uncertainty about the population as structure emerged.

The Shannon entropy was used to:

1. Quantify the complexity of the interaction network that was driving production of new automata (section 3.5.2)
2. Quantify the minimum information required to generate a niche (section 3.5.3)
3. Quantify the internal complexity of an automaton (section 3.5.4).

Each of these measures will now be described.

### 3.5.2 Interaction Network Complexity

The distribution of automaton types in a given population was structurally defined, and was responsible for the range of possible interactions. Changes in population structure, and the consequent diversity of interactions available, was quantified at each time step using the interaction network complexity ( $C_\mu(G)$ ), which measured the amount of information required to describe the probability that each interaction could occur in the population contingent on the current structure of the population [35],

$$(3.14) \quad C_\mu(G) = - \sum_{f_a, f_b, f_c} \frac{v_{ab}^c}{V} \log_2 \frac{v_{ab}^c}{V}$$

where

$$v_{ab}^c = \begin{cases} f_a f_b, & \text{if } T_c = T_b \circ T_a \text{ has occurred} \\ 0, & \text{otherwise.} \end{cases}$$

$V = \sum v^c$  is a normalising factor and  $f_a, f_b$  are the proportion of automaton types  $T_a$  and  $T_b$  in the population, respectively. Equation 3.15 determines the likelihood of an interaction occurring to produce  $T_c$  from the concentration of automata exhibiting the required functional composition. As the population evolves, some automaton types became extinct while others became more populous. As a consequence, automata produced by types that were increasing in concentration were more likely to be produced than those that were dependent on types that had become extinct. Such dynamics were reflected in the complexity of the interaction network, which reduced when some automaton types became extinct. Given that only one new automaton was produced at each time step, every interaction that occurred was competing with all other potential interactions. Subsequently, the probability of a specific interaction occurring was contrasted against the sum of the probability of all other possible interactions, as given by the normalisation term  $V$ . The probability of an interaction occurring to generate an automaton was the sum of the normalised frequencies of those automata responsible for its production. This normalised probability was calculated for each machine type in the population to yield a probability distribution. The information entropy of this probability distribution then yielded the interaction network complexity  $C_\mu(G)$ . As such, calculating  $C_\mu(G)$  provided a signature of the structure of the population at a given moment in time, and, when compared with the initial unstructured compositionally homogeneous population at the start of a simulation, provided a quantitative measure of the reduction in information entropy (or, conversely,

the amount of order that was being created within the population) as the network system evolved into a niche.

### 3.5.3 Information Content of a Population

Quantifying the minimum information required for niche generation was undertaken by defining the production threshold as a measure of the information required to describe the minimum number and type of automata that were required to be produced to create a niche. The production threshold for a niche was determined by calculating the Shannon entropy ( $H$ ) of the frequency distribution ( $X$ ) of each automaton type that would need to be produced within a given population,

$$(3.15) \quad H(X) = - \sum_{i=1}^T x_i \log_2 x_i,$$

where  $x_i$  is the proportion of interactions in the population that produce automaton type  $i$  and  $T$  is the set of all automaton types. The production threshold differed between niches depending on the number of constituent automata, with lower values for those niches in which not all automaton types were present. We used this measure to compare the information required to transition between niches, elucidate how the niches transitioned in response to perturbations in environmental conditions and explain why some niches were more robust than others. In general, the production threshold and interaction network complexity were complementary. The former quantified the information required to generate a niche, whereas the latter quantified the information required to describe a niche after it had evolved to a steady-state distribution, and any interactions that remained between the automata.

### 3.5.4 Structural Complexity

Given the specific properties of  $\epsilon$ -machines [113] - on which the automata were based - it was possible to quantify an automaton's structural complexity. The probability distribution over the states and the frequency with which each state was visited was calculated as:

$$(3.16) \quad C_\mu(T) \equiv - \sum_{v \in S} \rho_S^{(v)} \log_2 \rho_S^{(v)}$$

, where  $v \in S$  and  $\rho_S$  was the normalised left eigenvector associated with eigenvalue 1 of the transition matrix  $T \equiv \sum_{s \in A} T^{(s)}$ . This stated that the distribution of probabilities over

the internal states of an automaton determined the amount of information the automaton stored and, as such, its structural complexity. Structural complexity was different from Shannon entropy. The latter was a measure of randomness whilst the former was a measure of structure within a system.

The structural complexity was calculated for each new novel automata generated in the open-ended population simulations (see Chapter 9).

### 3.5.5 Information Processing Capacity of Automata

Each automaton had an information processing capacity ( $\varrho$ ) which indicated the domain and range of information that it could process (or, alternatively, the alphabet that it read and transmitted) and, therefore, the range of interactions it could have with other automata. The higher the interaction potential of an automaton the more possibilities it had to interact with a wider range of automata either as a  $T_a$  or a  $T_b$  automaton. This was measured directly from the automaton's structure. For example, the one-state automaton  $T_1$  accepted a '0' and emitted a '0' from the alphabet  $A = \{0, 1\}$  and therefore it had one input channel and one output channel for a total of two channels. Formally this was denoted as the logarithm  $\varrho(T_1) = \log_2(2) = 1\text{bit}$ . By comparison, the one-state automaton  $T_3$  accepted a '0' and emitted a '0' or a '1' for a total of three channels hence  $\varrho(T_3) = \log_2(3) = 1.6\text{bits}$ . The automata in the one-state population were partitioned in this manner to aid in the analysis of their competitive properties (see section 8.3.4).

## 3.6 Network Measures

A network was a collection of nodes joined by edges that signified the relationship that existed (an edge) between two nodes [46]. Two types of networks were implemented for executing and analysing the information niche and computation niche model: the interaction network ( $G$ ) - see section 3.3 which described which automata were produced from the interactions of other automata, and the membrane network ( $M$ ) - see section 3.4.2 which described the order in which automata interacted with each other. This section describes the methods used to capture the properties of these networks in one-state, two-state and multi-state automata populations.

### 3.6.1 Interaction Network

The interaction network ( $G$ ) was a directed graph where nodes represented automaton types and the directed edges indicated that the node at the beginning of the edge was  $T_a$  and

the node at the end of the edge was  $T_c$  in the functional composition operation  $T_b \circ T_a = T_c$  and the labelled edge indicated the automaton type  $T_b$  that was transforming the output of the  $T_a$  automaton to produce the  $T_c$  automaton. This network was mathematically represented as a  $T \times T$  matrix (where  $T$  was the set of automata in the population) where the rows ( $i$ ) indicated the  $T_a$  automaton types and the columns ( $j$ ) indicated the  $T_b$  automaton types. The value at the intersection of a row and column ( $G_{i,j}$ ) was the index of the automaton type that was produced ( $T_c$ ) by the interaction of  $T_a$  and  $T_b$ . For example, the automaton type  $T_2$  interacting with  $T_4$  creates the automaton type  $T_1$  and therefore the matrix entry was  $G_{2,4} = 1$  and this was represented graphically as shown in Figure 3.14.

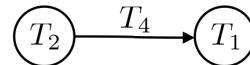


Figure 3.14: An example of the graphical representation of the interaction network ( $G$ ). The two nodes represent the  $T_a$  and  $T_c$  automata and the edge label represents the  $T_b$  automaton in the functional composition equation  $T_b \circ T_a = T_c$ .

### 3.6.2 Membrane Network

The membrane network ( $M$ ) was a directed graph where nodes represented automaton types and the directed edges indicated that the node at the beginning of the edge was  $T_a$  and the node at the end of the edge was  $T_b$  in the functional composition operation  $T_b \circ T_a = T_c$ . The network was mathematically represented as a  $T \times T$  matrix where the rows ( $i$ ) indicated the  $T_a$  automaton types and the columns ( $j$ ) indicated the  $T_b$  automaton types in the functional composition operation  $T_b \circ T_a = T_c$ . The intersection of a row and a column ( $M_{i,j}$ ) indicated the binary symbol that was transmitted from  $T_a$  to  $T_b$  if the range of the  $T_a$  automaton type was in the domain of the  $T_b$  automaton type and therefore the automaton type  $T_b$  could receive information from  $T_a$ . If this was not the case then a null value indicated that these automaton types do not communicate with each other in that particular ordering. The functional composition operation is non-commutative and therefore the ordering of the automata types was important in generating the matrix accurately. For example,  $T_2$  as  $T_a$  and  $T_1$  as  $T_b$  could not communicate and therefore  $M_{2,1} = 0$  but they could when  $T_1$  was  $T_a$  and  $T_2$  was  $T_b$  and therefore  $M_{1,2} = 1$ . Figure 3.15 illustrates the graphical representation of this flow of information.

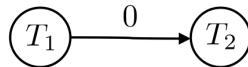


Figure 3.15: An example of the graphical representation of the membrane network ( $G$ ). The two nodes represent the  $T_a$  and  $T_b$  automata in the functional composition operation  $T_b \circ T_a = T_c$  and the edge label represents the binary symbol that was transmitted from  $T_a$  to  $T_b$ .

### 3.6.3 Topology and Degree Distribution

The general properties of the interaction network ( $G$ ) that represented the productions within the automata population were characterised as (i) the number of nodes and edges within the network, and (ii) the degree distribution [46] of those edges.

The number of nodes in the network at time  $t$  was calculated from examination of the interaction network matrix  $G$ . Where  $G_{i,-} \neq \emptyset$  or  $G_{-,i} \neq \emptyset$  and  $f_i > 0$  the automaton was deemed to exist in the population, available to interact with other automata and therefore was an active node in the interaction network.

The degree of a node ( $k$ ) in the network was the number of edges it had to other nodes - both incoming and outgoing edges - and the degree distribution ( $P(k)$ ) was the probability distribution of those degrees over the network i.e. the fraction of nodes in the network with a degree of  $k$ . Subsequently, with  $v$  the total number of nodes in the network,  $v_k$  the number of nodes with a degree  $k$  then the probability of a node with a degree of  $k$  occurring in the network was given by  $P(k) = v_k/v$ . The degree distribution revealed the structure of the network e.g. networks with a long tail degree distribution indicated that there were a very few, highly connected nodes whilst a network with a very narrow degree distribution indicated a highly connected network.

The topology and the degree distribution of the interaction network was examined in one-state (see Chapter 4, two-state (see Chapter 5, multi-state (see Chapter 9) and joint one-/two-state populations (see section 7).

### 3.6.4 Identifying strongly connected networks

Even in a relatively simple population of interacting entities the number of possible networks that describe all possible sequences of interactions could be significant. Identifying and examining all such sub-networks within a given population was used to identify specific networks that were responsible for self-organisation of the population into a niche. One of the drivers of self-organising behaviour was nonlinearity caused by positive feedback loops in the system [114], and this was manifested in an interaction network as a strongly connected cyclic topology [115],[116]. An algorithm was developed to identify and categorise any sub-network structures in the interaction network ( $G$ ) that had the motif of

a strongly connected network, i.e. whereby a subset of automata mutually produced each other:

Pseudocode for identifying strongly connected networks

```
begin
    W : The set of all possible combinations of sub-networks
    for each w in W
        create adjacency matrix A for w
        where  $A_i$  are outgoing edges and  $A_j$  are incoming edges
        if  $\text{SUM}(A_i) \geq 2$  AND  $\text{SUM}(A_j) \geq 2$  for EACH node in w
            then add w to S
    end
```

This was an exhaustive algorithm that examined all possible combinations ( $W$ ) of automaton interactions partitioned into many sub-networks ( $w$ ) ranging in size from two to 15 automaton types. An adjacency matrix ( $A$ ) was generated for each sub-network to describe the associated topology as a directed graph [46] with nodes and directed edges indicative of an individual automaton type and which automata interact to produce other automaton types, respectively. The adjacency matrix of each sub-network was tested for the characteristic of mutual production between members (i.e. a cycle), whereby each automaton (node) in the sub-network must have: (i) a minimum in-degree of two edges, implying that it was produced by at least one interaction of automata in the sub-network apart from with itself (self-replication), and (ii) a minimum out-degree of two edges, implying that the automaton produced one other automaton apart from itself within the same sub-network. A sub-network was considered to be a candidate for a strongly connected network only if all constituent automata fulfilled these criteria. The set of candidate strongly connected networks ( $S$ ) was then examined for dynamic stability.

### 3.6.5 Determining the dynamic stability of an interaction network

To identify dynamically stable networks equation 3.2 was numerically solved in MATLAB for each strongly connected network ( $S$ ) identified in the interaction network ( $G$ ). All sub-networks in  $S$  were examined for dynamic stability and the automaton types in the numerical simulation were restricted to those present in the sub-network under consideration. Networks whose production dynamics resulted in extinction of any of the constituent members, or which created new automata that were not original members of the network, were deemed unstable.

Pseudocode for testing the dynamic stability of an interaction network

```

begin
     $T$  : the set of automata in the population
     $S$  : the strongly connected interaction matrix that produces automaton  $i$ 
     $f$  : the normalised frequency vector of all automata in the population
     $Z$  : number of iterations of the simulation
    comment: Run the numerical simulation
    while  $z < Z$ 
        for each  $T_i$  in  $S$ 
            comment: Calculate changes in frequency of each automaton
             $f_i = f * S_i f^T$ 
            if  $f_i = 0$ 
                comment: Loss of this automaton - network deemed unstable
            end

```

### 3.6.6 Identifying and counting the unique states of the membrane network

Analysis of the activation history of the membrane's automata showed the set of unique states that the membrane occupied. A state here is the unique configuration of membrane automata activation status (i.e. on or off) recorded in the 15-element vector  $\Psi$ . An algorithm was developed (see Chapter 3) to examine the time-series data of membrane automata activation status  $\bar{\Psi}$  which had been recorded on each iteration of the simulation. The algorithm identified each unique state that the membrane entered and how often it entered that state during the simulation.

Pseudocode for identifying the unique states of the membrane network

```

begin
     $\overleftarrow{\Psi}$  : the history (of length  $Z$ ) of the activation status of each membrane automaton
     $\Psi_z$  : the activation status of each membrane automaton at a given point ( $z$ ) in history
     $\Sigma$  : the unique states of the membrane network that have been identified
     $s$  : a specific state of the membrane network
     $\Omega$  : the counted observations of a membrane network state in  $\overleftarrow{\Psi}$ 
    comment: Work through the history of the network membrane states
    for each  $\Psi_z$  in  $\overleftarrow{\Psi}$ 
        find  $\Psi_z$  in  $\Sigma$ 
        if found
            comment: A previously discovered network state observed again
             $\Omega_s + 1$ 
        else
            comment: A new network state discovered
             $i = |\Sigma| + 1$ 
             $\Sigma_i = \Psi_z$ 
             $\Omega_s = 1$ 
        end

```

Where:

$\Sigma$  is a  $|S| \times |\Psi|$  matrix where each row is a unique state of the membrane network ( $s$ ) and each column represents the activation status of each membrane automaton ( $M$ ) for that membrane state for each  $\Psi_i$  in  $\overleftarrow{\Psi}$ .

$\Omega$  is a  $1 \times |\Sigma|$  vector where each  $\Omega_i$  represents the counted observations of a membrane network state in  $\overleftarrow{\Psi}$ .

The number of unique states that the membrane network occupied during the simulation is given by  $|\Sigma|$  and the number of times that the membrane network occupied that state is given by  $\Omega$ . The Shannon entropy of the rate of occurrence of each network state  $H(\Omega_{norm})$  can be calculated from normalising  $\Omega$ .

### 3.7 Summary

This chapter has introduced the concepts of the information niche and the computation niche as complementary models of self-organising populations that examine the two core

processes of autopoiesis and cognition under a range of various and varying environmental conditions. The methods for identifying and measuring the emergent properties of these systems has also been discussed. Each Results chapter begins with an explanation of how the simulation of the information niche or computation niche model was set-up to generate the results that are discussed.



## RESULTS I - ONE-STATE INFORMATION NICHES

### 4.1 Reproduction of published paper: Emergence and Dynamics of Self-Producing Information Niches as a Step Towards Pre-Evolutionary Organization

Chapter 4 is a reproduction of the published paper, "Emergence and Dynamics of Self-Producing Information Niches as a Step Towards Pre-Evolutionary Organization" [47].

In summary, this paper describes the key properties of proto-autopoietic organisations that emerged from simulating a one-state automata population evolving under the influence of fixed and intermittent environmental conditions. The main contribution that this paper makes to the field of autopoiesis are twofold: (i) the proto-autopoietic organisations that emerge and that are analysed and quantified are formed from very simple conditions. As such, they represent a minimal beginning for an autopoietic system. The paper introduces the notion of an information niche as a particular instance of a proto-autopoietic system as a dynamically stable strongly connected network of mutually producing automata that form distinct organisational steady states under various environmental conditions. Critically it is noted that information can be lost or gained during a perturbation and, in some cases, this leaves the system unable to transform itself back to a prior configuration state. The environment can play the role of adding the necessary information back into the population in the form of a perturbation which proves sufficient for the population to transform to prior states. The paper is based on the information

niche model and made use of most of the information and network measures described in Chapter 3.

# INTERFACE

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## Research



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### Author for correspondence:

Stephen Mann

e-mail: [s.mann@bristol.ac.uk](mailto:s.mann@bristol.ac.uk)

# Emergence and dynamics of self-producing information niches as a step towards pre-evolutionary organization

Richard J. Carter<sup>1,2</sup>, Karoline Wiesner<sup>1,3</sup> and Stephen Mann<sup>2</sup>

<sup>1</sup>Bristol Centre for Complexity Sciences, <sup>2</sup>Centre for Protoproteobacterial Research, School of Chemistry, and <sup>3</sup>School of Mathematics, University of Bristol, Bristol BS8 1TS, UK

SM, 0000-0003-3012-8964

As a step towards understanding pre-evolutionary organization in non-genetic systems, we develop a model to investigate the emergence and dynamics of proto-autopoietic networks in an interacting population of simple information processing entities (automata). Our simulations indicate that dynamically stable strongly connected networks of mutually producing communication channels emerge under specific environmental conditions. We refer to these distinct organizational steady states as *information niches*. In each case, we measure the information content by the Shannon entropy, and determine the fitness landscape, robustness and transition pathways for information niches subjected to intermittent environmental perturbations under non-evolutionary conditions. By determining the information required to generate each niche, we show that niche transitions are only allowed if accompanied by an equal or increased level of information production that arises internally or via environmental perturbations that serve as an exogenous source of population diversification. Overall, our simulations show how proto-autopoietic networks of basic information processors form and compete, and under what conditions they persist over time or go extinct. These findings may be relevant to understanding how inanimate systems such as chemically communicating protocells can initiate the transition to living matter prior to the onset of contemporary evolutionary and genetic mechanisms.

## 1. Introduction

Theoretical models that attempt to distinguish living from non-living systems, such as Gánti's chemoton [1,2] and Eigen & Schuster's hypercycles [3], assume the presence of replicative molecular machinery, and are constrained in their outlook as they exclude the possibility of protolife behaviour under non-replicative, non-evolutionary conditions [4]. By comparison, the theory of autopoiesis [5] postulates that a living system is distinguished by an ability to continually produce and maintain itself. As these systems properties are not necessarily contingent on the presence of a functioning genetic apparatus, the study of autopoiesis may be critical not only for understanding the transition from (geo)chemistry to protobiology on a pre-Darwinian/pre-genetic early Earth [6] but also for the laboratory-based bottom-up design and construction of synthetic cellularity [7]. Previous computational models of autopoiesis have demonstrated properties such as spatial boundary formation and self-repair in artificial chemistry systems [8–10], but a major limitation of these simulations is their reliance on the pre-existence of an ideal chemistry. While these abstract models have helped to demonstrate the concept of autopoiesis, they do not address how such chemistries come into existence, persist or compete for space, materials and energy under complex reaction conditions. In contrast, other models of autopoiesis such as algorithmic chemistry [11], algebraic chemistry [12] and matrix chemistry [13] do not specify

an ideal chemistry but model the production of interacting entities to simulate the spontaneous formation of higher levels of organization.

In recent years, an alternative prebiotic evolutionary model, termed the finitary process soup [14], has been advanced. It is a model based on binary communication channels and their interaction. The channels take a single bit as input and produce a single bit as output. Since there is no stochasticity, these are deterministic input–output automata [15]. Reproduction, in this model, is represented as an interaction between two automata, with the potential of producing a new automaton. Crutchfield and Gornerup [14,16] present a detailed analysis of the structure and dynamics of this ‘soup’ of interacting automata. Interestingly, in this model, the emergence of higher level organization occurs spontaneously. Out of an initial set of 15 automata, subsets (networks) of mutually producing automata emerge. These automata networks (also called meta-machines) can be considered as self-producing, autonomous information processing entities. As such, the finitary process soup model represents a basic mechanism for the emergence of autopoiesis in an interacting population. While these findings contribute to the exploration of viable pathways to autopoiesis, they do not specifically pursue the question of how these networks form and compete, and why some networks persist over time while others go extinct.

In this paper, we extend the finitary process soup model to investigate the emergence of steady-state production networks under fixed or intermittent environmental conditions generated by changes in the degree of mixing within and influx rate into an interacting closed population of single-state automata. We find that different environmental conditions lead to different stable combinations, or networks, of mutually producing automata. We call these networks information niches, and we study their specific structural and dynamical properties. The model shows a variety of behaviour, from a small subset of mutually producing automata to a hierarchical network of automata maintaining a stable population. This is quite surprising, given that the model includes only the simplest types of input–output automata.

Furthermore, we investigated the population of automata under sudden environmental perturbations. We observed the emergence of a fitness landscape in which information niches are stable points, which the system can switch between upon perturbation. These results show how proto-autopoietic networks of basic information processors form and compete, and under what conditions they persist over time or go extinct. Thus, our model represents a mechanism for the formation of fitness landscapes under non-evolutionary conditions. These findings may be relevant to understanding how inanimate systems such as chemically communicating protocells can initiate the transition to living matter prior to the onset of contemporary evolutionary and genetic mechanisms.

## 2. Computational model and methods

### 2.1. Dynamics of information niches under fixed or intermittent environmental conditions

We employed a previously described computational model [14] to investigate the emergence of steady-state interacting networks and their mutual dependency within a population of interacting/replicating information processing automata.

The initial population consisted of 15 types ( $T_1$  to  $T_{15}$ ) of single-state automata that act as selective communication channels capable of receiving information from a binary alphabet ( $A = \{0,1\}$ ), processing the inputs using between one and four switching/non-switching binary transitions, and emitting the corresponding output in the form of a functional composition in which the sequential processing of the output from one automaton acts as the input for another (figure 1). In the original studies [14], these input–output automata were treated as a special category of finite-state transducers referred to as  $\epsilon$ -machines.

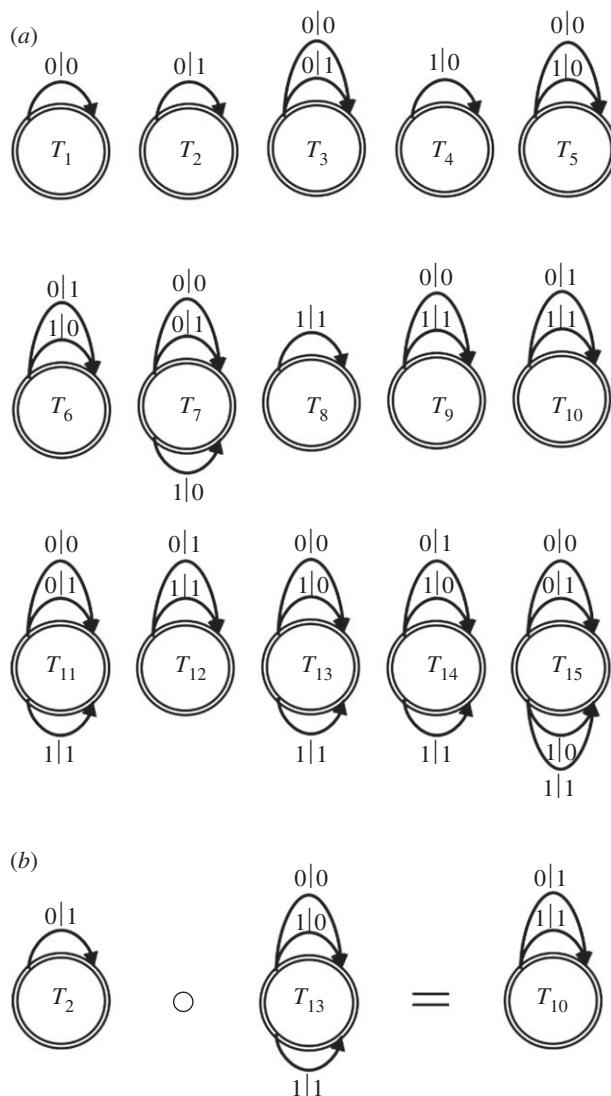
Significantly, the replicating population was compositionally closed because the binary interactions between various single-state automata were unable to generate information communication channels outside the original set of 15 members.

An environmental context was imposed on the interacting automata by initially distributing equal numbers of the 15 types randomly across a square lattice  $\Gamma$  of  $n \times n$  sites with each site occupied by an individual single-state automaton to give a population size of  $N = n^2 = 90\,000$ , which was then replicated iteratively using functional composition (figure 1b). The production of automata proceeded by randomly selecting a lattice site  $\Gamma_{ij}$  whose occupying automaton ( $T_d$ ) may or may not be replaced by a new type  $T_c$  depending on the competition between the environmental influx and internal production dynamics (figure 2). The probabilities that  $T_c$  is a randomly generated automaton entering from the external environment or alternatively derived from the functional composition of two neighbouring automata were given by  $\Phi$  and  $1 - \Phi$ , respectively. Production of  $T_c$  by either option replaced  $T_d$ , which was subsequently removed from the population to maintain a constant value for  $N$ . This constraint generated a survival selective pressure between different types of automata, which must be continually produced to prevent depletion from the population.

The production process was iterated for up to  $1 \times 10^7$  time steps to simulate the emergence of a number of distinct information niches. Changes in the structure and composition of the population were observed with increasing numbers of iterations, and this was captured at each time step by updating the frequency distribution ( $f$ ) of the information processing types present in the emerging community. The following differential equation described the changes in  $f$  on each time step [17]:

$$\frac{df_c}{dt} = (1 - f_c) \sum_{T_a \circ T_b = T_c} f_a f_b - f_c \sum_{\substack{T_a \circ T_b \neq T_c \\ T_a \circ T_b \neq T_0}} f_a f_b, \quad (2.1)$$

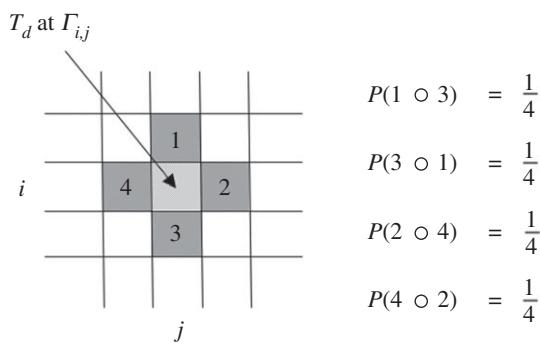
where  $T_a, T_b$  are the interacting machines,  $T_c$  is the new automaton produced from that interaction and  $f_a, f_b, f_c$  are their normalized frequencies of occurrence in the population.  $T_0$  is the transitionless automaton that represented an unsuccessful interaction and was prohibited in the population. Equation (2.1) determines two factors: (i) the probability of adding the automaton  $T_c$  is equal to the probability of selecting two neighbours  $T_a$  and  $T_b$  that produce  $T_c$  multiplied by the probability that the automaton that is being replaced ( $T_d$ ) is not the same as  $T_c$  and (ii) the probability of neither  $T_c$  nor  $T_0$  being produced. The invariant frequency distribution of machine types can therefore be determined by solving  $df/dt = 0$ . Here, discrete time is a good approximation for continuous time as only one lattice location is updated on each time step and so for large  $N$  (our minimum value for  $N$  is 90 000) this leads to a small change in the overall frequency distribution of all



**Figure 1.** (a) Schematic representation showing a compositionally closed population of 15 types of single-state automata ( $T$ ). The population includes four members that are capable of only one transition ( $T_1, T_2, T_4, T_8$ ), along with six ( $T_3, T_5, T_6, T_9, T_{10}, T_{12}$ ), four ( $T_7, T_{11}, T_{13}, T_{14}$ ) and one ( $T_{15}$ ) that exhibit two, three and four transitions, respectively. The binary numbers on the curved arrows on the top or bottom of the circles indicate the various possible transitions; for example,  $T_3$  operates only with an input signal of 0, transducing this to either 0 (non-switched output) or 1 (switched output) with 50% probability in each case. (b) Scheme showing an example of the functional composition of two machines (described by the non-commutative equation,  $T_2 \circ T_{13}$ , where  $\circ$  is the functional composition operator) to generate  $T_{10}$ . The three outputs from  $T_{13}$  are received with equal probability and transformed by  $T_2$  to produce  $T_{10}$ , which inherits the input domain from  $T_{13}$  and the output range of  $T_2$ . The number of possible unique binary interactions (207) is described by an interaction network ( $G$ ) in the form of a  $|T| \times |T|$  matrix; all functional compositions are members of the set of 15 types producing a compositionally closed population of interacting machines. Unsuccessful interactions between machines create the *transitionless* machine  $T_0$ , which is prohibited in our model of an interacting community.

automata. This equation assumes that all interactions are possible on each time step, which is consistent with a well-mixed environment with no influx of automata.

Spatial mixing occurred within the population during replication by randomly selecting a lattice site and exchanging the residing automaton with another type positioned on a



**Figure 2.** Graphic illustrating the computational model for generating internal production dynamics in a square lattice of  $nxn$  sites comprising single-state automata of type  $T$  [17]. The lattice has periodic boundary conditions, i.e. a regular toroid topology, and, as such, an automaton in the top two rows of the lattice can interact with automata directly opposite it in the bottom two rows of the lattice and vice versa. The same condition applies to an automaton on the left edge and right edge of the lattice. Spatial mixing also occurs in the same manner. An automaton ( $T_d$ ) on lattice site  $\Gamma_{ij}$  is chosen at random for replacement by functional composition involving types ( $T_a, T_b$ ) selected from the sites (1,2,3,4) adjacent to  $T_d$ . Only one pair of neighbours from the two possible pairwise combinations (1,3 or 2,4) is selected to interact according to the non-commutative equation  $T_b \circ T_a$  where the order of the interacting pair is selected randomly according to an equal probability of 1/4. If the functional composition generates a new automaton ( $T_c$ ), this replaces  $T_d$  at lattice position  $\Gamma_{ij}$ , which is subsequently removed from the population. If no interaction occurs, then a transitionless machine  $T_0$  is generated such that  $T_d$  is not replaced and remains on the lattice site. The new population is then subjected to different levels of spatial mixing.

different lattice site along one of the cardinal directions at a distance  $d$  selected from a one-dimensional Gaussian distribution with variance  $v$  and mean = 0 and rounding  $d$  to the nearest corresponding lattice site. This was repeated for  $c$  numbers of different sites per production time step. The combination of  $c$  and  $v$  approximated diffusion within the replicating population such that when  $c \rightarrow N$  and  $v \rightarrow n$  the population was well mixed, while for  $c \rightarrow 0$  and  $v \rightarrow 0$  the population of automaton had very low mobility [17]. To simulate the coupling of the replicating population to changes in an external environment, randomly generated automaton types replace randomly selected automata in the population at time  $t$  with a probability given by  $\Phi$ , where  $0 \leq \Phi \leq 1$ . With  $\Phi = 0$ , no random replacement occurred and population dynamics were driven entirely by the composition of existing automata. We refer to the process of random replacement as influx to convey the notion of the movement of externally generated automata into the population. In contrast, with  $\Phi = 1$ , the population dynamics were determined entirely by randomly generated automata entering the lattice from the external environment [14]. Twenty-five combinations of the spatial mixing ( $c, v$ ) and influx dynamics ( $\Phi$ ) parameters were used to simulate a range of fixed environmental conditions to assess the impact on the production dynamics of the automaton population and the emergence of the information niches.

We investigated the effect of intermittent changes in the environmental parameters on the robustness and transition pathways of the information niches to map the fitness landscape. For this, the following modifications in environmental conditions were imposed once a steady-state niche was attained: (i) inversion of the spatial mixing parameter such

that conditions contrary to those in which the niche was produced are imposed, e.g. if a niche was formed in a well-mixed environment then the environmental conditions were reset to simulate a highly restricted movement of the automata ( $c, v = 0$ ); (ii) inversion of the influx setting of new machines into the lattice, e.g. if a niche was produced in the absence of any influx of automata ( $\Phi = 0$ ) then this parameter was reset to  $0 < \Phi \leq 1$ ; (iii) simultaneous perturbations associated with modifications (i) and (ii); (iv) introduction of a type-restricted influx ( $\Phi'$ ) of automata that were randomly selected from the specified subset of automaton types ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ); and (v) simultaneous perturbations associated with modifications (i) and (iv). Perturbations on the initially produced steady-state niche were undertaken for a minimum of  $1 \times 10^6$  iterations, which was usually sufficient for the population to reconfigure into a new steady-state conformation. The perturbations were then removed by resetting the environmental parameters back to their original values, and changes to the population structure recorded. Consequently, the original (*primary*) niche was re-created or a new (*secondary*) niche was established by perturbing the primary niche.

## 2.2 Structure and dynamics of information niches

### 2.2.1. Quantifying niche structure, diversity and the minimum information required for niche generation

The distribution of automaton types in a given population was structurally defined, and was responsible for the range of possible interactions. Changes in population structure, and the consequent diversity of interactions available, was quantified at each time step using the interaction network complexity ( $C_\mu(G)$ ), which measured the amount of information required to describe the probability that each interaction could occur in the population contingent on the current structure of the population [14],

$$C_\mu(G) = - \sum_{f_a f_b f_c > 0} \frac{v_{ab}^c}{V} \log_2 \frac{v_{ab}^c}{V}, \quad (2.2)$$

where

$$v_{ab}^c = \begin{cases} f_a f_b, & \text{if } T_c = T_b \circ T_a \text{ has occurred} \\ 0, & \text{otherwise,} \end{cases}$$

$V = \Sigma v^c$  is a normalizing factor and  $f_a, f_b$  are the proportion of automaton types  $a$  and  $b$  in the population, respectively. Equation (2.2) determines the likelihood of an interaction occurring to produce  $T_c$  from the concentration of automata exhibiting the required functional composition. As the population evolves, some automaton types became extinct while others became more populous. As a consequence, automata produced by types that were increasing in concentration were more likely to be produced than those that were dependent on types that had become extinct. Such dynamics were reflected in the complexity of the interaction network, which reduced when some automaton types became extinct. Given that only one new automaton was produced at each time step, every interaction that occurred was competing with all other potential interactions. Subsequently, the probability of a specific interaction occurring was contrasted against the sum of the probability of all other possible interactions, as given by the normalization term  $V$ . The probability of an interaction occurring to generate an automaton was the sum of the normalized frequencies of those automata responsible for its production. This

normalized probability was calculated for each machine type in the population to yield a probability distribution. The information entropy of this probability distribution then yielded the interaction network complexity  $C_\mu(G)$ . As such, calculating  $C_\mu(G)$  provided a signature of the structure of the population at a given moment in time, and, when compared with the initial unstructured compositionally homogeneous population at the start of a simulation, provided a quantitative measure of the reduction in information entropy (or, conversely, the amount of order that was being created within the population) as the network system evolved into a niche.

Quantifying the minimum information required for niche generation was undertaken by defining the production threshold as a measure of the information required to describe the minimum number and type of automata that were required to be produced to create a niche. The production threshold for a niche was determined by calculating the Shannon entropy ( $H$ ) of the frequency distribution ( $X$ ) of each automaton type that would need to be produced within a given population,

$$H(X) = - \sum_{i=1}^{|T|} x_i \log_2 x_i, \quad (2.3)$$

where  $x_i$  is the proportion of interactions in the population that produce automaton type  $i$  and  $T$  is the set of all automaton types. The production threshold differed between niches depending on the number of constituent automata, with lower values for those niches in which not all automaton types were present. We used this measure to compare the information required to transition between niches, elucidate how the niches transitioned in response to perturbations in environmental conditions and explain why some niches were more robust than others. In general, the production threshold and interaction network complexity were complementary. The former quantified the information required to generate a niche, whereas the latter quantified the information required to describe a niche after it had evolved to a steady-state distribution, and any interactions that remained between the automata.

### 2.2.2. Identifying strongly connected production networks

Even in a relatively simple population of interacting entities the number of possible networks that describe all possible sequences of interactions can be significant. Identifying and examining all such sub-networks within a given population was used to identify specific networks responsible for self-organization of the population into a niche. One of the drivers of self-organizing behaviour was nonlinearity caused by positive feedback loops in the system [18], and this was manifested in an interaction network as a strongly connected cyclic topology [19,20]. We developed an algorithm to identify and categorize any sub-network structures in the interaction network ( $G$ ) that had the motif of a *strongly connected network*, i.e. whereby a subset of automata mutually produce each other:

begin

$W$  : The set of all possible combinations of sub-networks  
    for each  $w$  in  $W$

        create adjacency matrix  $A$  for  $w$  where  $A_i$  are outgoing edges  
        and  $A_j$  are incoming edges  
        if  $\text{SUM}(A_i) \geq 2$  AND  $\text{SUM}(A_j) \geq 2$  for EACH node in  $w$   
            then add  $w$  to  $S$

end

This is an exhaustive algorithm that examines all possible combinations ( $W$ ) of automaton interactions partitioned into many sub-networks ( $w$ ) ranging in size from two to 15 automaton types. An adjacency matrix ( $A$ ) was generated for each sub-network to describe the associated topology as a directed graph [21] with nodes and directed edges indicative of an individual automaton type and which automata interact to produce other automaton types, respectively. The adjacency matrix of each sub-network was tested for the characteristic of mutual production between members (i.e. a cycle), whereby each automaton (node) in the sub-network must have: (i) a minimum in-degree of two edges, implying that it is produced by at least one interaction of automata in the sub-network apart from with itself (self-replication), and (ii) a minimum out-degree of two edges, implying that the automaton produces one other automaton apart from itself within the sub-network. A sub-network was considered to be a candidate for a strongly connected network only if all constituent automata fulfil these criteria. The set of candidate strongly connected networks ( $S$ ) was then examined for dynamic stability.

### 2.2.3. Determining dynamically stable networks

To identify dynamically stable networks we numerically solved  $df/dt = 0$  of equation (2.1) for each strongly connected network ( $S$ ) identified in the interaction network ( $G$ ). All sub-networks in  $S$  were examined for dynamic stability and the automaton types in the numerical simulation were restricted to those present in the sub-network under consideration. Networks whose production dynamics resulted in extinction of any of the constituent members, or which created new information processors that were not original members of the network, were deemed unstable.

## 3. Results

### 3.1. Emergence and properties of primary information niches under fixed environmental conditions

Twenty-five environments were simulated by setting unique combinations of the spatial mixing ( $c, v$ ) and influx dynamics ( $\Phi$ ) parameters in the range of  $0 \leq c \leq N$ ,  $0 \leq v \leq n$  and  $0 \leq \Phi \leq 1$  for an evolving population of 90 000 interacting automata distributed equally across 15 different types. The emergence of steady-state network configurations (information niches) under fixed environmental conditions typically required between  $1 \times 10^6$  and  $1 \times 10^7$  iterations. After every iteration, the changes in frequency ( $f$ ) of each automaton type were determined until steady-state conditions were attained. Significantly, six distinct primary information niches ( $A-F$ ) comprising strongly connected components of self-producing communication channel networks were obtained (figure 3).

#### 3.1.1. Influence of spatial mixing and non-diffusivity

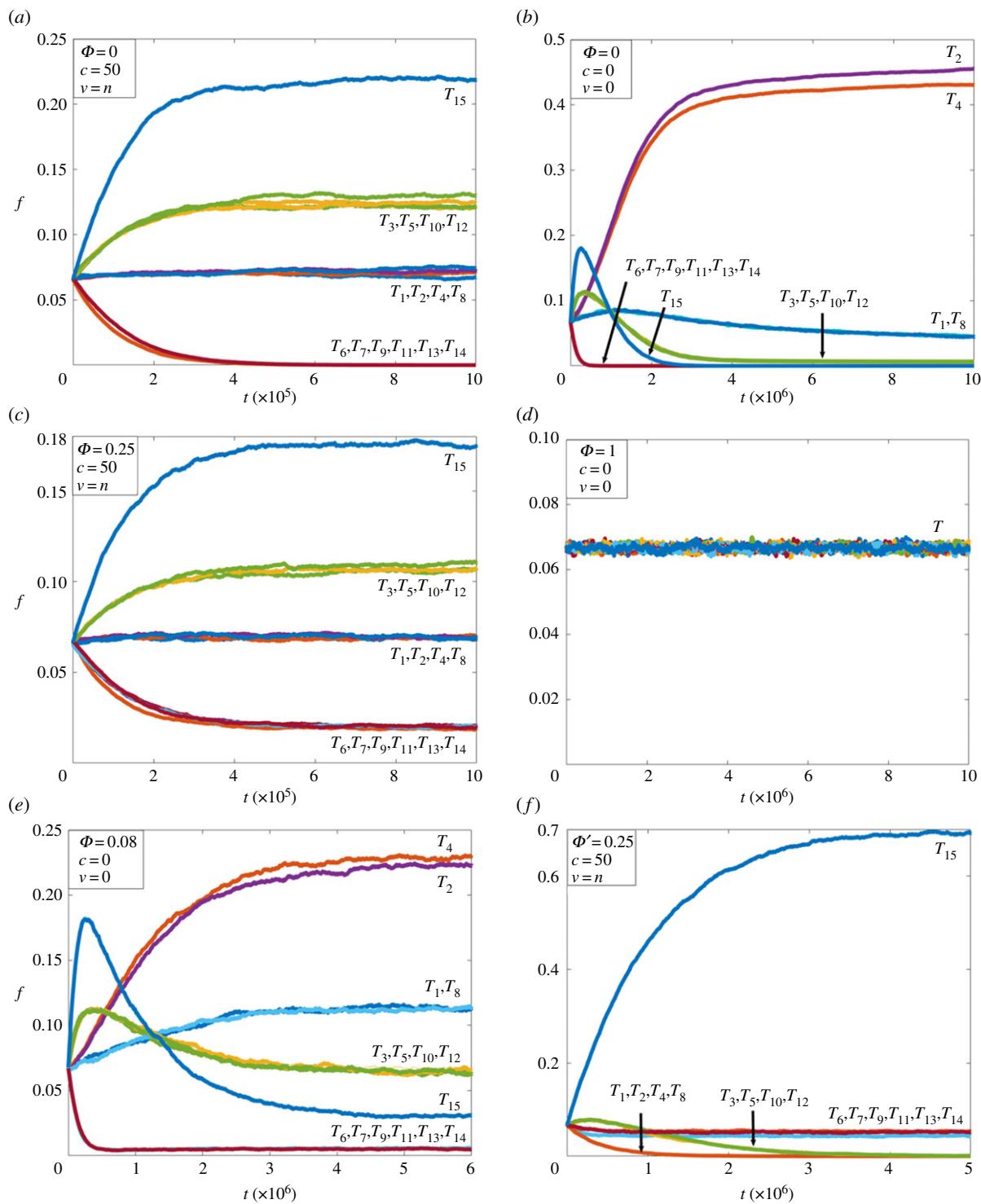
Niche  $A$  consisted of a steady-state network of nine automata that emerged from a well-mixed population ( $1 \leq c \leq N$ ,  $1 \leq v \leq n$ ) in the absence of an influx of randomly generated automata ( $\Phi = 0$ ). Six automata became extinct ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ) and the remaining nine types differentiated into three distinct clusters exhibiting no growth ( $T_1, T_2, T_4, T_8$ ), slow growth ( $T_3, T_5, T_{10}, T_{12}$ ) and fast growth ( $T_{15}$ ), all of which reached steady-state frequencies after  $t = 4 \times 10^5$  time steps (figure 3a).  $T_{15}$  was produced from 35 interactions and was

therefore the most frequently produced automaton. In comparison, automaton types in the slow and no growth clusters were generated from 21 or 15 interactions, respectively, while those that became extinct were produced from only eight interactions involving the ( $T_7, T_{11}, T_{13}, T_{14}$ ) (six interactions) and ( $T_6, T_9$ ) (two interactions) sub-groups. Interestingly, extinction of the six automata resulted in a drastic reduction in the number of interactions in the population from 207 to 63 interactions, which were then responsible for producing each of the remaining automata at an equal rate (seven interactions per automaton) and establishing steady-state conditions within the population.

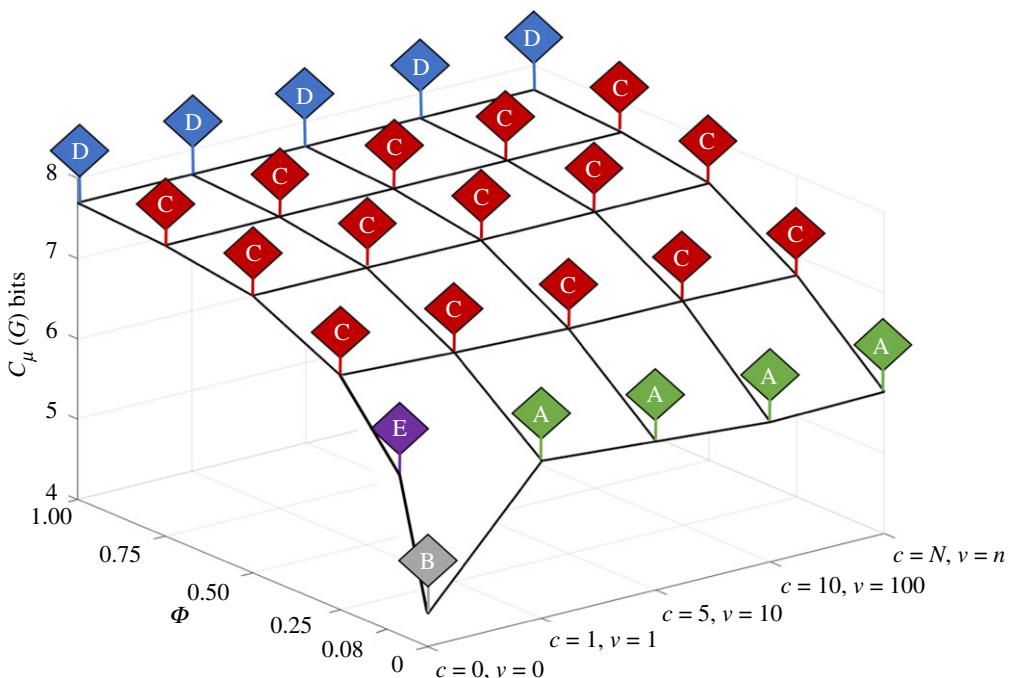
In contrast, simulations of the population production dynamics under fixed conditions of no spatial mixing ( $c = 0$ ,  $v = 0$ ) and no randomly generated influx ( $\Phi = 0$ ) produced niche  $B$ , which comprised a four-automaton steady-state network consisting of types  $T_1, T_2, T_4$  and  $T_8$  (figure 3b). The population dynamics initially mirrored those observed for a well-mixed environment (niche  $A$ ), but then exhibited a major transition at  $t = 2 \times 10^5$  after which the initial growth of  $T_{15}$  and the ( $T_3, T_5, T_{10}, T_{12}$ ) group was replaced by a rapid decrease in their frequency such that these automata became extinct after approximately  $3 \times 10^6$  iterations. As a consequence, the ( $T_1, T_2, T_4, T_8$ ) group, which exhibited no growth in a well-mixed environment (niche  $A$ ), differentiated into fast growing and non-growing populations of  $T_2$  and  $T_4$ , and  $T_1$  and  $T_8$ , respectively, with the ( $T_2, T_4$ ) pair occupying approximately 85% of the final population of niche  $B$  produced in the absence of spatial mixing. Under these conditions, interactions between the automata were spatially restricted such that short-range interactions dominated the population dynamics. As a consequence, two mechanisms were responsible for the fast growth of  $T_2$  and  $T_4$  in niche  $B$ : (i) independent interactions between  $T_2$  or  $T_4$  with a range of other automata gave rise to self-replication, or alternatively to production of  $T_1$  and  $T_8$ , which subsequently interacted with various other automata to generate  $T_2$  and  $T_4$  and (ii) local concentrations of  $T_2$  and  $T_4$  produced a spatial cluster (defined as a contiguous square area of the lattice consisting of nine  $T_2$  or  $T_4$  automata), which acted as a nucleation domain for protected outgrowth.

#### 3.1.2. Influence of influx dynamics

Having simulated the influence of spatial mixing and non-diffusivity on niche formation, we next investigated the effect of introducing an influx of randomly generated automata into an interacting population of automata under a range of mixing conditions. In the presence of both spatial mixing and significant influx dynamics ( $0 \leq c \leq N$ ,  $0 \leq v \leq n$  and  $0.25 \leq \Phi \leq 0.9$ ), the emerging steady-state population (niche  $C$ ) was structured similarly to niche  $A$  except that the ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ) group no longer became extinct (figure 3c). As a consequence, all 15 automaton types survived to produce a heterogeneous population structure comprising four steady-state clusters consisting of ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ) with a decreased frequency, ( $T_1, T_2, T_4, T_8$ ) with constant frequency, and ( $T_3, T_5, T_{10}, T_{12}$ ) and  $T_{15}$ , which exhibited slow and fast growth, respectively. In contrast, simulations of the population production dynamics under spatial mixing ( $0 \leq c \leq N$ ,  $0 \leq v \leq n$ ) and with a very high influx of randomly generated automata ( $0.9 < \Phi \leq 1$ ; niche  $D$ ) indicated that under these conditions the population dynamics were dominated by the influx



**Figure 3.** Plots of frequency distributions ( $f$ ) against iteration time step ( $t$ ) for interacting populations of automata under different simulated fixed environmental conditions. The simulations show the evolution of six distinct information niches comprising steady-state networks of selected and clustered information processing channels from an interacting population consisting of 90 000 single-state automata distributed at  $t = 0$  equally across 15 different types (shown in different colours) and subjected to three different environment inputs. (a) Niche A: population production dynamics in an environment with high spatial mixing of automata ( $1 \leq c \leq N$ ,  $1 \leq v \leq n$ ) and with no influx of randomly generated automata ( $\Phi = 0$ ) showing extinction of six automaton types and the emergence of a steady-state distribution of nine survival types arranged into three distinct clusters with one, four or four members after  $t = 4 \times 10^5$  time steps. (b) Niche B: extinction and steady-state survival of 11 and four binary automaton types, respectively, under a highly immobile environment exhibiting no diffusivity ( $c = 0$ ,  $v = 0$ ) and no randomly generated influx ( $\Phi = 0$ ). The survivors are arranged in three sub-groups containing one, one or two members. (c) Niche C: population production dynamics across a range of mixing conditions ( $0 \leq c \leq N$ ,  $0 \leq v \leq n$ ) and subjected to a considerable rate of influx of randomly generated automata ( $0.25 \leq \Phi \leq 0.9$ ). All automaton types survive to produce a heterogeneous population structure comprising four steady-state clusters consisting of one, four, four and six members. The population is structured similarly to niche A except that six members no longer become extinct. (d) Niche D: under all mixing conditions ( $0 \leq c \leq N$ ,  $0 \leq v \leq n$ ) and with  $\Phi > 0.9$  the population dynamics are dominated by the influx of new randomly generated automata from the environment such that the population remains unstructured and compositionally homogeneous over  $1 \times 10^5$  iterations. (e) Niche E: with no diffusive mixing on the lattice ( $c = 0$ ,  $v = 0$ ) and with a very low influx rate ( $0 < \Phi < 0.1$ ); the population is structurally similar to niche B except that three sub-groups of automaton types ( $(T_{15}), (T_3, T_5, T_{10}, T_{12})$  and  $(T_6, T_7, T_9, T_{11}, T_{13}, T_{14})$ ) no longer go extinct. (f) Niche F: with restricted automaton influx ( $\Phi' = 0.25$ ) and under a range of mixing conditions ( $0 \leq c \leq N$ ,  $0 \leq v \leq n$ ) the population evolves to three groups of automata ( $T_{15}$ ), ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ) and ( $T_3, T_5, T_{10}, T_{12}$ ), with the group ( $T_1, T_2, T_4, T_8$ ) going extinct.



**Figure 4.** Three-dimensional map of the interaction network complexity  $C_\mu(G)$  against environmental parameters ( $c, v, \Phi$ ) showing the information niche landscape. The information niches reside at different levels of  $C_\mu(G)$ . Note the prevalence of niche  $C$ . Niche  $F$ , which is produced under compositionally restricted influx ( $\Phi' = 0.25$ ), is not shown. There is little sensitivity to changes in the interaction network complexity measured for a wide range of values for  $c$  and  $v$ . In general, spatial mixing has a mild effect on population structure, and given that the interaction network complexity is contingent on structure, results in minor changes to the interaction network complexity.

rate from the environment. As a consequence, the population had no memory of previous interactions, and therefore remained unstructured with a composition uniformly distributed over all 15 automaton types even over  $1 \times 10^5$  iterations (figure 3d). We simulated the population production dynamics under conditions of no diffusive mixing on the lattice ( $c = 0, v = 0$ ) and with a very low influx rate ( $0 < \Phi < 0.1$ ). The resulting niche  $E$  was structurally similar to niche  $B$  ( $c = 0, v = 0; \Phi = 0$ ) but showed no automaton extinctions.

Finally, we simulated the population dynamics under a type-restricted influx ( $\Phi' = 0.25$ ) comprising randomly generated automata drawn from a specified subset of automaton types ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ). This specific subset was chosen as it represented the automaton types that were most frequently depleted from the population, or in the case of niches  $A$  and  $B$  became extinct. Thus, by restricting the environmental influx to this subset, we not only increased their concentration in the environment but also increased the probability that an automaton type from this subset would be re-introduced into the population during the simulation. As a consequence, rapid decay and extinction of ( $T_1, T_2, T_4, T_8$ ), slow decay and extinction of ( $T_3, T_5, T_{10}, T_{12}$ ) and rapid growth of  $T_{15}$  were observed to produce niche  $F$ . Niche  $F$  was structured into two groups consisting of a dominant automaton ( $T_{15}$ ) that occupied 70% of the population, along with a constant concentration of the ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ) cluster, which was sustained by the limited influx dynamics into the lattice. Significantly,  $T_{15}$  exhibited rapid growth because it was the only automaton produced (via eight interactions) by the restricted subset of influx automata ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ), and was the only self-replicator in the population.

### 3.1.3. Niche landscape and niche construction

Niche  $C$  was predominant across a wide range of fixed conditions of spatial mixing and random influx, indicating that

the network constellation producing the distinctive four clusters was extremely robust. In contrast, niches  $A$  and  $D$  were produced under a limited set of conditions ( $1 \leq c \leq N, 1 \leq v \leq n; \Phi = 0$  and  $0 \leq c \leq N, 0 \leq v \leq n; \Phi > 0.9$ , respectively), and  $B$  represented a singularity at  $c = 0, v = 0; \Phi = 0$ . The corresponding information landscape was mapped by plotting the interaction network complexity values ( $C_\mu(G)$ ) for niches produced under different environmental conditions (figure 4).

A niche with a higher interaction network complexity has more interactions and a more uniform distribution of automata and hence there is more uncertainty over what the next automaton to be produced will be. By contrast, there is less uncertainty in a lower complexity niche for the opposite reasons, i.e. fewer possible interactions and a non-uniform population and therefore more certainty over which automata are likely to be produced. An alternative interpretation is that more complex niches host a greater degree of competition between automata to reproduce due to each automaton having a lower probability of being produced than an automaton in a less complex niche (as measured by a lower interaction network complexity).

The initially unstructured and uniformly distributed population at  $t = 0$  had a  $C_\mu(G)$  value of 7.7 bits that represented all 207 possible interactions, and this reduced to 5.8 bits for niche  $A$  (63 interactions) and to 2.6 bits for niche  $B$  (eight interactions), indicative of higher levels of structuration particularly for niche  $B$ . In contrast, the  $C_\mu(G)$  value for niche  $C$  was 7.0 bits, which represented all 207 interactions and a small decrease in complexity (-0.7 bits) due to structuring of the population into four clusters. As niche  $D$  contained no changes in the frequency distribution of the original population, the  $C_\mu(G)$  value remained at 7.7 bits. Niche  $E$ , which had a similar spatial lattice structure to niche  $B$  but with inclusion of all automaton types in the population, had a  $C_\mu(G)$  value of 6 bits. This represented all 207 possible

interactions but with more and less structure than niche C and niche B, respectively. In general, the rates of formation of the information niches were decreased as the rate of spatial mixing decreased and/or the influx rate of new randomly generated automata increased. For example, growth of the ( $T_2, T_4$ ) group in niche B was reduced as  $0 < \Phi \leq 0.1$  and disappeared with  $0.1 < \Phi \leq 1$ . This indicated that increasing the number of automaton types persisting in the population due to a continuous influx from the environment ( $\Phi > 0$ ) destabilized the onset of structuration and the concomitant emergence of steady-state networks. In contrast, at  $\Phi = 0$ , 11 automaton types became extinct in niche B, which reduces the robustness of the network with respect to its ability to self-generate.

We executed an algorithm to identify interaction networks in a one-state automaton population that had strongly connected topologies characteristic of mutual production. The algorithm generated 7831 interaction networks ranging in size from two to 15 automata and exhibiting different levels of specialism (figure 5a–d). A subset of 129 networks was identified as strongly connected, implying that they were closed under composition. Of these, 29 were dynamically stable, i.e. under dynamical conditions each automaton in the network continued to be produced at a rate that no single automaton was over-produced (leading to complete dominance) or under-produced (leading to decay and ultimately extinction) within the population.

Such networks are similar to meta-machines [16], and endured indefinitely unless subjected to changes in the environmental conditions that disrupted the population dynamics. Of the 29 closed and stable networks, niche A (high spatial mixing ( $1 \leq c \leq N, 1 \leq v \leq n$ ) and no intake dynamics ( $\Phi = 0$ )) contained 28 (the closed and stable network  $\{T_6, T_9\}$  became extinct with time), while niche B with no lattice diffusion and no random influx ( $c = 0, v = 0; \Phi = 0$ ) contained only one. In contrast, niche C, which emerged under a wide range of population mixing and influx conditions ( $0 \leq c \leq N, 0 \leq v \leq n; 0.25 \leq \Phi \leq 0.9$ ), contained all 29 dynamically stable strongly connected networks. As expected, niche D produced under high levels of spatial mixing ( $0 \leq c \leq N, 0 \leq v \leq n$ ) and very high influx ( $\Phi > 0.9$ ) did not contain any stable networks.

We also searched for stable networks of production that were not only closed under composition but also irreducible. Production networks were irreducible if removal of one automaton resulted in dynamic instability that led to the decay of the network to a single automaton. Of the 29 dynamically stable networks, a subset of 12 networks termed *elementary networks* was identified as being closed, stable and irreducible (figure 5e). Niches A, B, C and D contained 11, 1, 12 and 0 elementary networks and niches E and F contained 12 and 0 elementary networks, respectively. Significantly, there was an association between niches with a higher number of elementary networks and their persistence across a range of environmental conditions, e.g. niches A and C collectively occupied approximately 75% of the information landscape (figure 4). While this was not a universal finding—niche E occurred only once and this was due to its formation exclusively in a low influx and low diffusive environment—it did suggest a degree of robustness conferred on a niche courtesy of the presence of more than one elementary network.

The presence of the elementary network  $\{T_6, T_9\}$  in niche C was a direct consequence of the influx of randomly generated automata from the environment as this elementary network

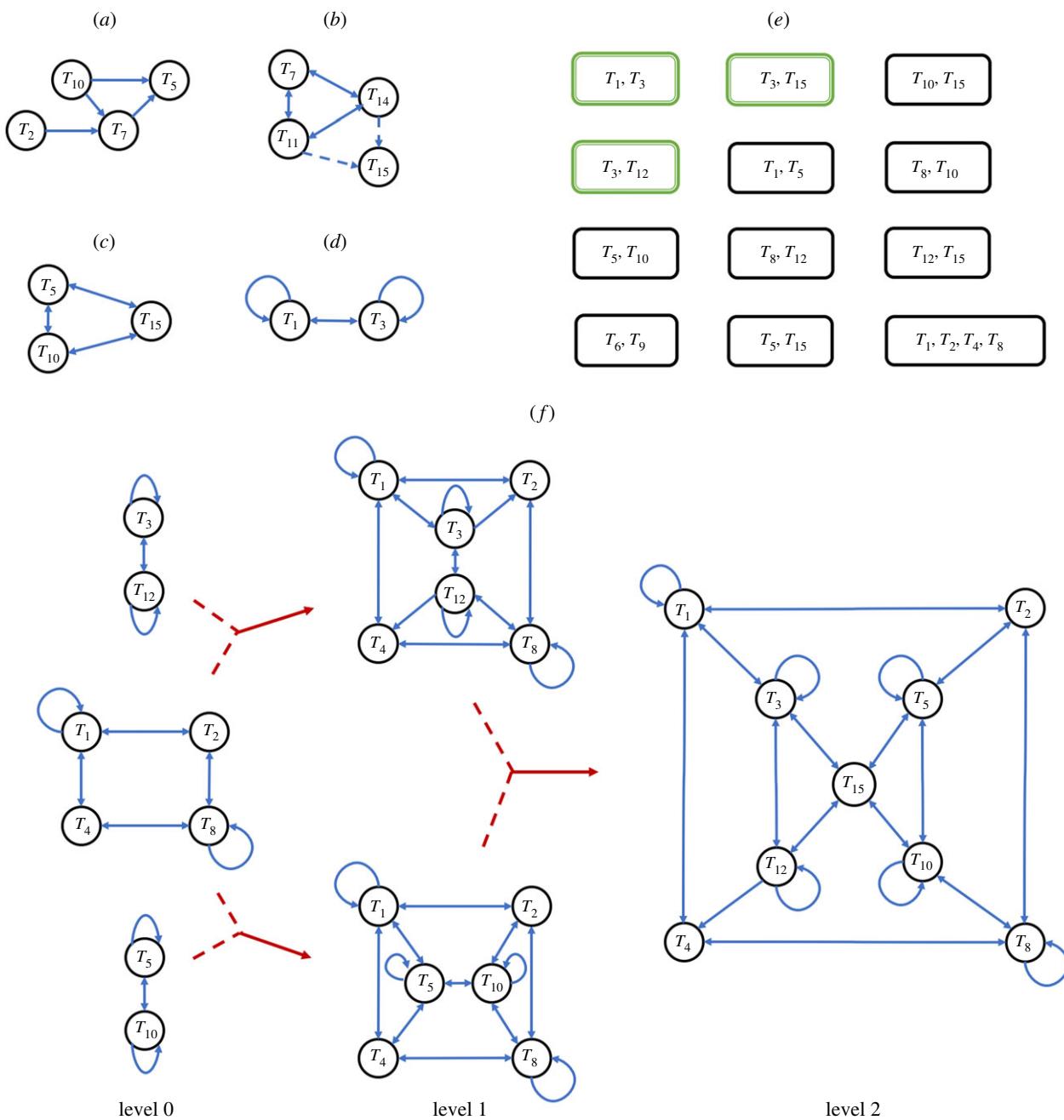
did not persist in the absence of any influx (niche A). Significantly, information niche A was constructed from a hierarchical organization in which the successive combination of elementary networks (level 0) produced intermediate networks (level 1), which in turn were integrated and embedded in a higher-order structure (level 2) (figure 5f). There were 15 construction pathways by which the higher-order network produced niche A, with each pathway the result of a unique combination of elementary and intermediate networks. Each network in the hierarchical organization was closed and dynamically stable. In contrast, niche B with a single elementary network was non-hierarchical.

The pathway to niche C involved the same elementary networks as niche A, except that in the presence of an influx of randomly generated automata ( $0 < \Phi \leq 0.9$ ) the group ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ) became organized into strongly connected networks that were dynamically unstable, and were therefore not part of the network hierarchy. Significantly, niches A and C consisted of automata that were each produced by at least two elementary networks, indicating a level of redundancy in the organization (figure 5f); for example, deconstruction of niche A indicated that the redundancy at level 1 involved decomposition of the intermediate networks into a subset of six ( $\{T_1, T_3\}, \{T_1, T_5\}, \{T_3, T_{12}\}, \{T_5, T_{10}\}, \{T_8, T_{10}\}, \{T_8, T_{12}\}$ ) of the total of 12 elementary networks.

### 3.2. Dynamics of information niches under environmental perturbations

To investigate the influence of environmental perturbations on the robustness and possible transitions of the primary information niches we simulated the response in the population dynamics to intermittent changes in the parameters  $c$ ,  $v$ ,  $\Phi$  and  $\Phi'$  (figure 6). These parameters were varied to simulate five types of perturbation that were imposed on each primary niche (niches A–F): (i) switching of lattice diffusivity to a value opposite to that initially associated with niche formation; (ii) switching of the influx rate to one of four possible values ( $\Phi = 0, 0 < \Phi < 0.1, 0.1 \leq \Phi \leq 0.9$  and  $0.9 < \Phi \leq 1$ ), which in each case corresponded to a parameter opposite to that initially associated with niche formation; (iii) application of (i) and (ii) concurrently; (iv) restricting the influx composition from a random selection of 15 automaton types to a confined group of six specified automata ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ) at a rate  $\Phi' = 0.25$ ; and (v) application of (i) and (iv) concurrently. In general, the results indicated that imposing environmental perturbations on the primary niches produces transformations in the internal structure of the population through the growth or decay in various automaton types, which under certain conditions (introducing diffusive mixing into niche B/E or removing influx into niche F) generated two new secondary niches (niche X and niche Y). We then perturbed these secondary niches by resetting the environmental parameters to those initially used for the formation of the associated primary niche to assess the reversibility of the niche transitions across the information landscape (figure 6c–d).

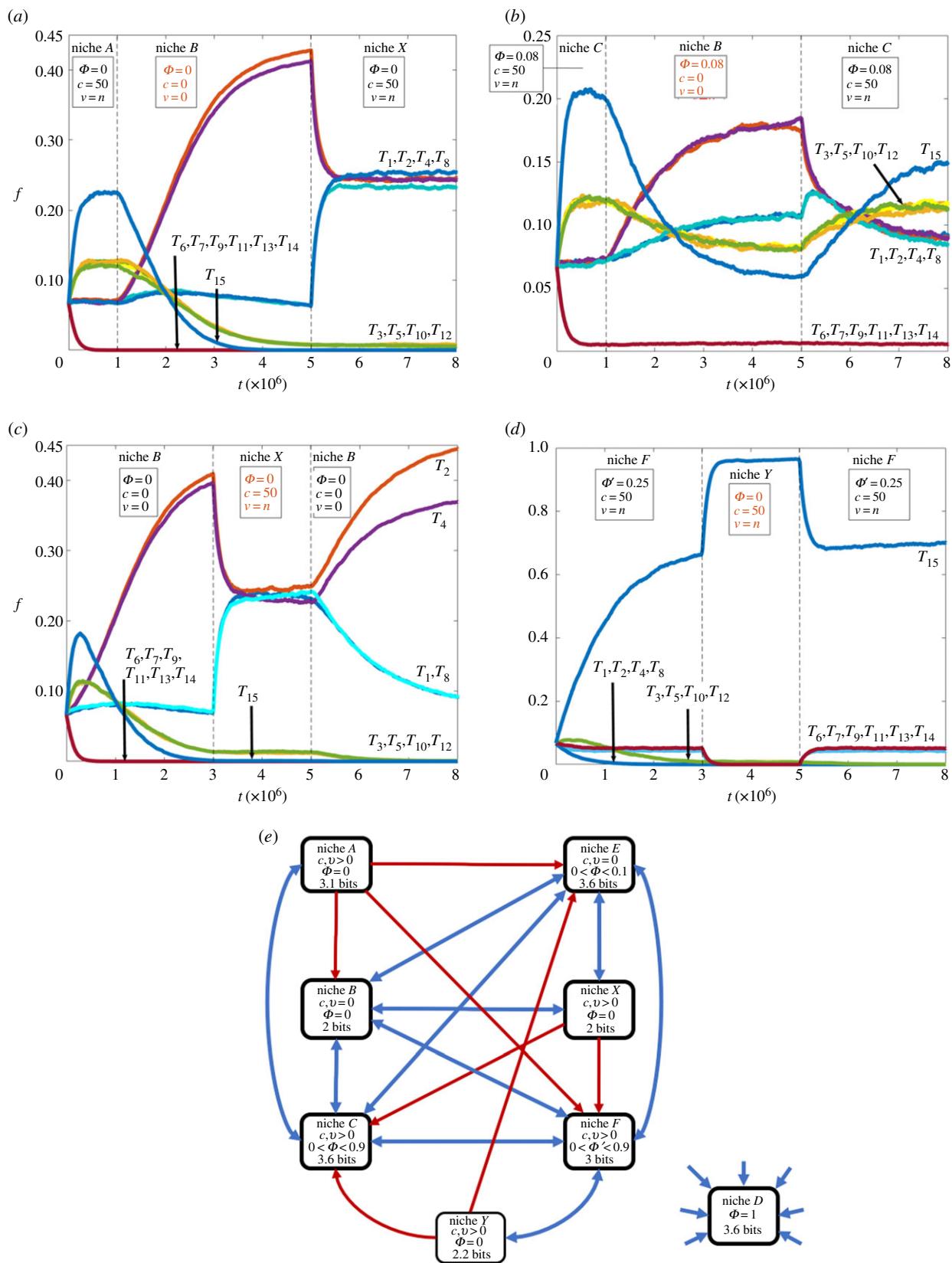
In total, 39 transitions between six primary niches and two secondary niches were identified (figure 6e). In some cases, the transitions were unidirectional. For example, niches A and C were established after  $7.5 \times 10^5$  iterations under well-mixed conditions with no or low intake dynamics ( $c = N, v = n; \Phi = 0$  or  $c = N, v = n; \Phi = 0.08$ ), respectively, and then



**Figure 5.** (a–d) Examples of the different types of network topologies generated from all combinations of interactions between automata in order of increasing specialism. (a) The most general topology (7702 identified types). The topology consists of a directed network in which each node represents an automaton and edges (arrows) signify that the automaton is involved in the production of the automaton positioned at the termination of the edge. For example, automata  $T_2$  and  $T_{10}$  interact to produce  $T_7$ , which interacts with  $T_{10}$  to produce  $T_5$ . In this example, the algorithm identifies the three networks  $\{T_2, T_7, T_{10}\}$ ,  $\{T_5, T_7, T_{10}\}$  and  $\{T_2, T_5, T_7, T_{10}\}$ . (b) Network with *apparent* strongly connected components (100 identified types), indicating that the constituent automata mutually produce each other; however, over time automata are also produced outside of the network (dashed arrows leading from  $T_{11}$  and  $T_{14}$ ), or the system becomes dynamically unstable because of competition within the same network that leads to extinction of one or more of its members. Edges with double arrows indicate that the connected automata are involved in producing each other. (c) Example of a strongly connected network (17 identified types) that only produces automata within the network, is dynamically stable and can be reduced into smaller sub-networks. (d) Example of a strongly connected network (12 identified types) that is dynamically stable and irreducible (elementary networks). A curved arrow indicates that the automaton is involved in its own production. (e) All 12 elementary networks of a one-state automaton population. Some automata are produced by more than one network and this is highlighted for  $T_3$  (green boxes). Multiple pathways to producing the same automaton (redundancy) confers a degree of robustness to the continued production of an automation even if an elementary network decays due to the extinction of one of its constituents. By comparison,  $T_6$  and  $T_9$  are only produced by one elementary network and these automata often become extinct. Niche A consists of all elementary networks except  $\{T_6, T_9\}$ ; niche B consists of only one network  $\{T_1, T_2, T_4, T_8\}$ ; and niche C consists of all of the elementary networks. (f) An example of a pathway to the bottom-up hierarchical construction of niche A based on the integration of three elementary networks (level 0) that combine to form two larger networks (level 1), which become embedded at level 2. Note that  $T_{15}$  is only produced when the level 1 networks are combined. Double arrows indicate that the associated automata are involved in producing each other and curved arrows indicate an automaton that is involved in self-production.

subjected to an extreme perturbation by switching the lattice diffusivity to zero ( $c = 0$ ,  $v = 0$ ). As a consequence, over  $1.25 \times 10^6$  iterations niches  $B$  and  $E$  emerged in each

population, respectively, with  $T_{15}$  experiencing a rapid decay while  $T_2$ ,  $T_4$  underwent fast growth. Once niches  $B$  or  $E$  were fully established, we re-adjusted the parameters to their original



**Figure 6.** Plots of frequency distributions ( $f$ ) against iteration time step ( $t$ ) showing the population dynamics when subjected to intermittent and extreme changes in environmental conditions (red text). (a) Primary information niche  $A$  was established after  $1 \times 10^6$  iterations, and then the lattice diffusivity reduced to zero. Niche  $B$  emerged within  $5 \times 10^6$  iterations and subsequently resetting the parameters to their original values formed a new secondary niche  $X$ , which was distinguished by two groups of automata ( $T_1, T_2, T_4, T_8$ ) and ( $T_3, T_5, T_{10}, T_{12}$ ). (b) Similarly, primary niche  $C$  was established after  $1 \times 10^6$  iterations and then the lattice diffusivity reduced to zero leading to the reversible emergence of niche  $E$  after  $5 \times 10^6$  iterations; resetting the parameters to their original values re-created niche  $C$ . (c) Formation of the secondary niche  $X$ ; niche  $B$  formed after  $3 \times 10^6$  iterations and then the lattice diffusivity was increased for  $2 \times 10^6$  iterations to generate niche  $X$  after which the perturbation was removed and the population transitioned back to niche  $B$ . (d) Primary niche  $F$  was established under type-restricted automaton influx ( $\Phi' = 0.25$ ), and then the population perturbed by removing the intake restriction to produce the homogenized secondary niche  $Y$  comprising the self-replicator  $T_{15}$ ; resetting the parameters led to the reverse transition back to niche  $F$ . (e) Information niche transition diagram; each box represents a niche and the associated environmental parameters indicate the conditions under which the information niche forms, and the production threshold of the niche in binary digits. Arrows between niches indicate possible transitions and whether they are irreversible (red single arrows) or reversible (blue double arrows). Niche  $D$  is a special case as it represents an unstructured, uniformly distributed population, which can be produced from perturbing all primary and secondary niches by setting  $\Phi = 1$ .

values, and assessed how the emerging populations responded. Niche C was re-established within  $1 \times 10^6$  iterations, indicating that the C to E transition was reversible across the information landscape under the imposed environmental conditions, while niche A was not re-established from niche B. Instead, niche B transitioned into a new niche (niche X), which consisted of eight automaton types clustered into two groups ( $T_1, T_2, T_4, T_8$ ) and ( $T_3, T_5, T_{10}, T_{12}$ ) (figure 6a,b). Secondary niche X was also produced from niche E by introducing lattice diffusivity into the simulations. Increasing the number of long-range interactions within the highly structured populations of niches B and E eliminated the  $T_2$  and  $T_4$  domains such that the production dynamics were dominated by the elementary network  $\{T_1, T_2, T_4, T_8\}$ , which produced each of its members with equal probability. This led to a transient period with a reduction in the number of  $T_2$  and  $T_4$  automata and corresponding increase in the number of  $T_1$  and  $T_8$  automata until a new steady state was reached after approximately  $5 \times 10^5$  iterations (figure 6c).

Secondary niche Y was generated by perturbation of primary niche F, which was produced under restricted influx conditions ( $\Phi = 0.25$ ) via switching off the partial influx of new automata ( $\Phi = 0$ ) (figure 6d). Under the new environmental conditions, the  $T_{15}$  frequency, which comprised approximately 70% of the population of niche F, increased rapidly to almost 100% in niche Y to produce a homogenized population. This was principally because (i)  $T_{15}$  could be generated from 21 interactions including a high level of self-replication and (ii) the clusters ( $T_7, T_{11}, T_{13}, T_{14}$ ) and ( $T_6, T_9$ ) were each produced from only six and two interactions, respectively, and collectively did not form a closed and stable network of production.

The production threshold was calculated for each niche and the loss or gain of information between niches undergoing reversible or non-reversible transitions examined. As shown in figure 6e, the production threshold of primary niches C, D and E was 3.6 bits, niche A was 3.1 bits, and niches F and B was 3 bits and 2 bits, respectively. The production thresholds for the secondary niches X and Y were 2 and 2.2 bits, respectively. As the production threshold relates to how much information is required for a niche to persist via the continual production of certain automata, in general transitions within the niche landscape occurred when there was a reduction or no significant change in the information content. However, transitions that resulted in a loss of information and a subsequent reduction in the production threshold of the population were irreversible unless sufficient information was added from the environment. For example, niche A (3.1 bits;  $0 < c \leq N, 0 < v \leq n; \Phi = 0$ ) transitioned to niche B by setting the lattice diffusivity to zero ( $c, v = 0$ ), which resulted in a reduced information content (2 bits) because extinction of  $T_{15}$  reduced the number of possible interactions in niche B. Re-setting the parameters to enable lattice diffusivity ( $0 < c \leq N, 0 < v \leq n; \Phi = 0$ ) did not re-establish niche A because increasing spatial mixing did not provide additional information content ( $T_{15}$  was irredeemably lost from the population). Instead, niche B transitioned into niche X (2 bits) that had the same information content as niche B but a different steady-state configuration. Indeed, the only way to re-gain lost information was through an influx of automata from outside the population by increasing the  $\Phi$  parameter. Thus, the transition from niche C ( $0 < c \leq N, 0 < v \leq n; 0 < \Phi < 0.9$ ) to B ( $c, v = 0; \Phi = 0$ ) was reversible because the initial perturbation step was linked with a reduction of information from 3.6 to 2 bits (figure 6e), and the return pathway associated with

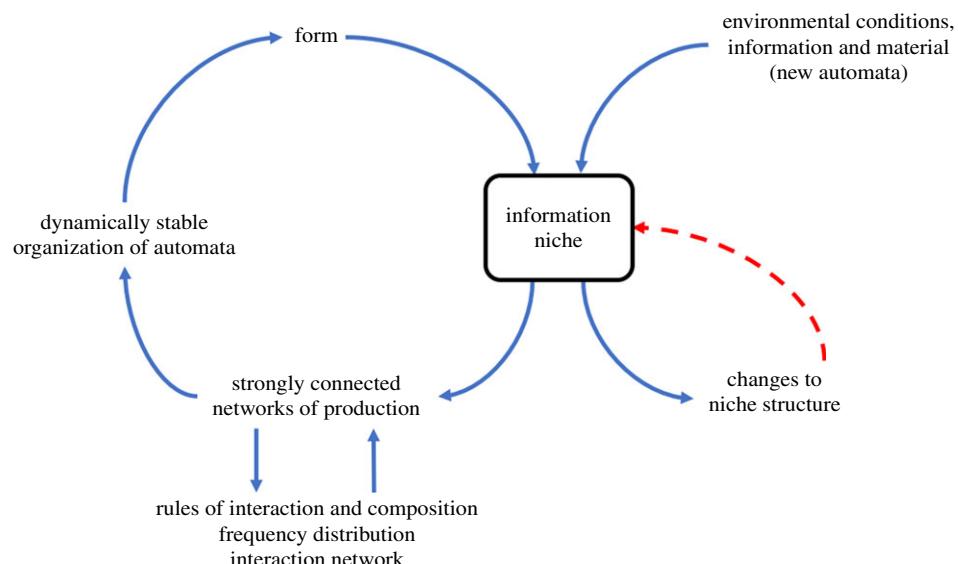
an increase in new information due to the re-established environmental influx of automata.

Based on the above analysis, the robustness of each niche within the information landscape was observed to be dependent on the environmental conditions under which it was formed, and the nature of any subsequent perturbations. In particular, niches that were generated under zero influx conditions resulted in the extinction of six ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ) of the 15 types of automata, while all the automaton types were retained in niches constructed under high influx conditions. Robust niches such as niches C, D, E and F could recover from any type of perturbation, and were associated with high information environments characterized by the presence of lattice diffusivity ( $0 < c \leq N, 0 < v \leq n$ ) and some environmental influx ( $0 < \Phi < 0.9$ ). Conversely, niches that were less robust were produced in low information environments characterized by zero diffusivity ( $c, v = 0$ ) and no influx of automata ( $\Phi = 0$ ).

## 4. Conclusion

We have examined a self-producing system in a pre-evolutionary/pre-genetic scenario by extending the finitary process soup model [14] to investigate the influence of environmental conditions and perturbations on the dynamics and emerging organizational complexity of an interacting population of single-state information processing entities (automata). Our simulations indicate that dynamically stable strongly connected networks of mutually producing automata emerge under specific environmental conditions associated with changes in the degree of spatial lattice mixing and influx dynamics. The emergence of a limited number of these information niches suggests an underlying fitness landscape, which sculpts the self-organizing community of interacting automata into a self-referential system that is contingent on the interplay of internal and external population production dynamics (figure 7). In this perspective, the information niche represents a nexus between four key processes: (i) the mutual production of automata and formation of closed and stable networks, (ii) emergence of a hierarchical interaction network structure, (iii) onset of dynamic stability in the networks of production, and (iv) redundancy within the population and interaction network.

Our simulations indicate that an information niche was more robust and viable with increasing levels of redundancy, as each automaton was produced by at least two different and independent elementary networks, and the associated modularity enables effective niche recovery when subjected to extreme environmental perturbations. Among the fitness landscape, niches C and E are able to reconstruct when subjected to fluctuating environmental parameters principally due to modulating the interface with the environment by coupling of the internal production dynamics to the randomly generated intake of new automata. Significantly, reversible niche transitions are only allowed if accompanied by an equal or increased level of information production. In some cases, the environmental perturbation generates additional information that drives the niche transition, and as such acts as an exogenous source of diversification of the population. Thus, taken together our simulations show that characteristics indicative of mutual production and redundancy confer resilience on the dynamics and emerging organizational complexity of interacting/replicating populations of simple information processing entities.



**Figure 7.** The information niche as a nexus: interactions between automata according to intrinsic (rules of composition and competition) and extrinsic (changes in frequency distribution and interaction network) factors generate strongly connected networks of production that evolve to dynamically stable organizations depending on the coupling with environmental factors (spatial mixing/intake dynamics) to form an information niche. The niche serves as a nexus as it is responsive to external factors such as changes in environmental conditions, information content and input dynamics, as well as to internal changes in structure. The circularity generates a compositionally closed system with the niche acting in a top-down manner to influence the networks of production, thereby maintaining its own identity and demonstrating proto-autopoietic properties.

Within a more general context, our model describes a basic mechanism for coupling environmental parameters into a community of interacting objects that function as communication channels, and therefore offers a new approach for studying the onset of autopoiesis within both a prebiological scenario and bottom-up synthetic biology context. We demonstrate that the emergence of information niches occurs without the introduction of novel forms into an environmental fitness landscape, suggesting that communities of interacting entities such as chemically active synthetic protocells [22,23] could become hierarchically structured and dynamically stable over time even in the absence of evolution. Such observations provide insights into how simple informational transitions between interacting members of a consortium could lead to self-sustaining structured populations comprising proto-autopoietic networks, and could therefore initiate a bridge in the transition from inanimate to living matter via a collective process of protocell self-production operating under non-evolutive/self-replication conditions. Moreover, this in turn might provide a resilient platform for the onset of evolutionary processes responsible, for example, for the emergence of protolife entities from pre-biotic inanimate systems. While closed systems based on single causal state automata are incapable of simulating evolution in the Darwinian sense due to the absence of novelty in

the automata types produced over successive generations, the functional composition of two-state automata is known to generate communication channels exhibiting entirely novel features [16], suggesting that the environmental dependence of such communities would provide a rich landscape for modelling more complex aspects of autopoiesis. Simulations based on these multi-state systems are the focus of future work.

**Data accessibility.** The information niche model has been implemented in Matlab and the code and associated files are available online at <https://github.com/rjcarte/Information-Niches>.

**Authors' contributions.** R.J.C. implemented and developed enhancements to the finitary process soup model in Matlab, designed and ran all simulations, and performed analysis of the simulation results. S.M. coordinated the study. All authors contributed to the conceptual development of the framework, discussed the simulation results and contributed to the writing of the manuscript. All authors gave final approval for publication.

**Competing interests.** We have no competing interests.

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## References

1. Gànti T. 2003 *Chemoton theory. Vol. 1. Theoretical foundations of fluid machineries*. New York, NY: Kluwer Academic/Plenum Publishers.
2. Gànti T. 2003 *Chemoton theory. Vol. 2. Theory of living systems*. New York, NY: Kluwer Academic/Plenum Publishers.
3. Eigen P, Schuster M. 1978 Part a: emergence of the hypercycle. *Naturwissenschaften* **65**, 7–41. (doi:10.1007/BF00420631)
4. Vádasz V, Fernando C, Santos M, Kauffman S, Szathmáry E. 2012 Evolution before genes. *Biol. Direct* **7**, 1. (doi:10.1186/1745-6150-7-1)
5. Maturana HR, Varela FG. 1980 *Autopoiesis and cognition: the realization of the living*. Boston Studies in the Philosophy and History of Science. Dordrecht, The Netherlands: Springer
6. Mann S. 2012 Systems of creation: the emergence of life from non-living matter. *Acc. Chem. Res.* **45**, 2131–2141. (doi:10.1021/ar200281t)

7. Li M, Huang X, Tang TYD, Mann S. 2014 Synthetic cellularity based on non-lipid micro-compartments and protocell models. *Curr. Opin. Chem. Biol.* **22**, 1–11. (doi:10.1016/j.cbpa.2014.05.018)
8. Varela FG, Maturana HR, Uribe R. 1974 Autopoiesis: the organization of living systems, its characterization and a model. *Biosystems* **5**, 187–196. (doi:10.1016/0303-2647(74)90031-8)
9. McMullin B. 1997 Computational autopoiesis: the original algorithm. Santa Fe Institute Working Paper (97-01-001); URL <https://www.santafe.edu/research/results/working-papers/computational-autopoiesis-the-original-algorithm>.
10. Zeleny M. 1981 *Autogenesis: on the self-organization of life*. New York, NY: Elsevier
11. Fontana W. 1991 *Algorithmic chemistry*, vol. X. Reading, MA: Addison-Wesley.
12. Dittrich P, Speroni di Fenizio P. 2007 Chemical organization theory. *Bull. Math. Biol.* **69**, 1199–1231. (doi:10.1007/s11538-006-9130-8)
13. Banzhaf W, Yamamoto L. 2015 *Artificial chemistries*. Cambridge, MA: The MIT Press.
14. Crutchfield JC, Gornerup O. 2006 Objects that make objects: the population dynamics of structural complexity. *J. R. Soc. Interface* **3**, 345–349. (doi:10.1098/rsif.2006.0114)
15. Ullman J, Hopcroft J. 1979 *Introduction to automata, theory, languages and computation*. Reading, MA: Addison-Wesley.
16. Gornerup O, Crutchfield JP. 2008 Hierarchical self-organization in the finitary process soup. *Artif. Life* **14**, 245–254. (doi:10.1162/artl.2008.14.3.14301)
17. Piantadosi ST, Crutchfield JP. 2013 How the dimension of space affects the products of pre-biotic evolution: the spatial dynamics of structural complexity and the emergence of membranes. (<https://arxiv.org/abs/1010.5019>)
18. Nicolis G, Prigogine I. 1989 *Exploring complexity*. New York, NY: W.H. Freeman and Company.
19. Klamt S, von Kamp A. 2009 Computing paths and cycles in biological interaction graphs.
20. Filisetti A, Villani M, Damiani C, Graudenzi A, Roli A, Hordijk W, Serra R. 2014 On RAF sets and autocatalytic cycles in random reaction networks. In *Advances in artificial life and evolutionary computation (WIVACE 2014)* (eds C Pizzuti, G Spezzano), pp. 113–126. Communications in Computer and Information Science, vol. 445.
21. Newman M. 2010 *Networks: an introduction*. Oxford, UK: Oxford University Press.
22. Qiao Y, Li M, Booth R, Mann S. 2017 Predatory behaviour in synthetic protocell communities. *Nat. Chem.* **9**, 110–119. (doi:10.1038/nchem.2617)
23. Tian L, Martin NC, Bassindale PG, Patil AJ, Li M, Barnes A, Drinkwater BW, Mann S. 2016 Spontaneous assembly of chemically encoded two-dimensional coacervate droplet arrays by acoustic wave patterning. *Nat. Commun.* **7**, 13068. (doi:10.1038/NCOMMS13068)



## RESULTS II - Two-State INFORMATION NICHES

### 5.1 Introduction

This chapter describes the results from simulating an exclusively two-state automata population. The following simulations were executed:

- Simulation of a two-state automata population self-organising to a niche under well-mixed conditions (see section 5.2)
- Simulation of a two-state automata population self-organising to a niche under low diffusivity conditions (see section 5.3)
- Simulation of a two-state automata population self-organising to a niche under conditions of (i) intermittent and, separately (ii) constant, influx of externally generated automata (see section 5.4)

To verify the results each simulation was repeated five times. All subsequent re-runs accurately re-produced the same outcomes and very minor differences due to the stochastic nature of the model were deemed inconsequential to the subsequent analysis and interpretation of the results.

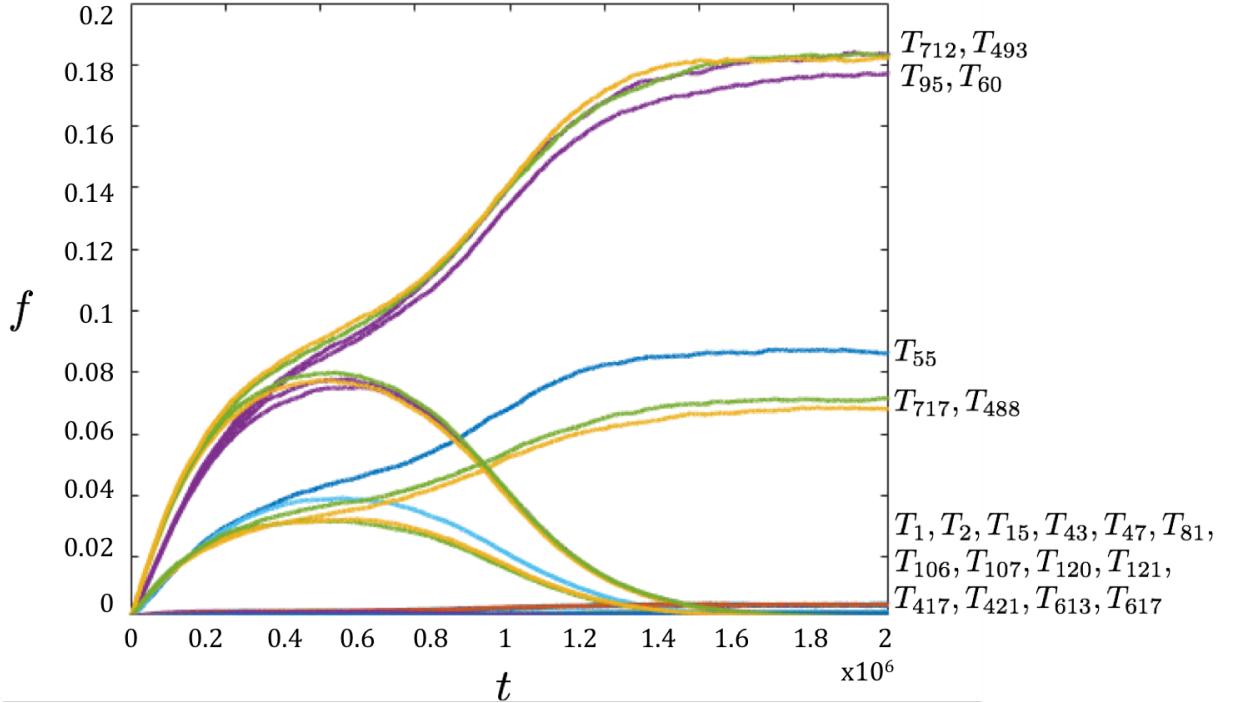


Figure 5.1: Simulation of a two-state population under well-mixed conditions shows an initial stage of competition between two different subsets of automata with one subset eventually dominating whilst the other decays rapidly. This *punctuated equilibrium* begins at the  $10^5$  iteration. The result was a niche consisting of 21 automata (niche 2A). Repeated simulations revealed that occasionally the other competing subset of automata came to dominate the population to create a new niche (niche 2B) with a very similar steady-state structure.

## 5.2 Emergence of a two-state automata niche under well-mixed conditions

The simulation was initialised with a population of 90,000 two-state automata on a  $300 \times 300$  lattice of 1,873 unique types equating to an average of 48 automata of each type. The simulation was run for  $2 \times 10^6$  iterations under environmental conditions of diffusive mixing ( $c = N, v = n$ ) and no influx of external automata ( $\Phi = 0$ ). This resulted in a niche (niche 2A) consisting of 21 automata with all other automata types going extinct (see Figure 5.1).

The simulation was repeated and produced a near identical steady-state structure with minor differences due to the stochastic nature of the automaton replacement algorithm. However, a third run produced a different niche (niche 2B) that had the same number of automata (21) as niche 2A but now consisted of the automata that had previously competed

## 5.2. EMERGENCE OF A TWO-STATE AUTOMATA NICHE UNDER WELL-MIXED CONDITIONS

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and decayed in the previous two simulations. Repeated simulation runs indicated that each niche could come to dominate and that this appeared to be probabilistically determined. Analysis of the interaction network revealed that these niches were generated from strongly connected networks whereby the automata constituting niche 2A mutually produced each other (and the same was true for niche 2B). This insight led to the observation that competition was occurring at two levels: at the individual automaton level where pairs of automatons were competing with each other e.g.  $T_{712}$  from niche 2B competes with  $T_{775}$  from niche 2A,  $T_{55}$  competes with  $T_{36}$ , and so on (see Table 5.1), and (ii) at the network level where collectively the performance of all automata in the two strongly connected networks constituting niche 2A and 2B had an impact on the individual competitiveness of each of their constituent automatons. As such, and given the interconnected nature of a niche, all automata in a given niche benefited from one or more of their members out-competing rival automata in the other niche. The likelihood of one niche out-competing the other appears to be probabilistically close to parity. The stochastic nature of how automata are chosen for interaction and therefore which automata were produced was determined as the reason for this alternating dominance between the two niches over repeated simulation runs.

category	niche 2A	$f$	niche 2B	no. edges	no. productions
Fast Growth	$T_{95}$	0.21	$T_{102}$	1,884	11,700
	$T_{60}$	0.2	$T_{39}$	1,884	11,700
	$T_{493}$	0.18	$T_{411}$	1,874	22,805
	$T_{712}$	0.17	$T_{775}$	1,522	22,805
Medium Growth	$T_{488}$	0.09	$T_{402}$	1,795	9,519
	$T_{717}$	0.09	$T_{766}$	1,874	22,805
	$T_{55}$	0.058	$T_{36}$	1,522	5,980
Slow Growth	$T_{15}$	0.0007	$T_{40}$	1,411	1,595
	$T_{107}$	0.0006	$T_{137}$	1,401	1,088
	$T_2$	0.0006	$T_4$	1,411	1,595
Slow Decay	$T_{47}$	0.0004	$T_{22}$	1,411	1,595
	$T_{81}$	0.0004	$T_{79}$	1,411	1,595
	$T_{106}$	0.0003	$T_{561}$	1,322	758
	$T_{617}$	0.0003	$T_{134}$	1,322	758
	$T_{120}$	0.0003	$T_{204}$	1,401	1,088
	$T_{417}$	0.0003	$T_{303}$	1,322	758
	$T_{421}$	0.0003	$T_{309}$	1,401	1,088
	$T_{613}$	0.0002	$T_{555}$	1,401	1,088
	$T_{121}$	0.0002	$T_{207}$	1,322	758
	$T_1$	0.0002	$T_3$	1,510	1,223
	$T_{43}$	0.0001	$T_{20}$	1,510	1,223

Table 5.1: The competing niches in a two-state population consist of symmetrical automata e.g. the automaton  $T_1$  in niche 2A with the transitions  $\{0|1,0|0\}$  has a symmetrical twin  $T_2$  in niche 2B with the transitions  $\{1|0,0|0\}$  however they do not interact to produce other two-state automata. Under well-mixed conditions these competing pairs contribute to, and benefit from, the replicative performance of the automata that also constitute their respective niches. The automata from each niche were categorised according to the rate at which they were produced with respect to their initial  $f$  which was 0.0005 for each automaton.

Compared to the one-state population (see Chapter 4) these results indicate that a population with a higher average structural complexity <sup>1</sup> there were now two levels of competition occurring: (i) competition between individual automata; and (ii) competition between niches. The figures 5.2 and figure 5.3 show the members of niche 2A and niche 2B respectively. As can be seen the automata in each niche were topographically identical and the information they processed was the mirror image of the other niche. Each niche processes the exact same information: 20 transitions of  $0|0$ , 20 transitions of  $0|1$ , 20 transitions of  $1|0$  and 20 transitions of  $1|1$ . Furthermore, as the population evolved with the large majority of automata going extinct each niche automaton was produced the same number of times (15) which led to the steady-state structure that defined the niche.

<sup>1</sup>all one-state automata have  $C_\mu(T)=0$  bits compared to an average of  $C_\mu(T)=0.94$  bits in the two-state population

5.2. EMERGENCE OF A TWO-STATE AUTOMATA NICHE UNDER WELL-MIXED CONDITIONS

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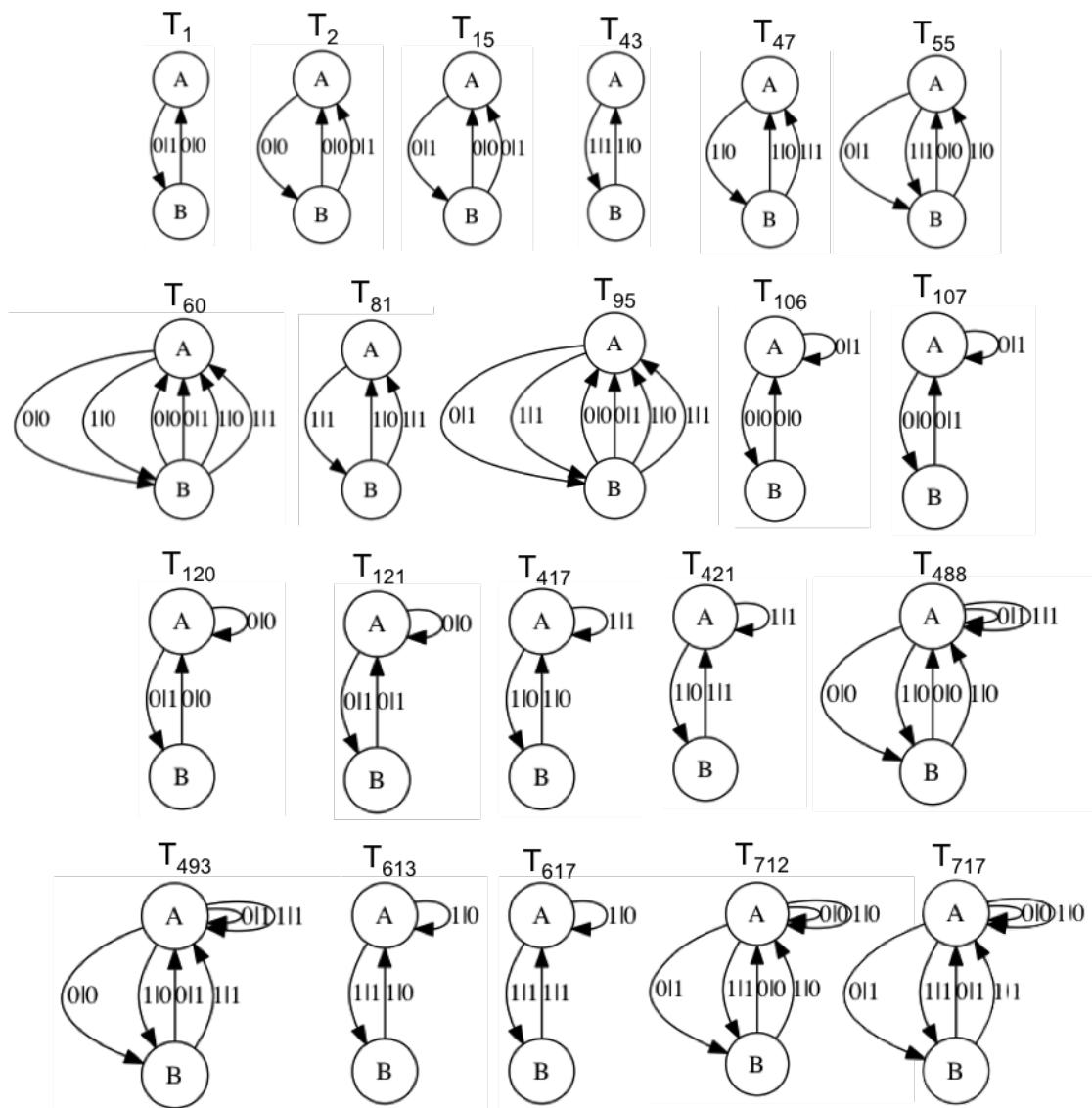


Figure 5.2: The 21 two-state automata types that constitute niche 2A.

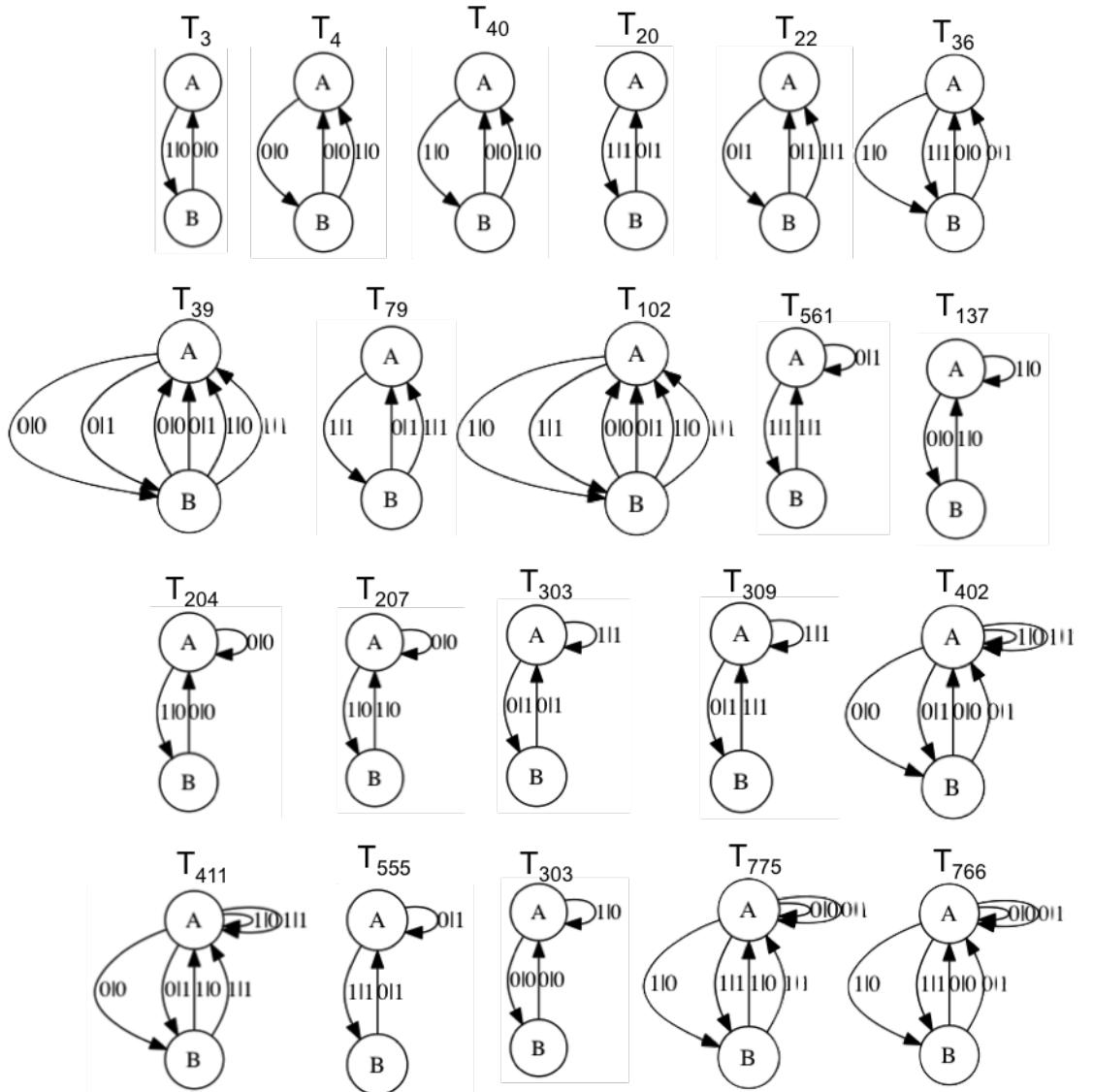


Figure 5.3: The 21 two-state automata types that constitute niche 2B. The topology of this niche's automata were identical to those in niche 2A whilst it processed a different domain and range of binary information.

The two-state interaction network consisted of 1,873 vertices and 355,484 edges representing the number of potential interactions that produce a two-state automaton. Of those potential interactions 220,476 produce the 42 automata that constitute the two niches 2A and 2B. For each niche there were 110,238 interactions that produce the automaton within that niche with 61.86% (68,189 interactions) producing the High Growth automata, 34.23% (37,737 interactions) producing the Medium Growth automata and 3.91% (4,312 interactions) producing the Slow Growth and Slow Decay automata. At the end of the

## 5.2. EMERGENCE OF A TWO-STATE AUTOMATA NICHE UNDER WELL-MIXED CONDITIONS

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simulation 1,852 two-state automata that were initially present have gone extinct leading to a reduction in the interaction network complexity from 19.22 bits at  $t = 0$  to 6.02 bits at  $t = 2 \times 10^6$ . 22.6% (424) of those extinct automata were not produced at all and the remainder were produced in very low numbers and were eventually selected for removal from the population. The analysis of the interaction network indicates that it is heavily skewed towards producing a small number of certain automata types in the population (see Table 5.2 and Figure 5.4).

As a large number of automata went extinct the interaction network complexity was drastically reduced as the number of interactions that are producing the niche automata are no longer possible (as the automata types that take part in those interactions are no longer present in the population), and this leads to production dynamics becoming dominated by the mutual production that occurs in the strongly connected networks of each niche. Given that each automata in the competing niches were produced in equal number then the eventual dominance of one niche over the other was a function of the history of productions i.e. the incidental advantage conferred on one niche over the other based on the chance that its constituent automata happened to of been produced more frequently up to that point.

Frequency of Production	No. of Automata Types
0	424
1-300	1,313
301-600	76
601-900	10
901-1200	16
1201-1500	8
1501-1800	12
..	..
6001-6300	2
..	..
9601-9900	4
..	..
12001-12300	4
..	..
20001-23000	4

Table 5.2: The histogram of the number of productions that occur in the interaction network and the number of automata that are produced in each bin. Analysis of the production of two-state automata showed that a very small number of automata (14 automata types representing 0.2% of the population) were produced considerably more often.

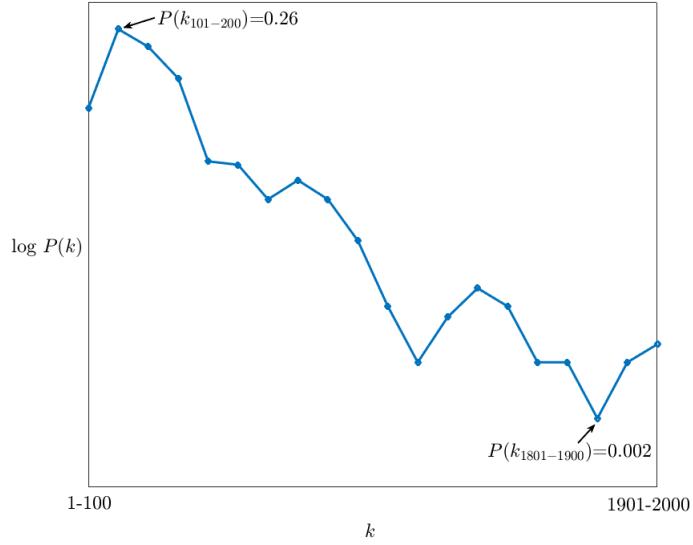


Figure 5.4: The degree distribution of the two-state interaction network. The  $x$ -axis are the  $k$  (total incoming and outgoing edges of each vertex which represents an automaton type) values allocated into bins of width 100. The  $y$ -axis are the  $\log P(k)$  values for each of the  $k$  bins. As can be seen the large majority of vertices in the network have fewer than 200 edges whilst a very small number of vertices have a large number of edges ( $> 1,000$ ) indicating a heterogenous network structure with a small number of highly connected 'hubs'.

The degree distribution varied significantly (see figure 5.4) indicating a heterogenous network structure consisting of a large number of vertices with a hundred or so edges and a very small number of vertices that are highly connected ( $> 1,000$  edges). In general, there was a direct relationship between an automaton degree of connectedness and the frequently with which it is produced e.g. the small subset of automata that are highly connected and highly produced are members of the set of automata that constitute the niches 2A and 2B.

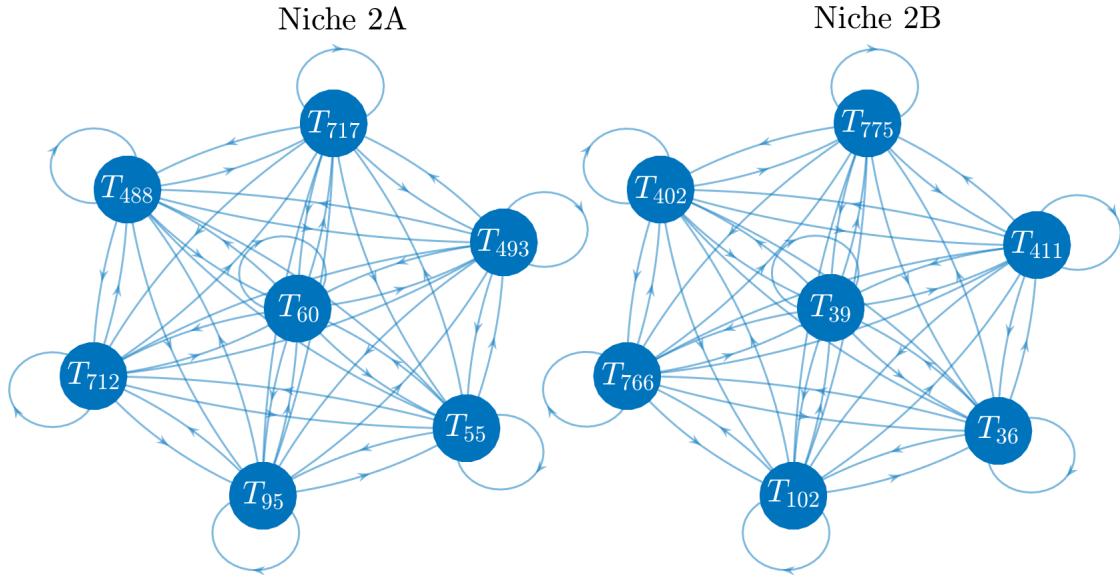


Figure 5.5: The competing interaction networks for niche 2A (blue) and 2B (black). Each network has an identical topology that is a fully connected network consisting of seven nodes and 49 edges. Neither network holds an intrinsic advantage and the 'punctuated equilibrium' that occurs is a result of chance.

### 5.3 Emergence of a two-state automata niche under non-diffusivity conditions

A population of 90,000 two-state automata consisting of 1,873 unique types (with an average of 48 of each type) were randomly distributed on a 300 by 300 lattice and the simulation iterated for  $5 \times 10^7$  iterations under environmental conditions of no diffusive mixing ( $c = 0, v = 0$ ) and no influx of external automata ( $\Phi = 0$ ). This resulted in the emergence of the niche 2C.

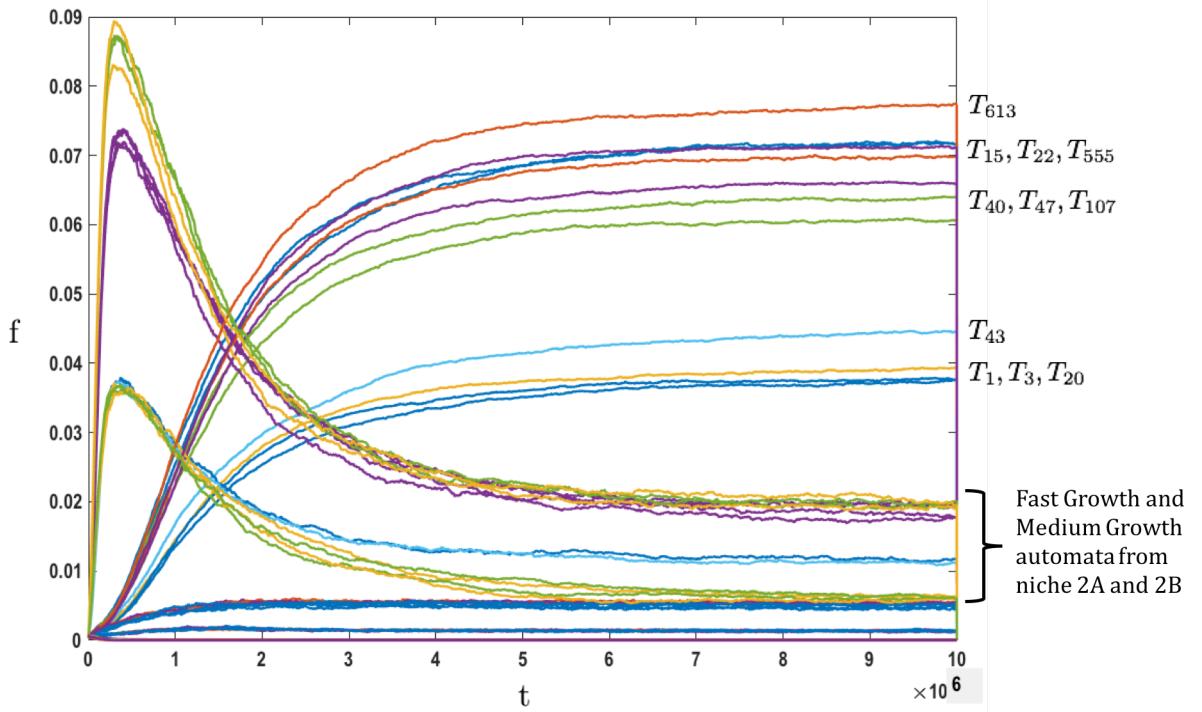


Figure 5.6: The population dynamics of a two-state automata population under conditions that emulate no diffusion ( $c = 0, v = 0$ ) which leads to the emergence of a new niche (2C). The first  $2.5 \times 10^5$  iterations follow the same trajectory as niches 2A and 2B however there is a sharp turning point thereafter with the Fast and Medium Growth groups of automata from those niches rapidly decaying. The 'No Growth' groups of automata from those niches instead experience rapid growth into two groups.

The population followed the same trajectory as the well-mixed environment (niches 2A and 2B) up to  $t = 10^5$  after which there was a turning point with the previously low frequency automata from niches 2A and 2B growing rapidly to the detriment of the previously dominant automata (see Figure 5.6). The competition between niche 2A and niche 2B was not evident and appeared to have been neutralised by the lack of spatial mixing within the population. Subsequently, the 42 automata of niches 2A and 2B co-existed within a new steady-state structure representing the new niche 2C. There were far fewer extinctions with 1,593 two-state automata types remaining in the population (280 had gone extinct). This results in a higher interaction network complexity of  $C_\mu(G) = 8.98$  bits compared to the  $C_\mu(G) = 6.02$  bits of niche 2A/2B.

### 5.3. EMERGENCE OF A TWO-STATE AUTOMATA NICHE UNDER NON-DIFFUSIVITY CONDITIONS

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label	automaton types	frequency group in 2A,2B	frequency group in 2C
A	$T_{39}, T_{60}, T_{95}, T_{102}, T_{411}, T_{493}, T_{712}, T_{775}$	high frequency	low frequency
B	$T_{36}, T_{55}, T_{402}, T_{488}, T_{717}, T_{766}$	medium frequency	low frequency
C	$T_{15}, T_{40}, T_{47}, T_{22}, T_{107}, T_{137}, T_{613}, T_{555}$	low frequency	high frequency
D	$T_1, T_3, T_{20}, T_{43}$	low frequency	medium frequency
E	$T_2, T_4, T_{81}, T_{79}, T_{106}, T_{561}, T_{120}, T_{204}, T_{121}, T_{207}, T_{417}, T_{303}, T_{421}, T_{309}, T_{617}, T_{134}$	low frequency	low frequency

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Table 5.3: The automata in the niches 2A,2B behave differently under low-diffusivity conditions. Analysis of the dynamics that is driving such different behaviour is aided by categorising the automata into the five groups (A – E) as shown.

The population transitioned through three phases (to aid in the analysis of the observed population dynamics the automata were allocated to four groups depending on their final frequency in niche 2A,2B and in niche 2C respectively as shown in Table 5.3):

Phase 1 was characterised by the extremely fast growth of the automaton groups A and B during the early stages of the simulation whilst the population was sufficiently well distributed across the lattice (thus re-producing the same dynamics as seen in the formation of niches 2A and 2B). These automaton groups quickly saturate the lattice where they are readily available for the automata in groups C and D to interact with to reproduce themselves. In this way, the A,B groups are a foodset for the C,D groups and this explains the growth in number of the automata in those latter groups C and D. This is a one-way relationship - the automata in C,D replicate themselves in interactions with the automata in A,B. The lack of any spatial mixing, and the depletion of the A,B foodset to produce more C,D automata leads to rapid precipitation of the population on the lattice leading to a marked drop-off in the diversity of interactions that can take place. Over time the rate of change in the composition of the neighbourhood of each automaton reduces significantly and this leads to a reduction in the concentration of the A,B automata groups.

Phase 2 marked a rapid transition of the structure of the population with the sudden and rapid decay of automata in the groups A and B and the continued growth of the automata in the C and D groups. The production advantage of groups A and B - that they self-replicate in any interaction with other members of their group leading to a higher intensity of production - becomes a disadvantage as this requires ready access to the other automata in their group and this was severely curtailed by the immobile population. By

comparison, the automata in groups *C* and *D* continue to be produced by the automata in groups *A* and *B* even whilst those groups are decaying. Simultaneously, groups *C* and *D* benefited from a 'lock-in' phenomenon whereby they did not readily interact with other expanding domains that shared the *A,B* foodset. This combination of maximising the foodset of groups *A,B* in a one-way beneficial relationship whilst not interacting readily with automata with similar characteristics meant that these domains of automata were very robust structures on the lattice. Such a 'replicate and lock-in' mechanism proved to be an effective survival strategy. However, it was not the only survival mechanism observed - an interesting observation was that the *A,B* automata did not go extinct and this was due to a 'mutual maintenance' mechanism whereby these automata would mutually produce each other whilst also performing self-replication. This had the effect of maintaining a more dynamic domain boundary between these domains that was able to partly counteract the 'lock-in' strategy of the automata in groups *C* and *D*.

Phase 3 is characterised by the extinction of a large number of automata which significantly reduces the diversity of the interaction network. Consequently, the number of possible interactions with which to maintain the remaining population of automata were significantly reduced and parity was seen in the interaction network. At this point the established domains were able to maintain their concentration across the lattice through the two competing processes of 'mutual survival' and 'replicate/lock-in' and this led to the emergence of the steady-state structure of niche 2*C*.

Chapter 6 provides a more detailed explanation of the competing mechanisms and the spatial dynamics that lead to the formation of niche 2*C*.

## 5.4 Emergence of a two-state automata niches under influx conditions

A population of 90,000 two-state automata consisting of 1,873 unique types (with an average of 48 of each type) were randomly distributed on a 300 by 300 lattice. Simulations were run for  $5 \times 10^7$  iterations under environmental conditions of no diffusive mixing ( $c = 0, v = 0$ ) and an influx of external automata at (i) a moderate rate ( $0.1 < \Phi \leq 0.7$ ), (ii) a high rate ( $0 < \Phi \leq 0.9$ ), and (iii) a very high rate ( $0.9 < \Phi \leq 1$ ).

With the influx rate in the range  $0 < \Phi \leq 0.7$  the niches 2*A* or 2*B* emerged albeit their formation was delayed when compared to an influx rate of  $\Phi = 0$  (as described in section 5.2). The higher the influx rate the longer the delay in formation of the niche. A similar observation was made about the one-state population (see Chapter 4).

#### 5.4. EMERGENCE OF A TWO-STATE AUTOMATA NICHES UNDER INFLUX CONDITIONS

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With the influx rate in the range  $0.7 < \Phi \leq 0.9$  a new niche (2D) formed (see Figure 5.7). This niche was characterised by the co-existence / co-habitation of niches 2A and 2B within the same space. The influx of automata had interrupted the intense competition in the earlier stages of evolution of the population and that would ordinarily lead to the punctuated equilibrium event observed previously. Under these conditions all automaton types survived leading to a more complex population structure.

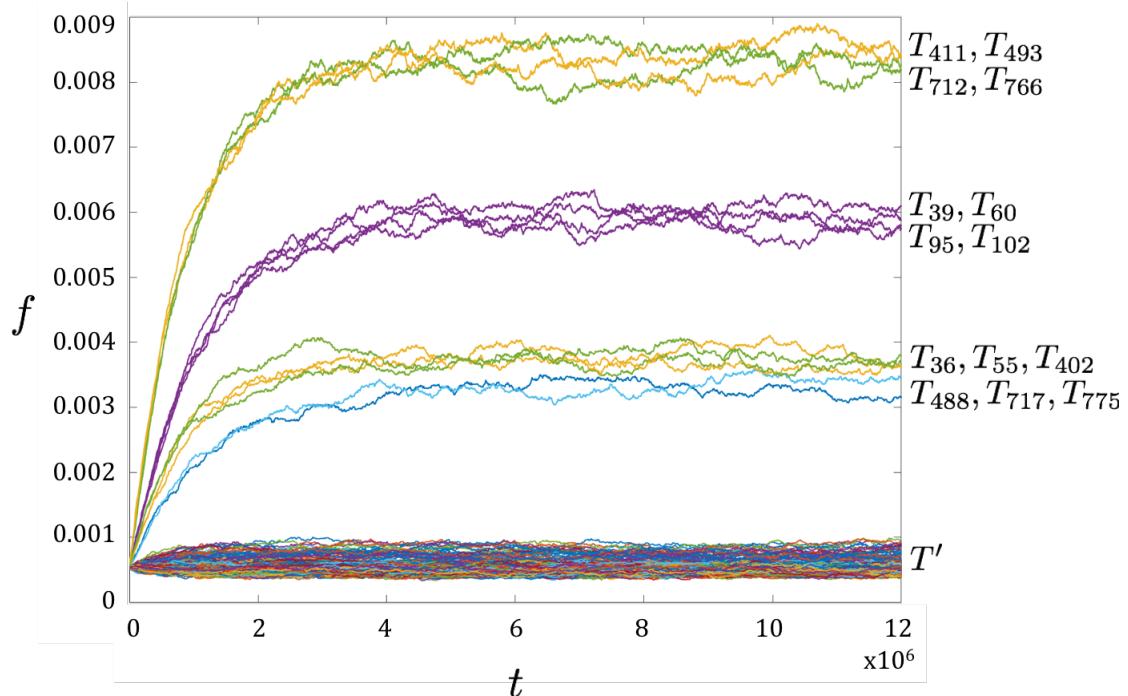


Figure 5.7: The emergence of niche 2D in the presence of an influx of external automata through random replacement at a rate  $0.7 < \Phi \leq 0.9$  had the effect of neutralising the initial competition between the niche 2A and 2B automata leading to their co-existence in the population. The three clusters of automata that have undergone significant growth from  $t = 0$  consist of equal numbers of automata from niches 2A and 2B e.g.  $T_{411}, T_{712}$  from niche 2A and  $T_{493}, T_{766}$  from niche 2B, and so on.  $T'$  represents all other automaton types in the population.

Finally, with  $0.9 < \Phi \leq 1$  there was a lack of any structure in the population as the replacement of automata on the lattice was dominated by externally generated automata. This had the effect of negating any structural 'memory' that the population could generate leading to an unstructured state. Whilst this state didn't represent a structured population, it was a possible state that could be reached by the population and, as such, was designated as niche 2E (see Figure 5.8).

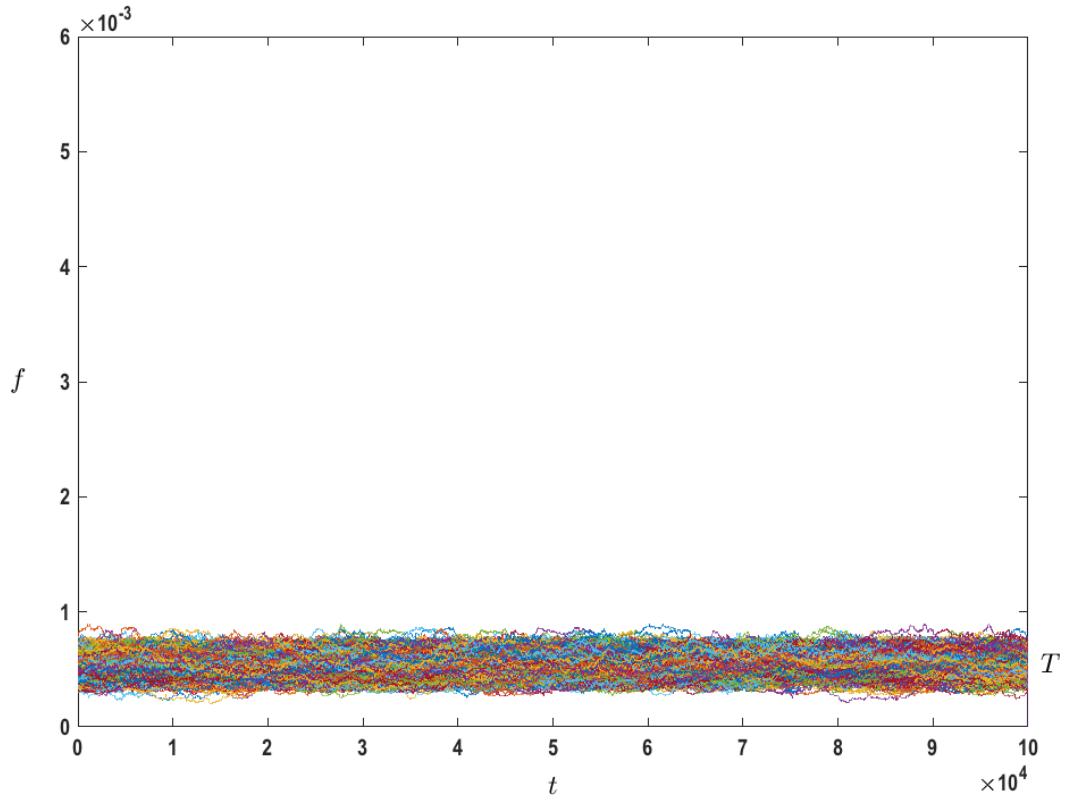


Figure 5.8: The emergence of niche  $2E$  in the presence of a very high rate of influx of external automata through random replacement at a rate  $0.9 < \Phi \leq 1$  and that leads to an unstructured population. The majority of new automata that were being introduced into the population were generated externally.

## 5.5 Quantitative Analysis of Niche Structures

The information content and complexity of each niche was measured by calculating their average structural complexity ( $C_\mu(T)$ ), their information content ( $H(f)$ ) and their interaction network complexity ( $C_\mu(G)$ ) respectively.

measure	niches				
	2A	2B	2C	2D	2E
average structural complexity ( $C_\mu(T)$ )	0.95	0.95	0.94	0.94	0.94
production threshold ( $H(f)$ )	3.03	3.03	5.05	7.99	10.87
interaction network complexity ( $C_\mu(G)$ )	6.02	6.02	8.98	11.58	18.43

Table 5.4: Comparison of (a) the average structural complexity ( $C_\mu(T)$ ) showing that the more highly structured niches consist of marginally more complex automata, (b) the information content ( $H(x)$ ) for each niche indicating an increase in the amount of information required to re-construct each niche as environmental disturbances are increased, and (c) the interaction network complexity  $C_\mu(G)$  which is an overall measure of the complexity of the niche and, as can be seen, the complexity of the niches increase with changes in environmental conditions. All measures were generated using the final frequency distribution of the automata in each niche (i.e. the population structure).

As can be seen niches 2A and 2B constitute a population of automata that were marginally of a higher average structural complexity compared to the other niches. The range of structural complexity in the complete two-state population was 0.72 bits to 1 bit compartmented into eight discrete and well-defined values:

$C_\mu(T)$ bits	0.722	0.845	0.89	0.971	0.918	0.985	0.998	1
No. automata	56	168	48	48	408	432	368	345

Table 5.5: The structural complexity measurements were compartmented into eight discrete and well-defined classes demonstrating the structural variation in the topology of the two-state automata population

By comparison, the range of structural complexity per automata in niches 2A or 2B were 0.92 to 1 bits suggesting that the niche automata resided in the higher structural complexity classes. Given that 99% of the population went extinct as niches 2A and 2B formed it can be surmised that the lower structural complexity automata were removed from the population. As such, the most highly structured niches consisted of a very small number of automata each of which had a higher-than-average structural complexity.

The production threshold - that is, the amount of information required to generate the niche - increased with the degree of environmental disturbance present during the formation of the niche. This was to be expected given that niches 2A and 2B consist of only 21 automata each compared to 1,593 automata in niche 2C, and 1,873 automata in niches 2D and 2E. The lower  $C(\mu)(G)$  value for niche 2D compared to 2E was due to the increased structure present in that niche.

Similarly, the interaction network complexity - the information required to describe the niche after it had evolved to a steady-state distribution and the possible interactions in that population - increased with the magnitude of environmental disturbance.

## 5.6 Summary

This chapter has simulated a two-state automata population evolving to five different information niches under various environmental conditions. The following niches were discovered:

1. Niche 2A and 2B emerged under well-mixed conditions with the population undergoing an initial period of intense competition with two groups of 21 automata each emerging as highly competitive, strongly connected networks that co-exist until  $2.5 \times 10^5$  at which point a 'punctuated equilibrium' event occurs with one of the groups spontaneously undergoing rapid decay leaving the remaining group to come and dominate the population. Repeated simulation runs reveal that either group can come to dominate leading to the formation of two separate niches 2A and 2B. The stochastic nature of the information niche model means that it was not possible to predict which niche would be likely to emerge as the 'winner'. Either niche was particularly robust and persisted even in the presence of an influx of externally generated automata (in the range  $0 \leq \Phi < 0.7$ )
2. Niche 2C emerged under low diffusivity conditions leading to the co-existence of the two groups of automata that had previously competed (leading to the formation of niche 2A or 2B). However, the previously low frequency automata of those niches now dominate leading to a different steady-state structure that constituted a new niche (2C). Two competing mechanisms were identified - the 'replicate/lock-in' and 'mutual maintenance' processes - which were not observed in the one-state information niche simulations. This suggests that a population with a higher average structural complexity generates concurrent mechanisms of competition and survival that lead to more complex competitive dynamics. These mechanisms are explored in more detail in Chapter 6.
3. A high level of influx of externally generated automata ( $0.7 \leq \Phi \leq 0.9$ ) had the effect of neutralising the competition between the two competing niches (2A,2B) leading to their co-existence in the population. The resulting steady-state organisation was designated as niche 2D.
4. With a very high rate of influx of external automata ( $0.9 < \Phi \leq 1$ ) the degree of disturbance was such that no structure emerged in the population. This was due to the loss of any 'history' of the populations endogenous productions meaning that no single automata could maintain a growth trajectory. The converse was also true in

that this also meant that uncompetitive automata could also not maintain a decay trajectory. The result was a homogenous state of the population known as niche  $2E$ .

Furthermore, the following general observations were made:

1. Two highly competitive automata groups emerged that had the following properties:  
(i) strongly connected networks of production ensuring that each member of the network was produced in equal number thus ensuring (ii) the dynamic stability of the network. This is consistent with the findings from simulating the information niche model with a simpler, one-state population of automata (see Chapter 4).
2. A two-state population of automata has a higher average structural complexity than produced more complex population dynamics than in a one-state population with zero structural complexity. For example, the two highly competitive groups of automata that emerged could co-exist under conditions where there was a high rate of influx of externally generated automata, whilst they competed intensely until the 'death' of one of groups under well-mixed ( $c = N, v = n$ ) and closed conditions ( $\Phi = 0$ ). This may be an indication that increasingly complex automata populations may be able to support numerous niches simultaneously. This is discussed further in Chapter 10.
3. The information niche model with a significantly larger and more diverse population did not generate an increased number of niches for the range of environmental conditions simulated. The two environmental parameters used to simulate environmental disturbances - spatial mixing and an influx of externally generated automata - may be a constraint on exhaustively examining the theoretical range of possible structural states of a two-state population. This is discussed further in Chapter 10.



## RESULTS III - SPATIAL PATTERNS

### 6.1 Introduction

This chapter presents the results of investigating the spatial patterns that formed on the lattice ( $\Gamma$ ) during the formation of one-state and two-state information niches under certain environmental conditions. Niche 1B from the one-state population and niche 2C from the two-state population emerged under non-diffusive conditions and were of particular interest as the lattice configuration demonstrated domain and boundary patterns. Autopoietic theory suggests that some form of compartmentation is required for the emergence of an autopoietic system [9]. Whilst this requirement is debatable (as discussed in Chapter 10) the formation of such structures warranted study.

### 6.2 Pattern formation on the lattice of a one-state information niche

The spatial configuration and topological structure associated with the emergence of the steady state niche 1B produced in the absence of both lattice site ( $\Gamma_{i,j}$ ) diffusion and influx of randomly generated automata ( $\Phi = 0$ ) was investigated. Compared with information niches 1A, 1C and 1D, which showed no spatial structure due to lattice diffusivity, a distinct spatial configuration was associated with niche 1B (see Figure 6.1a,b). This result was similar to that reported in [108]. In particular, amongst the two survival clusters,

the high frequency ( $T_2$ ,  $T_4$ ) group was de-mixed into a bi-continuous structure of  $T_2$ - and  $T_4$ -rich domains that were separated by a thin boundary layer comprising a low frequency population of  $T_1$  and  $T_8$  automata. The latter form specifically at the interface due to the non-commutative functional compositions:  $T_2 \circ T_4 = T_1$  and  $T_4 \circ T_2 = T_8$ . Growth of the  $T_2$ - and  $T_4$ -rich domains occurred through the generation of new members specifically in the boundary regions comprising an interfacial 'double-layer', and was associated with continuous repair of the ( $T_1, T_8$ ) boundary (Figure 6.1c-f).

## 6.2. PATTERN FORMATION ON THE LATTICE OF A ONE-STATE INFORMATION NICHE

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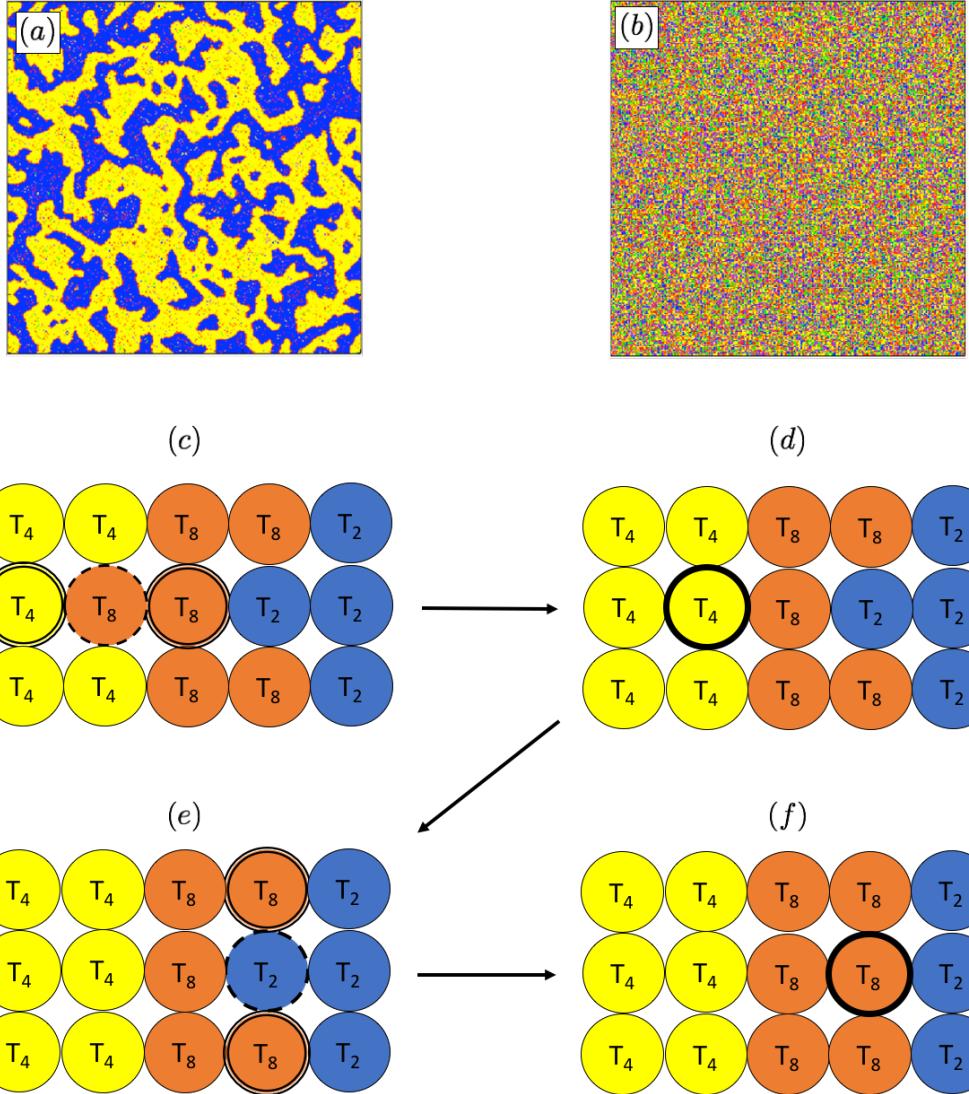


Figure 6.1: (a) Four-colour coded map showing the spatial configuration of the lattice associated with the emergence of niche 1B. A distinct topological structure consisting of a bi-continuous arrangement of  $T_2$ (blue)- and  $T_4$ (yellow)-rich domains separated by a thin interfacial layer of  $T_1$  (red) and  $T_8$  (orange) automata are shown; lattice  $x$  and  $y$  axes run from  $1 \rightarrow n$  from the top-left corner to the bottom-right, and  $(x,y)$  provides a unique index for each automaton sited on the lattice  $\Gamma_{x,y}$ . (b) Typical colour-coded map for niches 1A, 1C, or 1D showing no spatial structure due to the presence of spatial mixing. (c-f) Example of lattice domain growth (c,d), and boundary repair (e,f) for niche 1B: (c) A boundary automaton of different type to the adjacent domain automaton ( $T_8$ ; dashed circle) is randomly selected for replacement, and the interacting neighbours selected with a 25% probability are the functional composition  $T_8 \circ T_4$  (double circles). (d) As  $T_8 \circ T_4 = T_4$ , automaton  $T_4$  replaces  $T_8$ , thus leading to an increase in the size and coherence of the  $T_4$  domain. (e) In a later iteration, a  $T_2$  domain automaton, surrounded by three boundary automata is randomly selected to be replaced, (dashed circle), and the selected interacting neighbours are  $T_8 \circ T_8$  (double circles). (f) As  $T_8 \circ T_8 = T_8$ , automaton  $T_2$  is replaced by  $T_8$ , resulting in repair of the boundary and shrinkage of the adjacent domain. Thus, whilst growth of the domains produces a temporary decay in the boundary, the defects are subsequently repaired at the expense of another automaton in the adjacent domains. This dynamic produces a bi-continuous spatial configuration after  $10^7$  iterations as shown in (a). However, over a very large number of iterations ( $t \gg 10^7$ ), either the  $T_2$  or  $T_4$  domain completely dominated the lattice, resulting in extinction of all other automaton types and formation of a homogeneous population. Repeated simulations indicated that the eventual outcome was primarily due to the stochastic nature of the replication process and initial random configuration of the automata on the lattice.

Figure 6.1 illustrates the expansion of domains via. the outward growth of a boundary. Only four automaton types remain from a population of 15 automaton types and, under well-mixed conditions these types would experience no growth and they only maintain their concentration. However, under zero diffusivity conditions these automata become very competitive and come to dominate the population with the extinction of the other 11 automaton types.

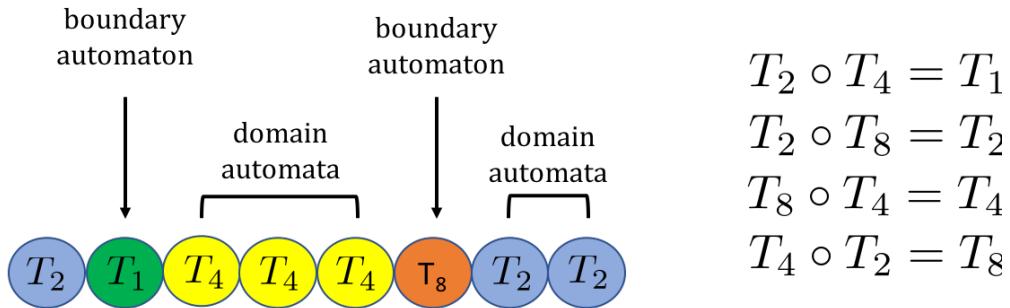


Figure 6.2: Illustration of the spatial configuration of niche 1B that consists of four automata types that take on two specific roles as domain and boundary automata.

Figure 6.2 illustrates the domain and boundary roles that the four automata  $T_1, T_2, T_4, T_8$  spontaneously take on under low diffusivity environmental conditions. Specifically, in this configuration:

$T_1, T_8$  self-replicate and are self-sustaining along the interface between the  $T_2$  and  $T_4$  domains.

$T_1$  was created by the interaction of  $T_2$  with  $T_4$  and hence wherever those two domains came into direct contact the boundary automaton  $T_1$  was produced

$T_2$  was created from the interaction of  $T_8$  with itself and also between  $T_1$  and itself. As such, formation of the  $T_2$  domain was totally dependent on the presence of boundary automata.

Similarly,  $T_4$  was created from the interaction of  $T_8$  and itself and also between  $T_1$  and itself. As such, the formation of  $T_4$  is dependent on the presence of boundary automata.

$T_8$  was created by the interaction of  $T_4$  and  $T_2$  and hence wherever those two domains came into direct contact the boundary automaton  $T_8$  was produced

Hence,  $T_2$  and  $T_4$  did not produce each other however they did participate in maintaining the boundary automata between their respective domains. These four automaton types formed an elementary network (dynamically stable, strongly connected) with specific spatial roles: two domains ( $T_2, T_4$ ) and two boundaries ( $T_1, T_8$ ) - that emerged from population interactions being restricted to immediate local neighbours. These automata types were the only combination of automata that produced each other in a manner whereby each domain could produce the boundary but it could not produce itself nor the other domain. By comparison, the boundary automata could produce themselves and the domain automata. This led to the 'protected outgrowth' of each domain because (a) decay of a domain could only occur via boundary dynamics and hence the interior of each domain was protected from being directly changed, and (b) the encroachment of a boundary into another domain enabled the other (competing) domain to expand into the space created by the extension of the boundary. Hence, the unique relationships between these four automata - that were competing with each other - a competitive strategy emerged which was subsequently termed 'protected outgrowth'. There was no evidence of the emergence of alternative competitive strategies from the interaction networks of other automata types which subsequently were expelled from the population.

### **6.3 Pattern formation on the lattice of a two-state information niche**

The spatial configuration and topological structure associated with the emergence of the steady state niche 2C produced in the absence of both lattice site diffusion ( $c = 0, v = 0$ ) and influx of randomly generated automata ( $\Phi = 0$ ) was investigated. Examination of the lattice did not indicate the presence of any automata that form and are maintained specifically at domain boundaries as was the case with niche 1B and instead the domains were in direct contact with each other (see Figures 6.6 and 6.5). The edge of a boundary was characterised as a mutually exclusive zone between two domains i.e. no possible interactions existed between adjacent domain automata and therefore no new automata could be produced at the interface between those domains.

Large regions of homogenous domains of automaton types formed from either:

- (a) automata with the ability to self-replicate and to mutually produce other self-replicators. Examination of the lattice revealed the motif of a domain surrounded by another (see Figure 6.5). This compartmentation of the interior domain was a result of two domains of automata mutually producing each other at their interface

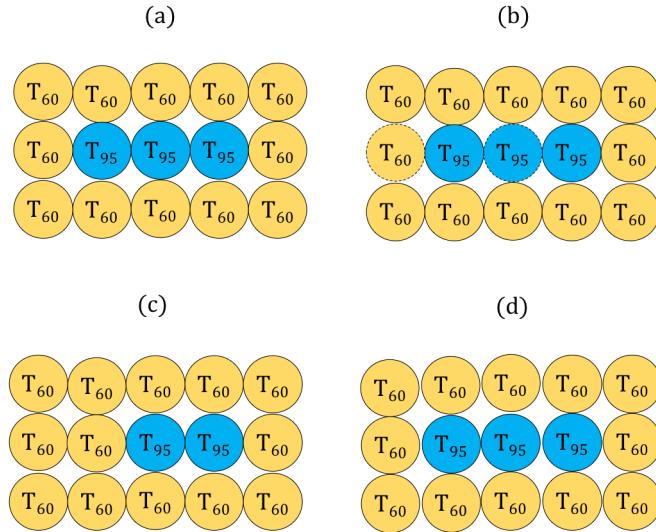


Figure 6.3: Illustration of the *mutual maintenance* strategy that emerged for a small group of automata under conditions of low diffusivity on the lattice. The example automata here are  $T_{60}$  and  $T_{95}$  which self-replicate and produce each other in any interactions between them: (a) a small subsection of the lattice illustrating the  $T_{60}$  automaton type surrounding the  $T_{95}$  automaton, (b) two automaton types are selected to interact  $T_{60} \circ T_{95} = T_{60}$ , (c) the interaction produces a new  $T_{60}$  automaton which replaces the  $T_{95}$  that was previously at that location, and (d) a sample of the same sub-section of the lattice at a later point in time indicates that the  $T_{95}$  has now successfully replicated itself in its interactions with the  $T_{60}$  automata according to  $T_{95} \circ T_{60} = T_{95}$

whilst simultaneously self-replicating within their interior (see Figure 6.3). This proved to be a reasonable survival strategy and the automata exhibiting such 'mutual maintenance' behaviour remained in the population albeit at a low frequency.

(b) used the automata in (a) as a foodset to produce themselves in non-reciprocal interactions thus leading to outgrowth from a 'seed' automata. This growth continued whilst there was either a sufficient foodset available in the neighbouring lattice sites, or until the outer edges of the domain met another domain with which it could not interact thus forming a hard domain boundary (see Figure 6.4). Once a domain was surrounded by other automata with which it could not interact no further growth - nor decay - of the domain was possible. In this way, and over time, all of the domains of this type became 'locked in'. This mechanism of domain growth followed by lock-in was a survival strategy adopted by the automata that came to dominate the niche. Such a competitive strategy emerged from the intrinsic information processing properties of the automaton and the nature of the properties it held with other automata in the population.

### 6.3. PATTERN FORMATION ON THE LATTICE OF A TWO-STATE INFORMATION NICHE

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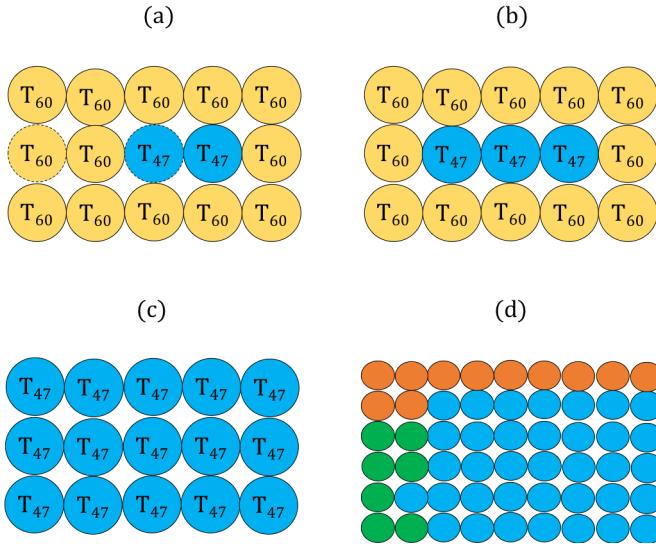


Figure 6.4: Illustration of the *replicate / lock-in* strategy that emerged during the simulation: (a) the  $T_{60}$  is a self-replicator and highly produced automaton that grew in number significantly in the earlier stages of the simulation and is highly concentrated on the lattice. Here it has surrounded the  $T_{47}$  which is a network replicator (i.e. it needs to interact with other automata apart from itself to produce replicants of itself), (b) in any interaction between these two automata the  $T_{47}$  automaton is produced and, as is seen here, replaces the  $T_{60}$  automaton, (c) this outward growth of the  $T_{47}$  automaton into the  $T_{60}$  rich lattice continues with the latter automaton acting as a foodset, and (d) this process continues until the  $T_{47}$  domain meets other domains consisting of automata that are also using the  $T_{60}$  type automata as a foodset. Where these domains meet the growth of the domain ceases as these automata do not interact with each other and, as such, these domains effectively become 'locked in' and no further growth of the domain occurs in the direction of the opposing domain.

These concurrent mechanisms of survival in the niche - 'replicate & lock-in' and 'mutual maintenance' - were in competition throughout the simulation. As discussed in section 5.3, as the population precipitates on the lattice (i.e. the frequency of changes to and the diversity of the neighbourhood of an automaton decreases as the simulation progressed) the selfish behaviour of the 'replicate & lock-in' automata became more effective. By comparison, the 'mutual maintenance' automata were dependent on the presence of other automaton in their neighbourhood with similar intrinsic properties that supported this survival mechanism. Figure 6.6 illustrates how these competing processes were reflected in both the patterns that emerged on the lattice over time and also in the time-series observations of the frequency distribution of the population.

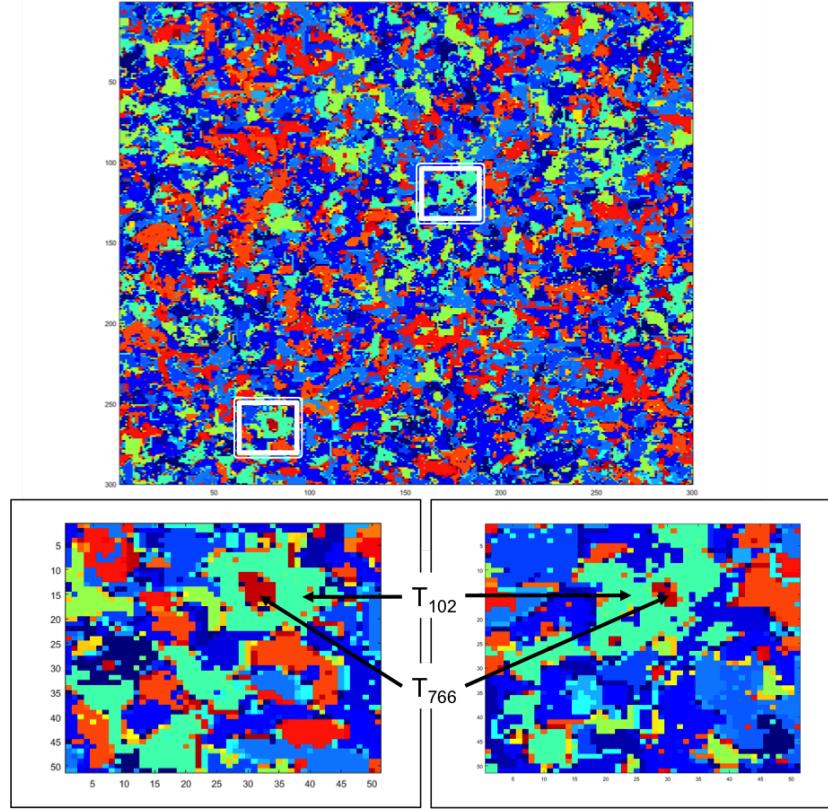


Figure 6.5: The spatial patterns of the lattice for the niche  $2C$  at  $5 \times 10^6$  showing two areas of interest where the  $T_{766}$  automaton is surrounded by the  $T_{107}$  automaton indicating the presence of the 'mutual maintenance' survival mechanism.

## 6.4 Summary

This short chapter has examined the spatial patterns that form on the two-dimensional lattice of the one-state information niche  $1B$  and the two-state information niche  $2C$  both of which emerged under low-diffusivity environmental conditions ( $c = 0, v = 0, \Phi = 0$ ). Both niches formed elaborate spatial patterns on the lattice that were characteristic of distinct domains and boundaries between those domains.

- Niche  $1B$  formed two domains each composed of a single automaton  $T_2$  or  $T_4$  that compete through a mechanism of 'protected outgrowth' whereby each domain is seeking to extend its boundary via. production of the boundary automata that separate the domains ( $T_1, T_8$ ) into the space of a competing domain. This competitive process leads to the formation of complex spatial patterns that are reminiscent of

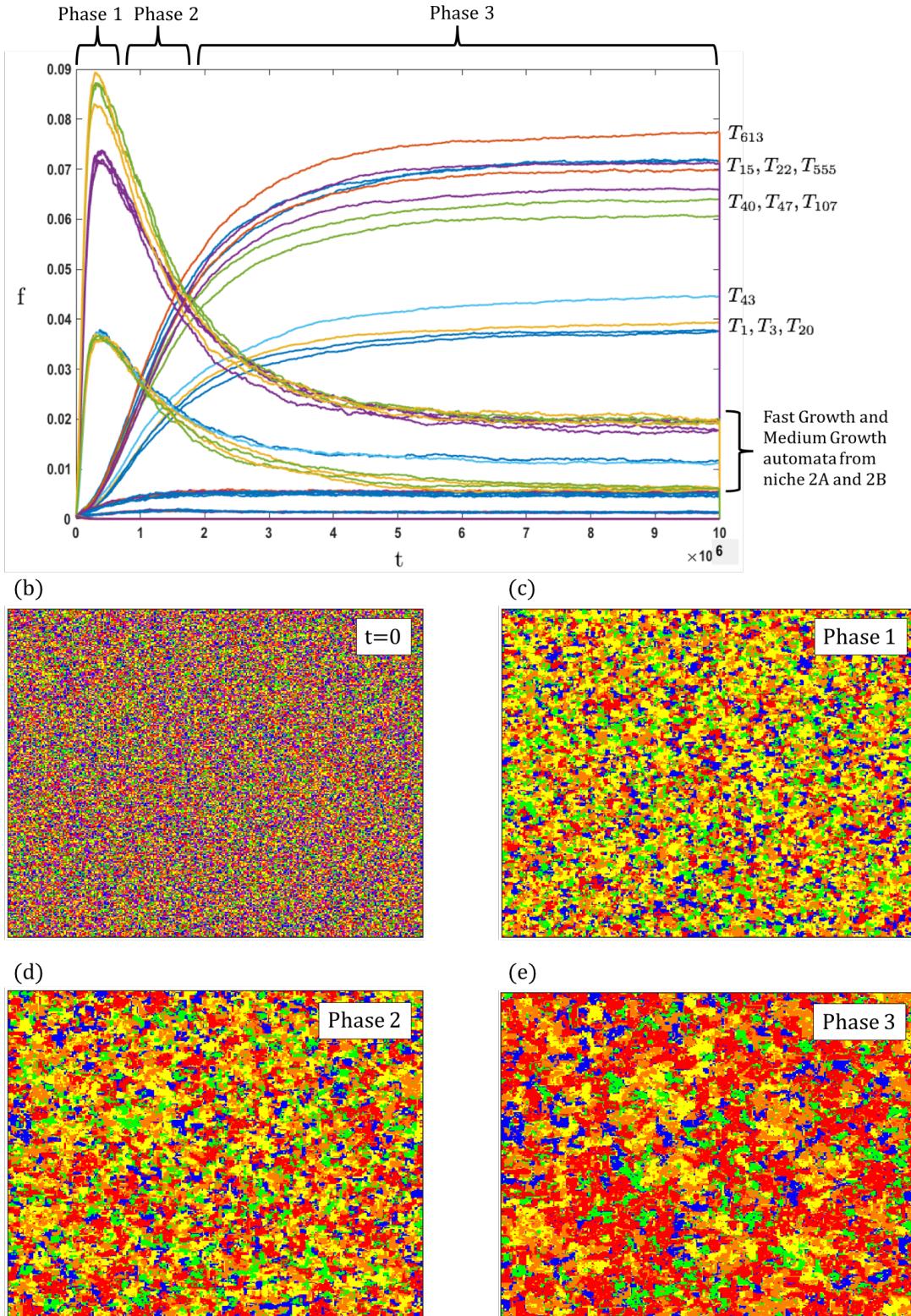


Figure 6.6: Evolution of niche 2C illustrated by the spatial patterns during the different phases of the evolution of niche 2C: (a) the time-series of the frequency distribution of the population with the three phases of evolution indicated, (b) the state of the lattice at  $t = 0$  with the 1,873 two-state automata types randomly distributed across the 300 by 300 lattice, (c) the lattice at  $t = 0.5 \times 10^6$  indicating the peak of concentration of the small subset of 14 automaton types that self-replicate and mutually produce each other (yellow regions), (d) the lattice at the start of the crossover point (at  $t = 1.5 \times 10^6$ ) where the dominant automata from Phase 1 have decayed significantly as they were used as the foodset for the production of automata which had now replaced them as the dominant automata in the niche (red, orange and blue regions), and (e) the final state of the lattice at  $t = 10 \times 10^6$  with increased dominance of the lattice by the 'replicate & lock-in' automata.

those discovered in physical systems such as spinodal decomposition (see Chapter 10). The non-trivial dynamics that lead to the evolution of such spatial patterns was surprising given that a very small population of just four automata was responsible for such complexity.

- Niche 2C formed domains that were not composed of any boundary automata. Rather the domains were immediately adjacent to each other. Two competing mechanisms were identified - 'replicate & lock-in' and 'mutual maintenance' - with the automata that were part of the former the most competitive and coming to dominate the population. The automata operating as part of the latter were still present in the population over extended periods of time and, hence, were judged to be operating an effective survival strategy. Both of these mechanisms arose as a result of the intrinsic information processing capability of different automata types and the relationships between them.
- Automata operating the 'replicate & lock-in' strategy would produce themselves in the vast majority of interactions with other automata and, critical to their success, in any interaction with the group of automata that grow exponentially at the beginning of the simulation. This rich foodset of self-replicating and fast growing automata rapidly populated the lattice, however, as they met the 'replicate & lock-in' automata they were unable to compete as they were transformed into these other automata without any reciprocation. This rapid transformation of the fast-growing self-replicating automata to replicate themselves proceeded until these domains reached other domains of similar types of automata with which they were unable to *not* interact. This resulted in mutually exclusive zones of production at the interface of these domains that prevented further growth of those domains (hence the 'lock-in' aspect of this mechanism).
- By comparison, the 'mutual maintenance' domains consisted of self-replicators that were effective at dynamically reproducing other self-replicating automaton domains at their interface. This had the effect of maintaining the domains of self-replicators in proximity to other self-replicating domains. However, this was not an effective strategy for expanding the domains across the lattice but it was an effective strategy for protecting and maintaining the co-operating domains.
- The information niche model has demonstrated non-trivial spatial patterning on the lattice in a one-state and two-state automata population. Three novel, competing mechanisms emerged through the intrinsic information processing nature of the

automata and the relationships between them and these directly led to the formation of the spatial patterns observed. Whether a 2D lattice with discrete, fixed locations for automata - the lattice is technically an asynchronous cellular automata model - is a constraint on all possible spatial dynamics of a one-state or two-state automata population is discussed in Chapter 10.



## RESULTS IV - INTERACTING ONE-STATE AND TWO-STATE INFORMATION NICHES

### 7.1 Introduction

A key characteristic of an autopoietic system is its ability to maintain its identity in the presence of external disturbances. The process by which it does this is called cognition [13] which can be decomposed into two steps [2] (see Figure 7.1):

1. Assimilation. A change in the internal structure of the system via. the absorption in some way of elements that are presently external to the entity and their subsequent integration into the inner processes of the entity, whilst maintaining the original identity and viability of the system. This process is termed *assimilation* and it leads to a *temporary* change in the entity's structure without any loss of its global organisation. Entities that are able to contribute to the production processes are said to be actively assimilated whilst those entities that are more neutral and non-participatory are deemed to be passively assimilated with the latter type eventually being expelled from the system [14].
2. Accommodation (or Adaptation as per [2]). A disturbance that permanently changes the autopoietic system and leads to a re-organisation of the system. This *discrete evolution* of the autopoietic system [13] equips the recently modified system to process further disturbances of the same kind in a more efficient way. The re-organisation must continue to re-generate an autopoietic system.

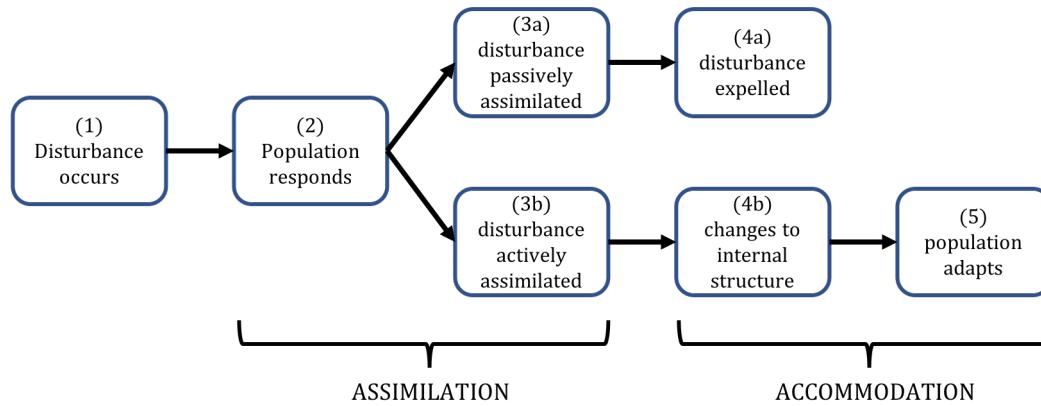


Figure 7.1: The cognition process [2] within the context of an automata population indicating the two types of adaptation that can occur: (a) assimilation where a new entity or disturbance becomes part of the structure of the system without changing its overall organisation, and (b) accommodation where a new entity or disturbance triggers a re-organisation of the system without loss of identity.

This chapter is part one of a two part investigation into cognition in a self-producing population of one-state and two-state automata. The focus of these simulations was on the effect of material disturbances either through the influx of externally generated automata from an established neighbouring niche or the co-location of automata from two previously separate populations. Two specific questions were posed: (i) does the identity of either a one-state or two-state niche re-generate and emerge even when co-located with other automata?, and (ii) does the identity of an established niche maintain itself or is it lost in the presence of material disturbances?

The second part of investigating cognition is covered in Chapter 8 which examined the effect of information as environmental 'noise' on the formation of a one-state niche.

## 7.2 Simulation Set-up

Two developments were made to the information niche model:

1. Allow an influx of automata from an established two-state niche (2A) into an existing one-state niche (1A)

A two-state population under well-mixed conditions was generated to a steady-state structure that corresponded to niche 2A (see chapter 5). In addition, a one-state population under well-mixed conditions was also generated to a steady-state structure that corresponded to niche 1A (see chapter 4). The simulation model was extended to handle the productions that arose from the interactions between

the one-state and two-state automata that constituted these niches. The model was configured so that there was a unidirectional flow of two-state automata into the one-state population.

## 2. Co-located one-state/two-state automata populations

A joint one-state/two-state population was evolved from an initially uniform state under well-mixed conditions. This required the *a priori* generation of a joint interaction network matrix ( $G_{1,2}$ ) of 1,888 unique automata types representing 400,744 interactions that produced one-state and two-state automata exclusively: 207 interactions exclusively between one-state automata, 355,484 interactions exclusively between two-state automata and 45,053 interactions between one-state and two-state automata. This joint one-state/two-state population had an initial interaction network complexity of  $C_\mu(G) = 18.61$  bits, an average structural complexity of  $C_\mu(T) = 0.93$  bits, and a production threshold of  $H(f) = 7.45$  bits.

Once these enhancements were developed and tested the following simulations were performed:

- Simulation of an intermixed one-state and two-state population consisting of 1,888 automaton types under well-mixed (section 7.3) and low diffusivity conditions (section 7.4)
- Automata from the niche 1A consisting of nine one-state automata combined with the automata of the niche 2A consisting of 21 two-state automata simulated firstly under uniform initial conditions (section 7.5) and secondly with the initial distribution of automata corresponding to the proportions of each automata type as per their original niche structures (section 7.6)
- An established two-state automata niche 2A disturbing the one-state niche 1A via. the influx of a single two-state automaton per time step at a rate  $\Phi = 0.5$  (see section 7.7)

### 7.3 The dynamics of a joint one-state/two-state population under well-mixed conditions

The joint population consisted of all 15 one-state automaton types ( $T_{1..T_{15}}$ ) and all 1,873 two-state automaton types ( $T_{16..T_{1888}}$ <sup>1</sup> representing a total of 1,888 unique automata types. An interaction matrix  $G$  was generated that identified 400,744 interactions between all one-state and two-state automata: 207 of those interactions were exclusively between one-state automata, 355,484 interactions were exclusively between two-state automata and 45,053 interactions were new interactions between one-state and two-state automata. In all cases only interactions that produced one-state and two-state automata were allowed and added to the joint interaction matrix. The characteristics of this interaction network is shown in Figure 7.2.

The joint one-state/two-state population had an initial interaction network complexity of 18.61 bits and an average structural complexity of 0.93 bits. The population was distributed across a 300 by 300 lattice with an average count of 48 of each type of automaton. The simulation was run under well-mixed conditions ( $c = N, v = n, \Phi = 0$ ) for  $10^7$  iterations (see Figure 7.3).

From an initial population of 1,888 automaton types only 35 automaton types remained. The composition of the surviving population was:

- All nine of the one-state automata types present in niche 1A and that accounted for 98% of the joint population. The one-state niche (1A) had therefore successfully re-generated its identity with a slightly altered structure with the proportional difference between automata more accentuated with  $T_{15}$  more populous than in the original niche. Examination of the interaction network revealed that from the beginning of the simulation a total of 172,239 interactions could produce the one-state automata.
- 20 of the 42 automata that represented most of the Fast Growth/Medium Growth category automata from niches 2A/2B which, collectively, occupied 1.99% of the joint population. Niches 2A and 2B therefore did not re-generate in the joint population. Only the high performing two-state automata from those niches were able to survive.
- Very low frequency (0.01%) of six two-state automata that do not belong to any previously observed niches were being continually produced. The presence of one-

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<sup>1</sup>the indexing used to identify each unique automaton type was  $i = 1 \rightarrow 1,8888$  and so automaton type  $T_{16}$  in the joint population corresponds to the two-state automaton type  $T_1$  and automaton type  $T_{1888}$  corresponds to the two-state automaton type  $T_{1873}$  from the two-state population as per Chapter 5

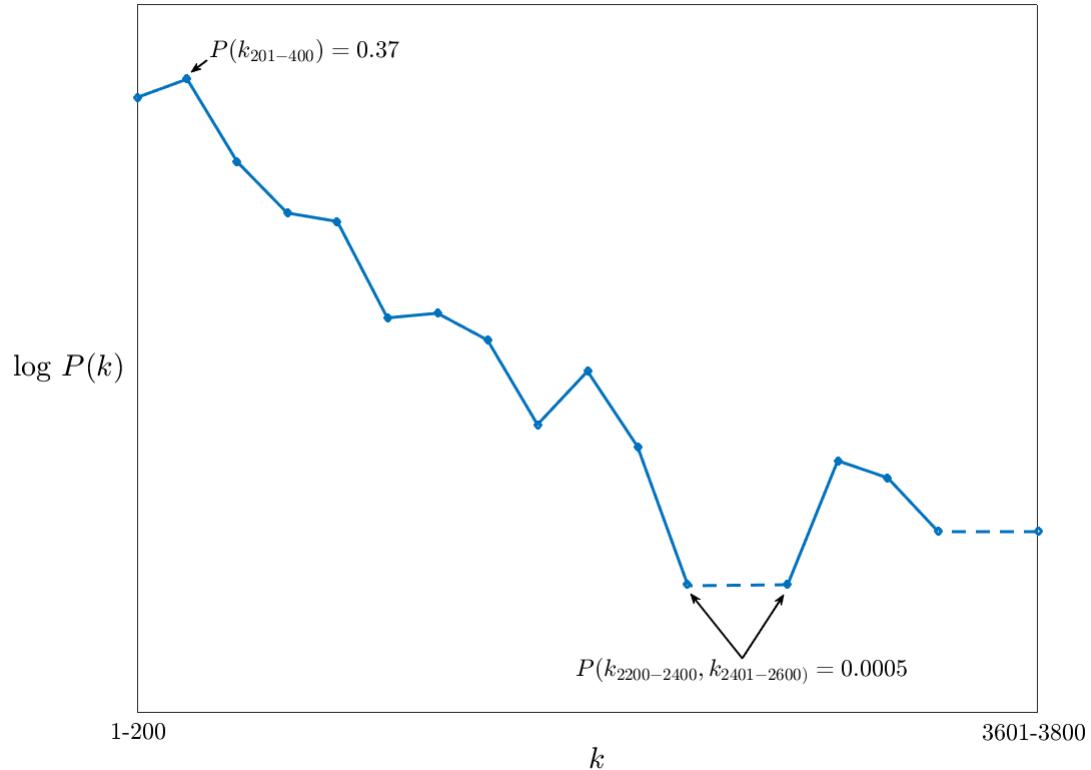


Figure 7.2: The degree distribution of the joint one-state/two-state interaction network. The  $x$ -axis was the  $k$  values (incoming and outgoing links from each node in the network) allocated into bins of width 200. The  $y$ -axis are the  $\log P(k)$  values for each of the  $k$  bins. As can be seen the large majority of nodes in the network have fewer than 400 edges whilst a very small number of vertices have a large number of edges indicating a heterogenous network structure with a small number of highly connected 'hubs'. Compared to the two-state interaction network the joint one-state/two-state network has more hubs (with  $> 2,000$  edges) due to the inclusion of the highly connected one-state automata.

state and two-state automata had led to the continual production of the automata  $T_{21}$ ,  $T_{24}$ ,  $T_{43}$ ,  $T_{64}$ ,  $T_{80}$ ,  $T_{87}$  within the joint population that previously did not survive in an exclusively two-state population. This may indicate the assimilation of new automata.

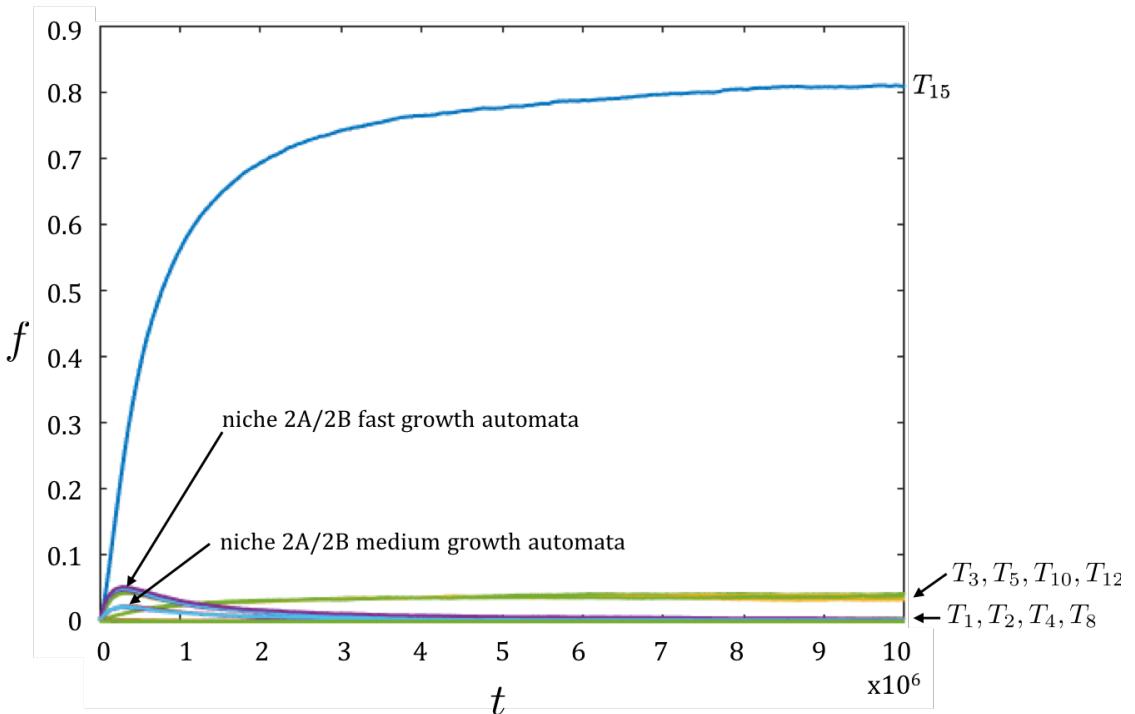


Figure 7.3: A graph showing the time-series frequency distribution of the joint one-state/two-state population over  $10^7$  iterations showing that: (i) the one-state niche (1A) was reproduced albeit with a different structure that accentuated the frequency gap between the four automata clusters 'Fast Growth' ( $T_{15}$ ), 'Slow Growth' ( $T_3, T_5, T_{10}, T_{12}$ ), 'No Growth' ( $T_1, T_2, T_4, T_8$ ) and 'Slow Decay' ( $T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$ ) - see Chapter 4 - and, (ii) that the automata from both two-state niches (2A and 2B) were also present in the same proportions as the original niches albeit they were at a very low concentration representing just 3.3% of the population. All three niches were able to co-habit within the same space demonstrating a large degree of robustness of their respective organisations in maintaining their respective identities.

## 7.4 The dynamics of a joint one-state/two-state population under low diffusivity conditions

The joint population of one-state and two-state automata was simulated for  $10^7$  iterations under conditions of low diffusivity on the lattice ( $c = 0, v = 0, \Phi = 0$ ). The results show a strong re-generation of niche 1B with  $T_4$  (47%) and  $T_2$  (44%) dominating the niche with the one-state 'boundary' automata  $T_1$  and  $T_8$  also increasing their concentration to collectively occupy 5% of the lattice. The remaining automata consist of a low frequency of the one-state automata  $T_3, T_5, T_{10}, T_{12}$  (3%) and then a very low frequency of 12 two-state automata (1%) that were originally the dominant automata in niche 2C.

The structure of the one-state automata was consistent with niche 1B and hence the one-state niche was successfully re-constructed in a competing population of 1,888

#### 7.4. THE DYNAMICS OF A JOINT ONE-STATE/TWO-STATE POPULATION UNDER LOW DIFFUSIVITY CONDITIONS

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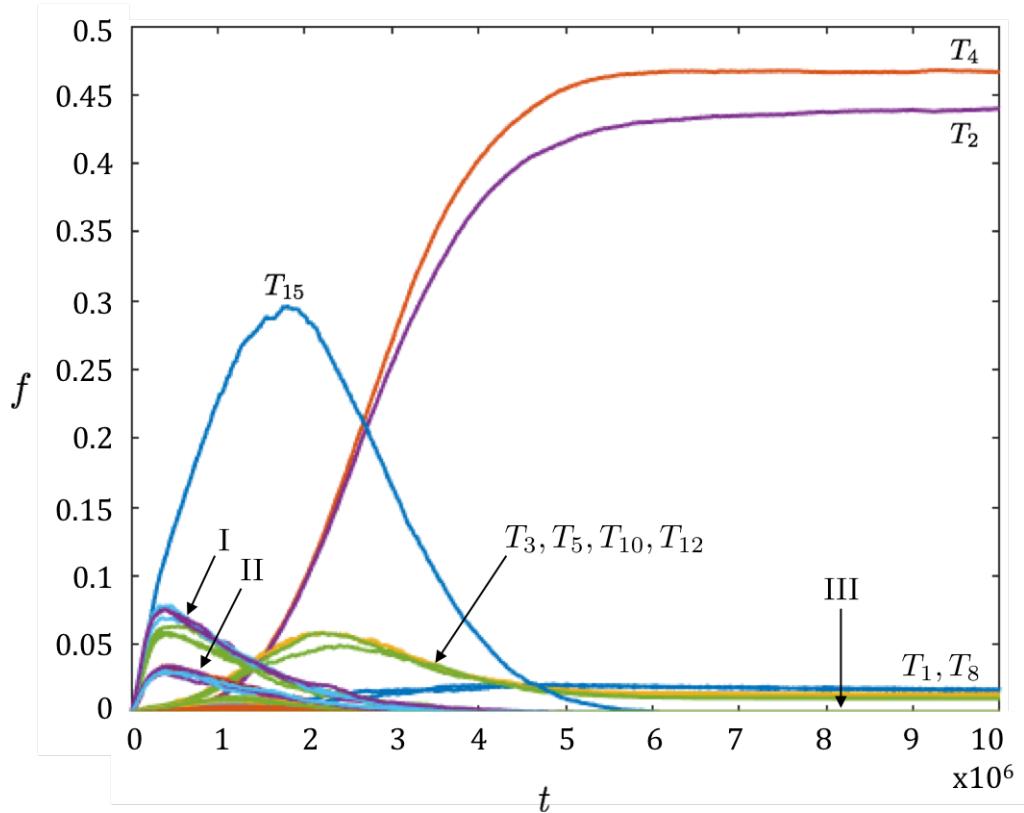


Figure 7.4: The time-series frequency distribution plot for the joint population of one-state and two-state automata under conditions of non-diffusivity ( $c = 0, v = 0, \Phi = 0$ ). As can be seen the one-state niche 1B formed readily (as indicated by the frequency distribution of automata  $T_1, T_2, T_4, T_8$  at  $t = 10^7$ ) and which came to dominate the population. The two-state population followed a similar trajectory to that which formed niche 2C however the 'mutual maintenance' automata that grew quickly early in the simulation (I and II) decayed rapidly after  $t = 0.5 \times 10^6$  and eventually went extinct leaving only the 'replicate & lock-in' automata (III) which were able to survive in the joint population albeit at a very low frequency.

automata types. The surviving two-state automata were those that were operating the 'replicate & lock-in' survival mechanism which, although this was not a superior strategy to the 'protected outgrowth' mechanism of the one-state population, nevertheless provided a degree of competitiveness. Interestingly, all two-state automata that were operating the 'mutual maintenance' survival mechanism went extinct even though they initially grew in number more rapidly than any other two-state automata in the early stages of the simulation (see the automata  $T_{95}, T_{102}$  indicated in Figure 7.4 at  $t = 1.5 \times 10^6$ ).

Examination of the one-state/two-state joint interaction matrix indicates that the 'mutual maintenance' two-state automata produce the one-state automata in the majority of interactions that occurred. As such, and as was the case with the 'replication & lock-in' two-state automata (see Chapter 5), the one-state automata were using the 'mutual main-

niche	$H(f)$ bits	$\langle C_\mu(T) \rangle$ bits	$C_\mu(G)$ bits
joint	4.65	0.78	3.56
1B	2	0	2.6
2C	5.05	0.94	8.98

Table 7.1: Comparison of key measurements between the joint population, niche 1B and niche 2C

tenance' automata as a foodset in their own production. Given the very high concentration of one-state automata on the lattice this led to a high intensity consumption of this foodset at a rate that did not give the 'mutual maintenance' automata pairs enough time to produce (maintain) each other thus disrupting this survival mechanism. Consequentially, they were rapidly depleted from the population. The one-state automata appeared to be little affected by this extinction event. By comparison, the two-state 'replicate & lock-in' automata decayed in number and this was exacerbated as most of the interactions they had with the dominant one-state automata generated more highly competitive one-state automata. Nevertheless, this group of two-state automata did persist in the population over extensive time periods and this was confirmed with multiple re-runs of the simulation (i.e. multiple simulations were performed and after  $10^7$  iterations the population was examined and demonstrated the continued presence of these 14 two-state automata albeit at a very low frequency).

At  $t = 1$  the production threshold for the joint population was  $H(f) = 7.4$  bits, the average structural complexity was  $C_\mu(T) = 0.93$  bits and the interaction network complexity was  $C_\mu(G) = 18.6$  bits. At  $t = 10^7$  these were:  $H(f) = 4.65$  bits,  $C_\mu(T) = 0.78$  bits and  $C_\mu(G) = 3.56$  bits. Compared to the equivalent measurements from niche 1B and niche 2C were:

As can be seen in Table 7.1 the steady-state joint population had lower information content compared to the two-state niche 2C (with a production threshold of 4.65 bits compared to 5.05 bits). The primary reason for these differences are that there are fewer remaining automata in the joint one-state/two-state population of 20 automata compared to 42 surviving automata in niche 2C. For similar reasons the interaction network complexity is also lower in the joint population than niche 2C and, indeed, the difference here is accentuated due to the more uniformly spread frequency of automata in niche 2C (i.e. a more uniformly spread population increases our uncertainty over which automaton will interact in the next time-step). It is clear from examination of the population structure of the joint population vs. niche 2C that the former has two highly dominant automata that account for nearly 90% of the population thus we have more certainty over which automata are likely to interact in the next time step (and hence a lower interaction network

complexity measurement).

## **7.5 The dynamics of the automata of niche 1A combined with the automata of niche 2B under initial uniform conditions**

The nine automata from the one-state niche 1A and the 21 automata from the two-state niche 2B were combined into a single population consisting of 30 one-state/two-state automata. The interaction network for this population was generated  $G_{1A,2B}$  and analysis of the network revealed that new interactions had been created between the one-state and two-state automata (see Figure 7.5). Through these new interactions the 1A automata could potentially now be produced from 252 interactions and the 2B automata from 462 interactions. In their original independent niches there were 63 and 315 interactions and, as such, the automata were benefiting significantly with an additional 189 interactions (producing 1A automata) and 147 interactions (producing 2B automata) respectively as a result of their co-location.

A simulation of 90,000 automata interacting under well-mixed conditions that were initially distributed evenly giving a uniform frequency distribution at  $t = 1$ . The simulation was iterated for  $10^7$  iterations and the time-series of the frequency distribution (see Figure 7.6) clearly shows that the 1A niche automata came to dominate the population from the outset. By comparison, the 2B niche automata rapidly decayed to occupy just 1.3% of the population although none went extinct. As such, even though the two-state automata were not competitive under these conditions they do persist. Examination of the interaction network showed that each of the one-state automata had a production advantage over the two-state automata by each being potentially produced from 28 interactions compared to 22 interactions for each of the two-state automata respectively. The persistence of the two-state automata was partly courtesy of their interactions with highly concentrated one-state automata that allowed them to replicate themselves (Figure 7.5 illustrates the mutual production between the two sets of automata). However, the 1A niche automata did not re-construct the niche 1A structure because each of these automata were produced in equal amounts (from 28 interactions each) and the final order of these automata was due to the stochasticity of the selection of interacting automata (the simulation was repeated several times and this confirmed this observation).

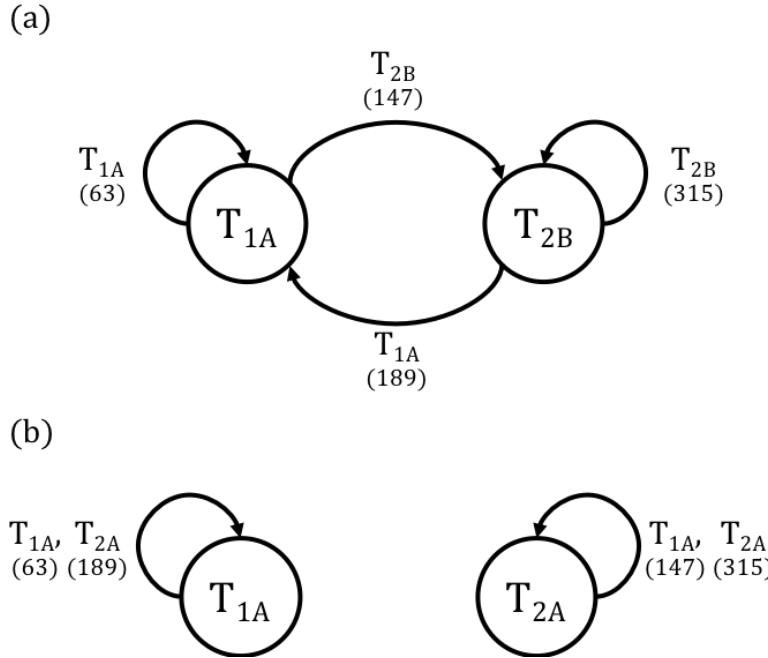


Figure 7.5: The interaction networks for the set of automata from the one-state niche 1A ( $T_{1A}$ ), the two-state niche 2A ( $T_{2A}$ ) and the two-state niche 2B ( $T_{2B}$ ). This diagram captures the  $T_b \circ T_a = T_c$  relationship with the direction of the arrow indicating the  $T_a$  to  $T_c$  relationship which is transformed by the  $T_b$  automata as indicated on the edge label: (a) the one-state niche 1A and two-state niche 2B automata interaction network where 63 interactions ( $T_{1A} \circ T_{1A} = T_{1A}$ ) are the one-state automata reproducing each other, 147 interactions involving both  $T_{1A}$  and  $T_{2B}$  automata that generated all of the  $T_{2B}$  automata types according to  $T_{2B} \circ T_{1A} = T_{2B}$ , 315 interactions generated exclusively from two-state automata  $T_{2B} \circ T_{2B} = T_{2B}$  that only generated 2B automata and 189 interactions whereby the two-state automata interacted with one-state automata produced one-state automata ( $T_{2B} \circ T_{1A} = T_{1A}$ ); (b) the interaction network of the 1A niche and 2A niche automata showing a different structure to (a). Here the transformation of the output from  $T_{1A}$  automata by a  $T_{2A}$  automata produced more  $T_{1A}$  automata and, likewise, the transformation of the output from the  $T_{2A}$  automata by  $T_{1A}$  automata produced  $T_{2A}$  automata.

## 7.6 The dynamics of the automata from the one-state niche 1A combined with the two-state niche 2B automata initialised to their original structures

A joint population was created as per section 7.5 consisting of 30 automata types: nine automata types from niche 1A and 21 automata types from niche 2B. The initial frequencies of the automata was in proportion to their frequency of occurrence in their original niches. The assumption here was that each niche initially contributes towards 50% of the population and, as such, with a population size of 90,000 each niche was represented by 45,000 automata. Within that allocation the original niche frequency distributions were

7.6. THE DYNAMICS OF THE AUTOMATA FROM THE ONE-STATE NICHE 1A  
COMBINED WITH THE TWO-STATE NICHE 2B AUTOMATA INITIALISED TO THEIR  
ORIGINAL STRUCTURES

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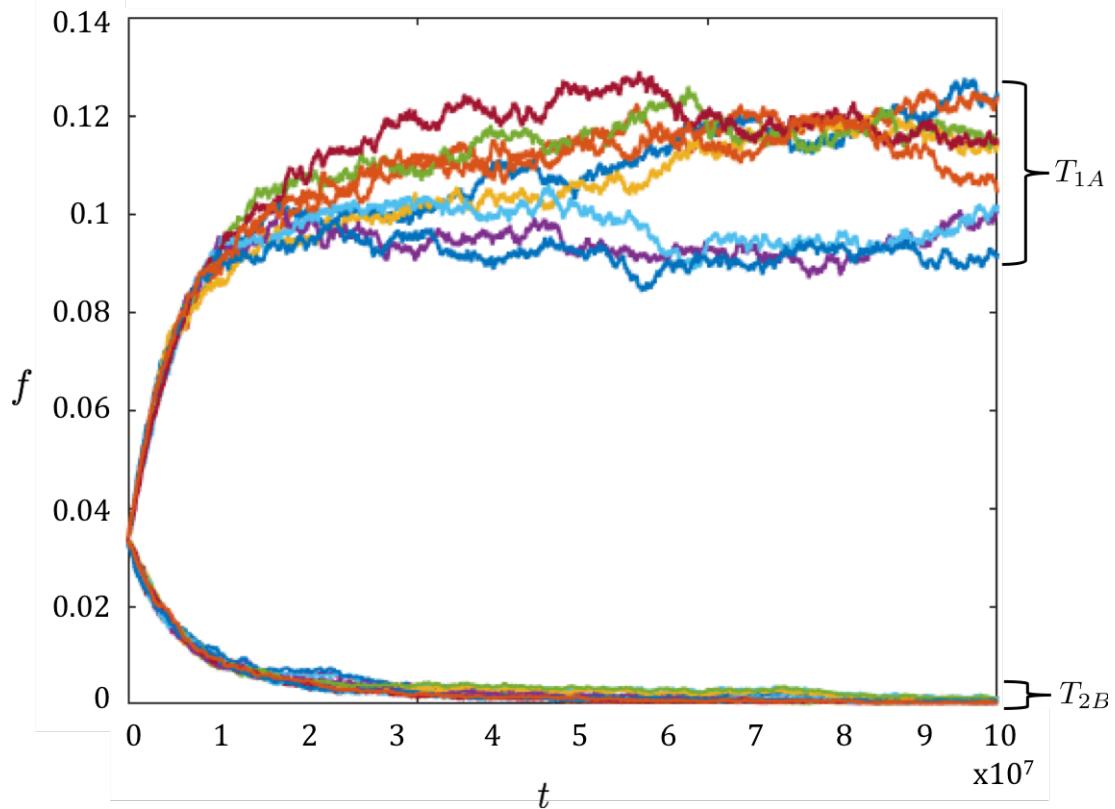


Figure 7.6: Population dynamics of the joint population of automata from niche 1A and 2B distributed evenly at  $t = 1$  and evolved under well-mixed conditions ( $c, v = 0$  and  $\Phi = 0$ ) for  $10^7$  iterations.

re-created e.g. the  $T_{15}$  automaton type occupied 22% of niche 1A and, as such, would occupy 22% of the 50% allocated to niche 1A giving its initial concentration in the joint population as 11%. Table 7.2 shows the initial frequencies allocated to each of the 30 automaton types at  $t = 1$ .

	$T_i$	initial $f_i$	final $f_i$	difference	$C_\mu(G_i)$
niche 1A	$T_1$	0.034	0.017	-0.017	2.8
	$T_2$	0.034	0.024	-0.01	2.8
	$T_3$	0.07	0.035	-0.035	2.8
	$T_4$	0.035	0.028	-0.007	2.8
	$T_5$	0.06	0.17	0.11	4.6
	$T_8$	0.033	0.038	0.005	2.8
	$T_{10}$	0.062	0.25	0.188	4.6
	$T_{12}$	0.062	0.056	-0.006	2.8
	$T_{15}$	0.11	0.35	0.24	4.6
$\sum_i f_i$		0.5	0.97	0.47	
niche 2B	$T_3$	0.0001	0	-0.0001	1.6
	$T_4$	0.0003	0.0001	-0.0002	1.6
	$T_{20}$	0.00005	0	-0.00005	1.6
	$T_{22}$	0.0002	0.0005	0.0003	1.6
	$T_{36}$	0.032	0	-0.032	3.2
	$T_{39}$	0.1	0.003	-0.097	3.2
	$T_{40}$	0.0003	0.001	0.0007	1.6
	$T_{79}$	0.0002	0.0017	0.0015	1.6
	$T_{102}$	0.11	0.01	-0.1	3.2
	$T_{134}$	0.0001	0	-0.0001	1.6
	$T_{137}$	0.0003	0.0001	-0.0002	1.6
	$T_{204}$	0.0001	0.0005	0.0004	1.6
	$T_{207}$	0.0001	0.0003	0.0002	1.6
	$T_{303}$	0.0001	0	-0.0001	1.6
	$T_{309}$	0.0001	0.0002	0.0001	1.6
	$T_{402}$	0.05	0	-0.05	3.2
	$T_{411}$	0.09	0.0016	-0.084	3.2
	$T_{555}$	0.0001	0.0007	0.0006	1.6
	$T_{561}$	0.0001	0.0005	0.0004	1.6
	$T_{766}$	0.04	0.005	-0.035	3.2
	$T_{775}$	0.08	0.003	-0.077	3.2
$\sum_i f_i$		0.5	0.03	-0.47	

Table 7.2: Comparison of the initial and final frequencies of each automaton type in the joint one-state niche (1A) and two-state niche (2B) population. The interaction network complexity  $C_\mu(G_i)$  of each automaton type is also shown. NOTE: the indices for the niche 2B have been used to aid referencing back to the results of Chapter 5 and should not be confused with the niche 1A automata with the same index number. The simulation used the indices  $i = 1\dots30$  for each automata with niche 1A automata indexed  $i = 1\text{to}9$  and the niche 2B automata indexed as  $i = 10\text{to}30$

**7.6. THE DYNAMICS OF THE AUTOMATA FROM THE ONE-STATE NICHE 1A COMBINED WITH THE TWO-STATE NICHE 2B AUTOMATA INITIALISED TO THEIR ORIGINAL STRUCTURES**

The simulation was run for  $10^7$  iterations and the resulting population dynamics were as shown in Figure 7.7. The initial concentration of each automaton was proportional to its frequency of occurrence in its original niche formation. As can be seen the one-state automata grow significantly from constituting 50% of the population at  $t = 1$  to 97% of the population at  $t = 10^7$  leaving the two-state population to shrink to just 3% of the population. The interaction network complexity  $C_\mu(G)$  for each automaton was measured at  $t = 0$  and again at the conclusion of the simulation although this showed that all  $C_\mu(G)$  measurements had centred on the value of 2.4 bits (for brevity this is not included in the table).

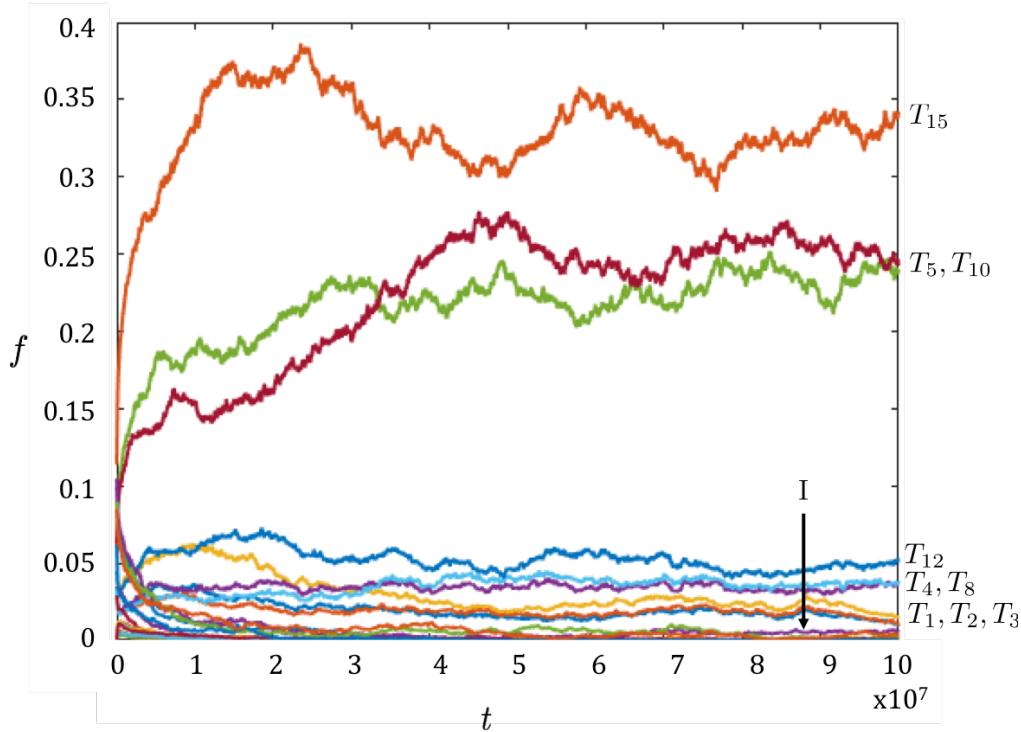


Figure 7.7: Population dynamics of the joint population of automata from niche 1A and 2B distributed at  $t = 1$  according to their proportions in their original niches. The population was evolved under well-mixed conditions ( $c, v = 0$  and  $\Phi = 0$ ) for  $10^7$  iterations. As can be seen the three 1A niche automata ( $T_5, T_{10}, T_{15}$ ) experienced rapid growth and came to dominate the population whilst six 2B niche automata went extinct leaving a reduced number of two-state automata (I).

As can be seen from column (final  $f_i$ ) from Table 7.2 and Figure 7.7 the 1A niche automata grow significantly from occupying 50% of the population to 97%. This led to the subsequent reduction of the 2B niche automata to accounting for just 3% of the joint population. The dominant automata ( $T_{15}, T_5, T_{10}$ ) benefited from an increase in the number of times that they were produced in a joint 1A,2C niche population combined with a higher

initial frequency relative to the rest of the population <sup>2</sup>. This advantage was quantified by calculating the interaction network complexity ( $C_\mu(G)$ ) for each automaton type at  $t = 0$  and the results are shown in the last column of Table 7.2. For the 1A niche automata there was an association of a higher  $C_\mu(G)$  with better overall performance throughout the simulation e.g.  $T_5, T_{10}, T_{15}$  had the highest  $C_\mu(G)$  values at 4.6 bits each which was significantly higher than the next lower measurement at 3.2 bits which was measured for seven 2B niche automata. A larger number of interactions involving automata that have a higher frequency in the population will yield a higher  $C_\mu(G)$  value e.g. the total frequency of all automata at  $t = 1$  that could interact to produce:  $T_{15}$  was 0.86,  $T_1$  was 0.23 and the two-state automaton  $T_{775}$  was 0.73. As the population reached a steady-state it was interesting to note that the  $C_\mu(G)$  values for the interaction network for each automaton were reaching parity at 2.4 bits. This indicates that the increased order that emerged in the population as it evolved had reduced the uncertainty about which automaton will be produced. Examination of the interaction network showed that the loss of six two-state automata had reduced the production rate of all automata e.g. one-state automata were produced from 16 interactions rather than 28 initially, and the remaining two-state automata were produced from 11 interactions from 22 initially.

## 7.7 Disturbance of the one-state niche 1A via. influx of two-state niche 2B automata

To examine the effect of an inflow of automata from an established two-state niche (2B) into an existing one-state niche (1A) a series of simulations were run with a uni-directional flow of the 2B automata into the 1A automata niche at various rates in the range  $0 < \Phi < 1$ . On each iteration of the algorithm either a new automaton was created from interactions within the existing population or from the random replacement of an existing automaton with an automaton selected from niche 2B. The automaton transferred from niche 2B was selected probabilistically from the frequency distribution of the 2B population and, as such, higher frequency automata were more likely to be selected to be transferred into niche 1A. It was assumed that the contributing niche 2B continually produced automata to maintain its steady-state structure and that the loss of its automata to niche 1A was inconsequential (at most, only one automaton would be removed from niche 2B on each iteration which would represent a very small fraction of that niche's population). Niche 2B

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<sup>2</sup>The 1A niche automata  $T_3, T_{12}$  which were as competitive and populous as the  $T_5, T_{10}$  in an isolated 1A niche environment were not produced as often from interactions with the 2B niche automata and were able to endure in the joint niche population

## 7.7. DISTURBANCE OF THE ONE-STATE NICHE 1A VIA. INFLUX OF TWO-STATE NICHE 2B AUTOMATA

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automata entering niche 1A were able to interact with incumbent automata in the niche and this caused changes to the interaction network in the receiving niche. Each two-state automaton transferred in this way replaced an incumbent automata in the receiving niche. Over time this meant that two-state automata that had become part of the receiving niche - either through influx or from endogenous production - were themselves possibly replaced by incoming automata. The simulation was initialised by setting the frequency of the automata in both niches to the proportions that they were present in their steady-state niches and the simulation was run for  $10^7$  iterations.

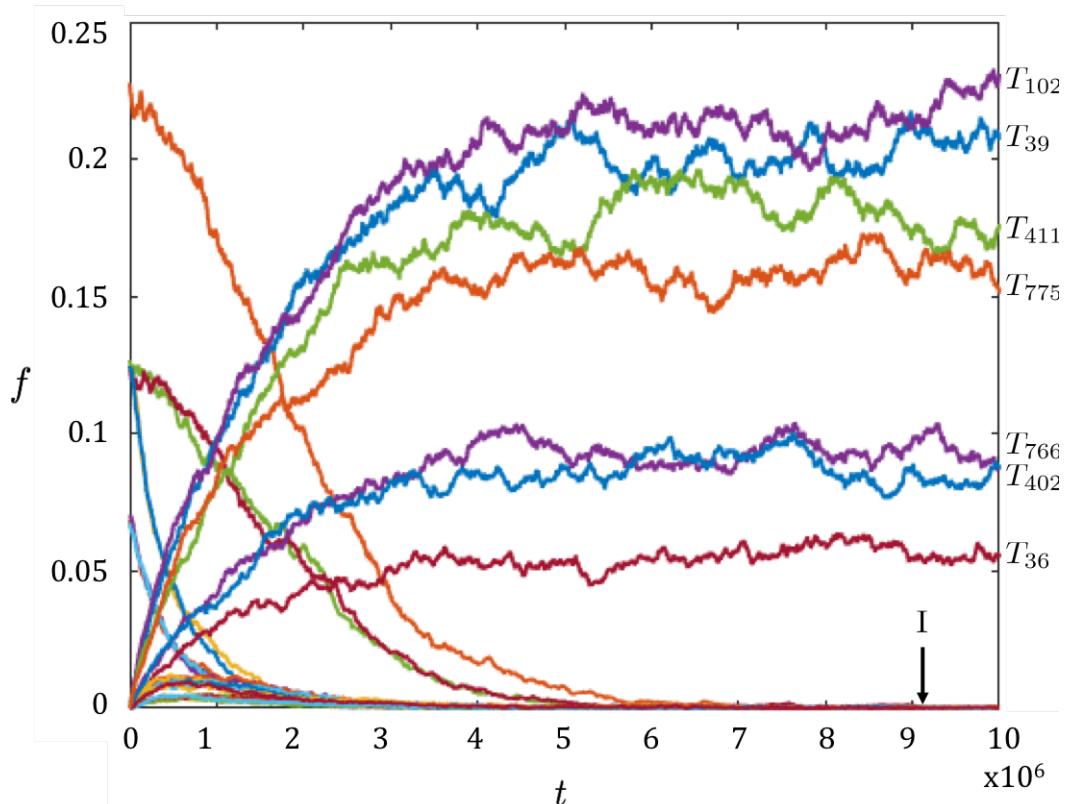


Figure 7.8: Time-series frequency distribution for a simulation of the random replacement of incumbent niche 1A automata with two-state automata from niche 2B. Selection of automata from niche 2B was randomly determined with higher frequency automata in that niche more likely to be selected to replace an incumbent automata. The initial population is exclusively the one-state automata from niche 1B ordered in the proportions in which they persist in their original niche. As can be seen even with a very low rate of replacement of  $\Phi = 0.05$  the two-state niche 2C is reproduced in this population to the detriment of the incumbent one-state automata. NB: I are the low frequency automata from niche 2B.

As can be seen in Figure 4 with  $\Phi = 0.05$  the structure of niche 2B was reproduced entirely in the 1A niche with the complete loss of all one-state automata. Examination of the interaction network in the incumbent population showed that the two-state automata

were being produced from 462 interactions compared to 252 interactions that produced the one-state automata. As the one-state automata went extinct this reduced the number of two-state interactions to 315 interactions however this was in the absence of any competition from the one-state automata. For all values of  $0 < \Phi \leq 1$  the two-state niche was reconstructed in the one-state population and came to dominate the population with a subsequent loss and ultimately extinction of the one-state automata. The value of  $\Phi$  determined how quickly this was realised. In other words, given enough time the interaction network of the two-state niche will be re-constructed in the one-state niche where it produced members of its own network at almost twice the rate that the one-state automata network were able to. The higher the value for  $\Phi$  the quicker that this occurred and the quicker the two-state niche was re-generated in the one-state population.

## 7.8 Perturbation of a one-state population via. the influx of two-state automata

The simulation was set-up according to that described in section 7.7 except that the receiving population was now the unstructured one-state population of 15 automata types and the contributing population was the unstructured two-state population of 1,873 automata types. Four simulations were each run for  $5 \times 10^6$  iterations with  $\Phi = 0.05, \Phi = 0.5, \Phi = 0.8, \Phi = 0.9$  respectively and the results are shown in Figure 7.9.

Figure 7.9a is the result of a very low rate of influx ( $\Phi = 0.05$ ) where there is a 5% chance of a two-state automata replacing an incumbent automata in the population. There was a slow decay of all incumbent one-state automata as they are replaced by the influx of two-state automata.  $T_{15}$  initially undergoes fast growth which begins to level off towards the end of the simulation. The incoming two-state automata are self-organising with the niche 2A and 2B automata being produced at a rate faster than new two-state automata are fluxing into the population. This led to a delineation of the 2A, 2B automata from other two-state automata as the former were now being produced endogenously to the point where the fast growth automata  $T_{95}$  and  $T_{102}$  from niches 2A and 2B respectively now outnumber the previously competitive one-state automata  $T_3, T_5, T_{10}, T_{12}$ . The very low rate of influx allows the interaction network to dominate population dynamics.

By comparision, Figures 7.9b-d demonstrate the opposite effect whereby the influx rate was at a rate where the effect of the interaction network was heavily inhibited in driving population dynamics. For example, the two-state automata that are now present in the incumbent population do not self-organise into niches 2A, 2B but rather stay as an

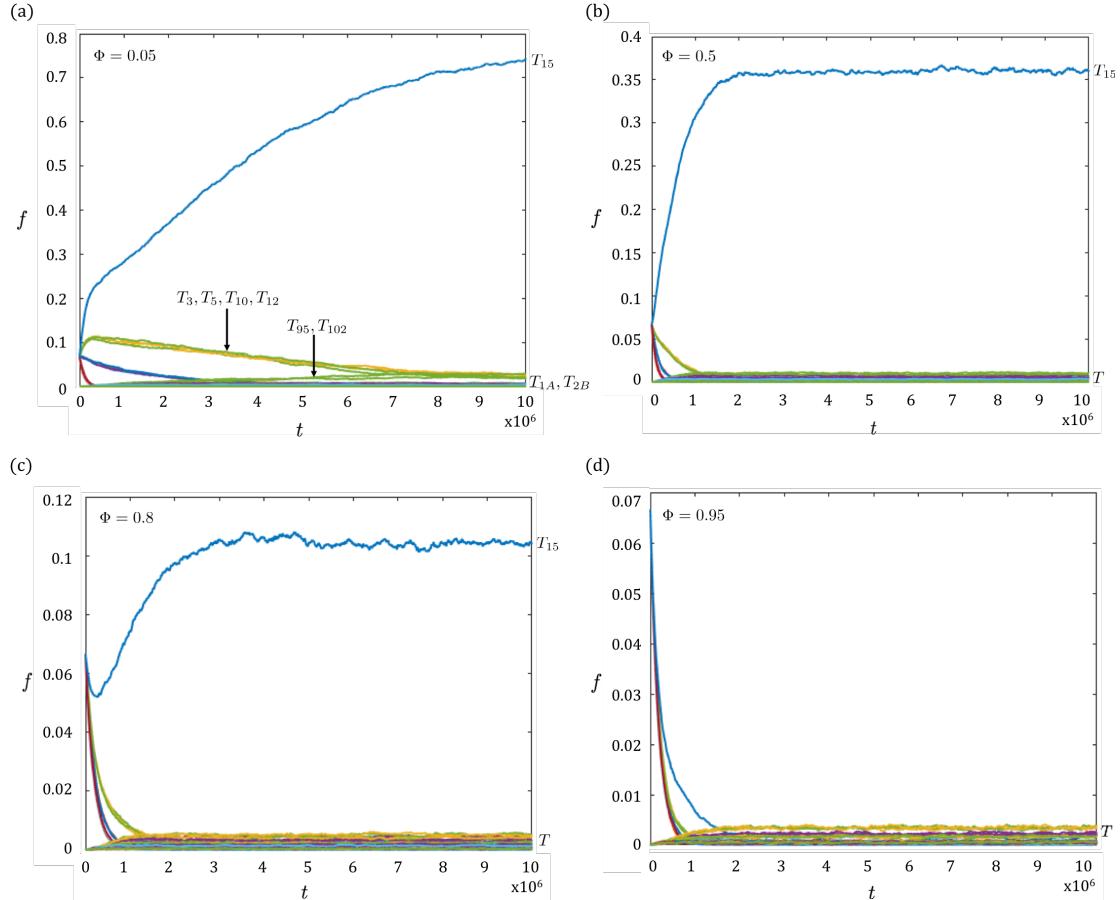


Figure 7.9: Time-series frequency distribution for four simulations of the random replacement of incumbent one-state automata population (15 types) with two-state automata population (1,873 types) for various values of  $\Phi$  over  $10^7$  iterations: (a) with  $\Phi = 0.05$  the one-state automaton  $T_{15}$  undergoes rapid and continued growth to dominate the population whilst the remaining one-state undergo a reduction in concentration whilst incoming two-state automata established

unstructured sub-population. In Figures 7.9b-c the  $T_{15}$  automaton was able to continue to be produced 50% and 20% of the time respectively and therefore was able to persist under moderate to high influx of two-state automata. However, as shown in Figure 7.9d all structure is lost as the population dynamics are driven 95% of the time by sampling from an unstructured population of 1,873 two-state automata.

### 7.8.1 The effect of removing the perturbation

To examine whether the two-state automata arriving in the one-state population are being 'assimilated' or 'accommodated' four simulations were run that examined the effect of 'switching off' the influx of two-state automata into the one-state population and, in two

simulations, re-enabling the influx but at a reduced rate. The influx rates of  $\Phi = 0.85$  and  $\Phi = 0.95$  were chosen empirically. The results of these four simulations are shown in Figure 7.10.

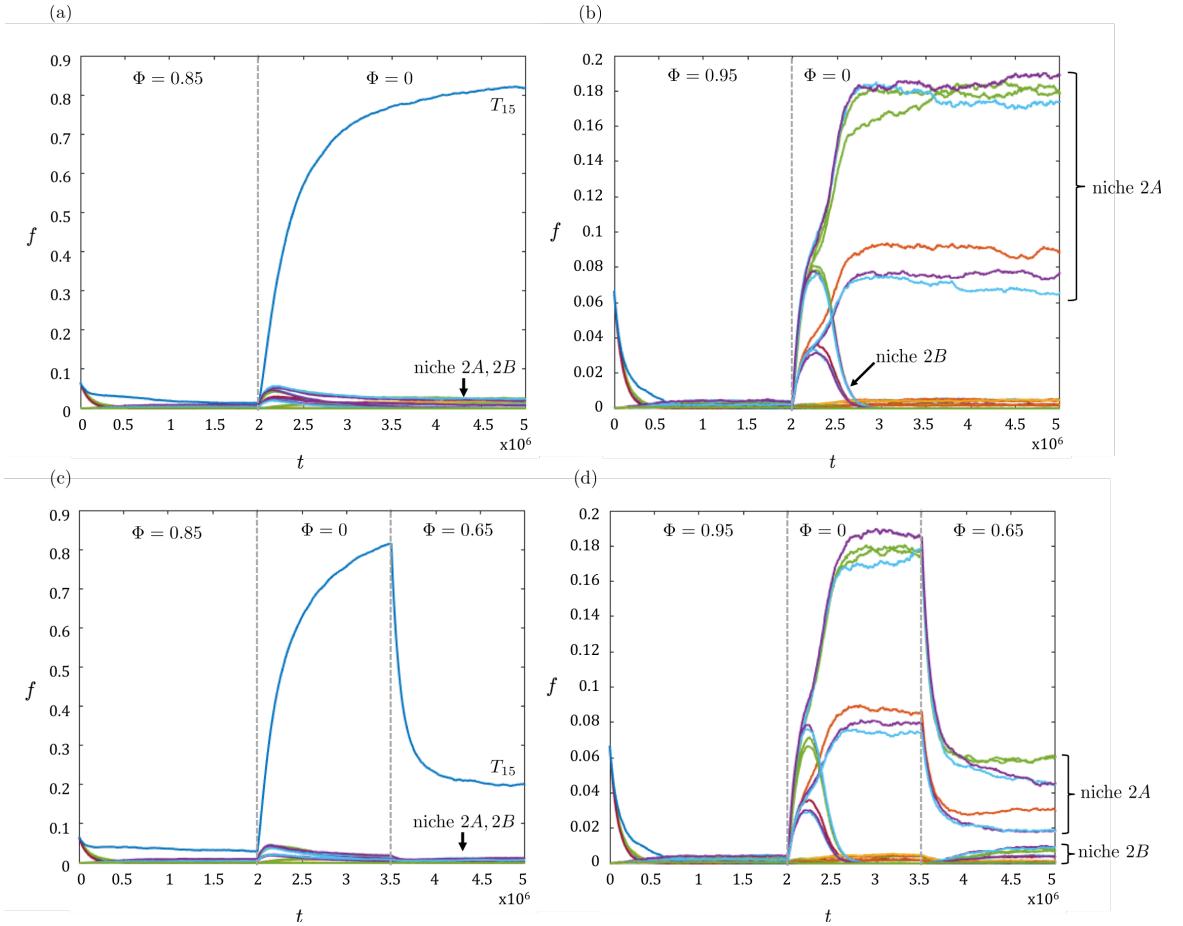


Figure 7.10: Time-series frequency distribution for four simulations where (a) from  $t = 1$  the influx of two-state automata was at the rate  $\Phi = 0.85$  and was then halted ( $\Phi = 0$ ) at the  $t = 2^6$  iteration for the remainder of the simulation showing the dominance of the  $T_{15}$  one-state automaton and the presence of the two-state automata from niche 2A and 2B; (b) from  $t = 1$  the influx of two-state automata was at the more aggressive rate of  $\Phi = 0.95$  leading to the extinction of all one-state automata by the  $2^6$  iteration at which point the influx of automata was halted ( $\Phi = 0$ ) for the remainder of the simulation leading to the co-existence of niche 2A and 2B until the punctuated equilibrium event at the  $2.25 \times 10^6$  iteration leading to the domination of the population by the niche 2A automata; (c) the same settings and timings were used as per (a) except at the  $3.5 \times 10^6$  iteration the influx of two-state automata is re-enabled at a lower rate of  $\Phi = 0.65$  for the remainder of the simulation showing a significant reduction in the concentration of  $T_{15}$  until a new steady-state is reached; and (d) the same settings and timings were used as per (b) except that at the  $3.5 \times 10^6$  iteration the influx of two-state automata was re-enabled at  $\Phi = 0.65$  which led to the reduction in concentration of the niche 2A automata and an increase in the concentration of niche 2B automata.

Figure 7.10a shows that the one-state automata underwent a steady decline in con-

centration in the presence of an influx of two-state automata at the high rate of  $\Phi = 0.85$  and this led to the extinction of all one-state automata except  $T_{15}$ . Once the influx of two-state automata had been disabled ( $\Phi = 0$ ) at  $t = 2^6$  then the one-state  $T_{15}$  automaton very quickly dominates the population. This was because the interactions between the two-state automata produced the  $T_{15}$  automaton more often than they did each other. As  $T_{15}$  grew in concentration it was selected more and more frequently to interact with another automaton which was also likely to be  $T_{15}$  to create the interaction  $T_{15} \circ T_{15} = T_{15}$  and hence replicated itself. The decrease in the rate at which  $T_{15}$  came to dominate the population was due to the process of selecting an automaton to remove from the population which, due to the method used, means that the greater the concentration of an automaton the more likely it is to be selected for removal from the population. Given the stochastic nature of the interaction and removal process on some iterations non- $T_{15}$  automata were removed as shown by the gradual decline of the remaining automata types. Incidentally, those remaining automata were primarily the niche 2A and 2B automata which continued to persist. The population dynamics from  $t = 2^6$  were driven entirely by the interaction network which enabled the self-producing networks of this population to emerge to form a steady state population structure characterised by the dominance of  $T_{15}$ . This population has adapted to the two-state automata as they are now able to continually produce themselves independently of a steady influx of their type from outside i.e. the 'operational limits' of this autopoietic system is entirely enclosed within the population and is not dependent on any external processes.

Figure 7.10c shows the results of re-introducing an influx of two-state automata (at a rate  $\Phi = 0.65$ ) at the  $3.5 \times 10^6$  iteration which leads to the reduction in concentration of  $T_{15}$  and the niche 2A, 2B automata as the production of new automata is disrupted by the influx of two-state automata.

Figure 7.10b shows the one-state automata decaying quickly due to the very high influx rate ( $\Phi = 0.95$ ) of two-state automata into the population to the extent that they go extinct. This is evident once the influx rate is disabled ( $\Phi = 0$ ) and the two-state automata completely dominate the population and re-create the production dynamics seen with the formation of niche 2A (see Chapter 5).

Figure 7.10d shows the effect of re-introducing an influx of two-state automata (at a rate  $\Phi = 0.65$ ) which, predictably, disrupts the internal production dynamics to reduce the concentration of the niche 2A automata whilst increasing the concentration of the niche 2B automata. The effect of an external perturbation on two-state automata production dynamics was discussed in Chapter 5 and is seen again here with the neutralisation of the competition between those two niches to the extent that they can co-habit the population.

The rate of  $\Phi = 0.65$  was empirically determined to be the maximum rate at which the population structure is retained. With  $\Phi > 0.65$  the population structure collapses due to the significant interruption of the internal production dynamics caused by the high rate of influx of two-state automata.

These simulations demonstrate how 'fragments' of two-state automata networks can re-build the network required to reproduce a two-state niche via. the accommodation of two-state automata into an initially one-state population. This supports Maturana's proposed mechanism by which autopoietic systems reproduce [13].

These simulation results revealed an interesting sequence of phases (see Figure 7.11) that the population went through beginning with the destruction of the incumbent population via. the rapid assimilation of foreign automata (at a rate  $\Phi = 0.95$ ) through to the establishment of internal production dynamics (with an impermeable boundary with  $\Phi = 0$ ) to continually produce those foreign automata which become the incumbent automata to form either niche 2A or 2B even in the presence of an influx of two-state automata (to a maximum rate of  $\Phi = 0.65$ ).

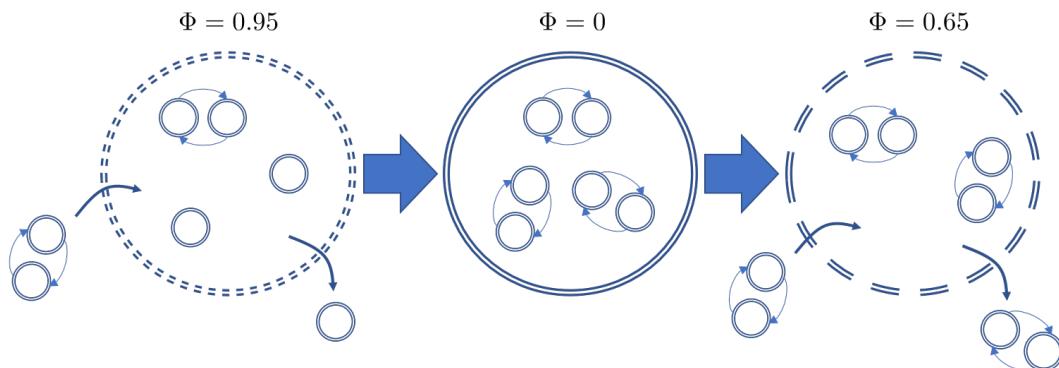


Figure 7.11: With  $\Phi = 0.95$  two-state automata flux into the one-state population which displaces primarily one-state automata which are removed. At such a high rate of influx all one-state automata are depleted from the population leaving just two-state automata. With  $\Phi = 0$  the internal production dynamics dominate and this leads to the formation of either niche 2A or 2B. With  $\Phi = 0.65$  there is an inflow and outflow of two-state automata however the niche structure is maintained. The boundary lines signify the rate of influx of automata with solid double lines indicating no flux  $\Phi = 0$  to small dashed lines indicating a highly permeable boundary.

In a chemical or biological setting this implies that a foreign material that has successfully entered into a space and displaced the previous incumbents needs to somehow spontaneously form and regulate its systems interface to prevent the continued flow of foreign material into the recently claimed space (i.e.  $\Phi = 0$ ). This would be necessary to allow the relationships between those now encapsulated entities to form a network of interactions leading to the self-production and the emergence of some sort of steady-state organisation. This would be the reproduction of a niche within a new space. Once

established this niche would 're-enable' its systems interface to allow a regulated flow (e.g.  $\Phi = 0.65$ ) of foreign material that is sufficient to allow it to structurally couple to its environment. This is the essence of autopoiesis.

## 7.9 Summary

This chapter has investigated whether one-state and two-state populations form niches that previously emerged in exclusively one-state or two-state populations. Three approaches were taken: a joint population of 1,888 one-state and two-state automata, a small population consisting of only those automata that constitute the niches 1A and 2B, and the one-state niche 1A as the incumbent population with a uni-directional flow of two-state niche 2B automata replacing incumbent automata at a constant rate ( $\Phi$ ).

The following simulation results were presented and discussed:

- A joint one-state/two-state population consisting of 1,888 unique automaton types interacting over  $10^6$  iterations under well-mixed conditions ( $c = N, v = n, \Phi = 0$ ) demonstrating that all three niches 1A, 2A and 2B emerged and persisted within the same population. Niche 1A dominated and occupied 97% of the population with the two-state niches sharing the remaining 3.3% available.
- Joint one-state/two-state population consisting of 1,888 unique automaton types interacting over  $10^6$  iterations under low-diffusivity conditions ( $c = 0, v = 0, \Phi = 0$ ) demonstrating that niche 1B emerges and dominates the population. Niche 2C does not emerge although the dominant automata from that niche - the 'replicate & lock-in' automata - do persist at a very low frequency. The 'mutual maintenance' two-state automata from niche 2C do not survive and went extinct.
- A joint population consisting of the niche 1A automata and the niche 2B automata set to an initially equal concentration interacting over  $10^7$  iterations under well-mixed conditions demonstrating that the 1A automata dominate. However, there was no discernible structure to the one-state automata whereas the two-state automata - although of a very low frequency - were proportioned in accordance with niche 2B. The dominance of the one-state automata was determined to be due to the additional interactions that produce them that were introduced by the presence of the two-state automata. The original niche structures did not emerge.
- A joint population consisting of the niche 1A automata and the niche 2B automata set to initial frequency distribution that represented their proportions in their original

niche configurations. This population interacted over  $10^7$  iterations under well-mixed conditions. The one-state automata experience growth at various rates in the early stages of the simulation whilst the two-state automata decay rapidly. The original niche structures were not maintained.

- A one-state automata population of 15 different types perturbed by two-state automata of 1,873 automata types replacing incumbent one-state automata at the rates  $\Phi = 0.05, \Phi = 0.5, \Phi = 0.8, \Phi = 0.95$  respectively. The one-state automaton  $T_{15}$  proves to be very robust and a very high rate ( $\Phi = 0.95$ ) of incoming two-state automata are required before it succumbs and eventually goes extinct. All other one-state ultimately went extinct in the presence of any disturbance of two-state automata. Further simulations were run to examine the effect of disabling the influx of automata (i.e.  $\Phi = 0$ ) after  $2^6$  iterations and in the case where all one-state automata had gone extinct this led to the formation of niche 2A or 2B and where  $T_{15}$  was still present this led to it dominating the population. Re-enabling the influx of two-state automata ( $\Phi = 0.65$ ) led to these population structures maintaining themselves; with  $\Phi > 0.65$  the influx of two-state automata disrupted endogenous production to a degree that population structure was removed.

Analysis of the above results led to the following observations:

- A uni-directional flow of automata from one niche to another leads to the reproduction of the structure of the donating niche in the recipient group; the velocity with which this reproduction is achieved increases as the influx flow rate increases to a maximum of  $\Phi = 1$ .
- The co-location of one-state and two-state automata did not affect the ability for those automata to evolve to their steady-state niches under well-mixed conditions. However, the actual structure of those niches were significantly different e.g. the one-state niche was characterised by a very high frequency of  $T_{15}$  and a significantly lower frequency of the other one-state automata that constitute niche 1A. Nevertheless, the ordering and therefore the identity of the niche was reproduced. For the two-state niche the proportions of each automata was found to be closer to that found in the original niche 2A however, as a proportion of the total population (which included the one-state automata), the two-state automata occupied a very small number (3%). In a 90,000 automata population this equates to 2,700 two-state automata which demonstrates that small populations are able to support the formation of steady-state organisations.

- An injection of two-state automata drawn from an established niche ( $2B$ ) of 21 automata was far more effective in reproducing itself than two-state automata drawn from a uniform, unstructured ensemble of 1,873 two-state automata types. This indicates that an efficient, optimised group of automata (as per the  $2B$  niche automata) was able to reproduce its own steady-state structure at a far faster rate across a wider range of conditions (where  $0 < \Phi \leq 1$  then the niche would be reproduced). By comparison, an unstructured population of two-state automata required a specific change in conditions (i.e. the disabling of an influx of two-state automata where  $\Phi = 0$ ) before any kind of structure could emerge. Within  $2^6$  iterations of the simulation a two-state population would be assimilated within a one-state population with the subsequent effect on the receiving population determined by the rate at which incumbent automata had been replaced by external two-state automata ( $\Phi$ ): (a) with  $0 < \Phi < 0.95$  the incoming two-state automata were able to establish their own production dynamics albeit at a very low concentration with the  $T_{15}$  one-state automata was still present in the population thus demonstrating that the foreign two-state automata had been accommodated in the population; and (b) with  $0.95 \leq \Phi \leq 1$  the one-state population had been eliminated leading to the complete dominance and reproduction of the external two-state population. However, for this two-state population to form any kind of structure required the removal of any influx from the external two-state population. From there the ordinary population dynamics of a two-state population under well-mixed conditions (see Chapter 5) were only possible when there was no influx of external automata (i.e.  $\Phi = 0$ ). This is a demonstrable example of the importance of the 'operational closure' concept of an autopoietic system.
- The less structured and diverse that the source of automata is that is replacing incumbent automata the more likely it is that the incumbent population will persist. Conversely, the more structured and efficient the source of automata is then the less likely the incumbent population will be able to compete and persist. Hence, in a more general chemical or biological setting the nature of and maturity of neighbouring cells or systems will play a contingent role on the viability of an autopoietic system that can exchange material with its environment.
- All simulation results exhibited the *active* assimilation of two-state automata alongside, or into, a one-state population that led to changes in the internal structure of the population. This was due to the interactivity that existed between the one-state and two-state automata. The *passive* form of assimilation would only be present

where there was no interaction between automata however this would only occur in extremely simple (and therefore trivial) populations e.g. where the range of the incumbent population of automata do not match the domain of any of the incoming automata, and vice versa. As a general notion this means that one set of automata can only ever process say the '0' symbol and the other set of automata can only ever process the '1' symbol. Given the assumption that these subsets of automata are self-producing and maintaining means that such mutual exclusion (or disjoint automata sets) are only possible where both sets actually consist of just one self-replicating automata each e.g. the  $T_1$  and  $T_8$  one state automata.

This chapter has examined the cognition process of autopoiesis as the influx and presence of foreign molecules into unstructured or evolved populations. The next chapter examines cognition as a flow of information between a self-producing population and its environment.

## RESULTS V - ONE-STATE COMPUTATION NICHE SIMULATIONS

### 8.1 Introduction

This chapter investigates a one-state automata population evolving in the computation niche model. The three components that constituted the computation niche model were an environment, a membrane, and an internal replicating population. A total of 140 simulations were run:

- Four simulations to examine the effect of the membrane on the internal self-producing population under the following conditions: no environment ( $E = \emptyset$ ), a random environment ( $E = P(e = 0, e = 1) = [0.5, 0.5]$ ), a constant 0 environment ( $E = P(e = 0, e = 1) = [1, 0]$ ), and a constant 1 environment ( $E = P(e = 0, e = 1) = [0, 1]$ ). See section 8.3.
- 11 simulations of the computation niche under the influence of varying environmental noise that changed in .1 increments ( $E = \{[0, 1], [0.1, 0.9], \dots, [0.9, 0.1], [1, 0]\}$ ). See section 8.3.5.
- 121 simulations of the computation niche under the influence of random environmental noise that increased in intensity in .1 increments ( $\Phi_{in} = [0, 0.1, \dots, 0.9, 1]$ ) repeated for each of the 11 environmental settings ( $(E = \{[0, 1], [0.1, 0.9], \dots, [0.9, 0.1], [1, 0]\})$ ). See section 8.3.6.
- Four simulations of the niche coupled to the environment with coupling strength increasing in .25 increments from  $\Phi_{out} = \{0, 0.25, 0.5, 0.75\}$ . See section 8.3.7.

## 8.2 Set up of the Computation Niche membrane

To examine the effect of a membrane on the production dynamics of a self-producing population a membrane network ( $M$ ) was initialised consisting of 15 one-state automata types. The membrane network consisted of 15 vertices and a total of 207 edges (see Figure 3.10). The weightings ( $\lambda$ ) on each edge were initialised to the normalised frequencies of the uniform distribution of the population at  $t = 0$  e.g. in a 15 automata population the concentration of each automaton type was 1/15th. Therefore, at  $t = 0$  each edge in the membrane network was equally weighted at  $\lambda = 0.0048$ . The initial cumulative weightings of the communication channels received by each membrane automaton ( $M_i$ ) - relative to all other automata in the membrane - is shown in Table 8.1.

$M_i$	in-degree ( $k_{in}$ )	out-degree ( $k_{out}$ )	$\sum \lambda_i$ at $t = 0$	$\sum \lambda_i$ at $t_{max}$ with $E = \emptyset$	$\sum \lambda_i$ $t_{max}$ with $E = [0.5, 0.5]$
$M_1$	12	12	0.058	0.056	0.057
$M_2$	12	12	0.058	0.056	0.057
$M_3$	12	15	0.058	0.056	0.057
$M_4$	12	12	0.058	0.056	0.057
$M_5$	15	12	0.0725	0.074	0.073
$M_6$	15	15	0.0725	0.074	0.073
$M_7$	15	15	0.0725	0.074	0.073
$M_8$	12	12	0.058	0.056	0.057
$M_9$	15	15	0.0725	0.074	0.073
$M_{10}$	15	12	0.0725	0.074	0.073
$M_{11}$	15	15	0.0725	0.074	0.073
$M_{12}$	12	15	0.058	0.056	0.057
$M_{13}$	15	15	0.0725	0.074	0.073
$M_{14}$	15	15	0.0725	0.074	0.073
$M_{15}$	15	15	0.0725	0.074	0.073
Total	207	207	1	1	1

Table 8.1: The cumulative weightings of the incoming edges for each target membrane automaton ( $i$ ) comparing the initial weightings ( $t = 0$ ) with the final weightings ( $t = t_{max}$ ) with and without environmental noise present ( $E = \emptyset, E = [0.5, 0.5]$  respectively). The final cumulative weightings of each membrane automaton's incoming edges under those two environmental settings were different from each other and the initial values. This demonstrated how the membrane adapts to reflect the changing structure of the internal self-producing population.

At  $t = 0$  the membrane automata had not yet received an input and, as such, they were all set to spontaneously emit their nominal output as given by their internal structure. Where an automaton had the possibility of outputting a 0 or a 1 then the output was chosen

with equal probability. The probabilities - as shown in Table 8.2 - were always the same value at  $t = 0$  for successive simulation runs when there was no environmental noise<sup>1</sup>.

automaton	Outgoing Edges		Incoming Edges		Accepts 0	Accepts 1	$P_{max}^{active}$
	$P(y_i = 0)$	$P(y_i = 1)$	$P(x_i = 0)$	$P(x_i = 1)$			
$M_1$	1	0	0.625	0.375	y	n	0.625
$M_2$	0	1	0.625	0.375	y	n	0.625
$M_3$	0.5	0.5	0.625	0.375	y	n	0.625
$M_4$	1	0	0.375	0.625	n	y	0.625
$M_5$	1	0	0.5	0.5	y	y	0.5
$M_6$	0.5	0.5	0.5	0.5	y	y	0.5
$M_7$	0.67	0.33	0.5	0.5	y	y	0.5
$M_8$	0	1	0.375	0.625	n	y	0.625
$M_9$	0.5	0.5	0.5	0.5	y	y	0.5
$M_{10}$	0	1	0.5	0.5	y	y	0.5
$M_{11}$	0.33	0.67	0.5	0.5	y	y	0.5
$M_{12}$	0.5	0.5	0.375	0.625	n	y	0.625
$M_{13}$	0.67	0.33	0.5	0.5	y	y	0.5
$M_{14}$	0.33	0.67	0.5	0.5	y	y	0.5
$M_{15}$	0.5	0.5	0.5	0.5	y	y	0.5

Table 8.2: The information processing behaviour of each membrane automaton showing the probability of the automaton emitting ( $P(Y)$ ) a symbol '0' or '1', the probability of the automaton receiving ( $P(X)$ ) a '0' or a '1' and the probability of the activation threshold ( $P_{max}^{active}$ ) being surpassed to activate the membrane automaton.

Table 8.2 shows the probabilities of each membrane automaton receiving ( $X$ ) and emitting ( $Y$ ) binary information in the absence of environmental information. Incoming edges ( $X$ ) to a membrane automaton could carry symbols that were outside of its domain. This was because some transmitting automata had an output range that surpassed that of the domain of the receiving automaton e.g. a dual output automaton can emit a '0' or '1' at different time-steps whilst a mono input automaton could only ever process a '0' or '1' but not both. Subsequently, mono input channel automata ignored (i.e. did not process) information that was outside of their domain. The event of triggering a membrane automaton was independent for each input symbol, and as such, the input probabilities  $X_i$  were not additive e.g. the  $T_6$  automaton can accept both '0' and '1' symbols but can only execute a transition based on one of those inputs. The input that surpassed the activation threshold of the automaton was chosen as the transition. The probability of an automaton activating at time  $t$  was the maximum probability of one of its inputs. Examination of the membrane network determined the nominal  $P_{max}^{active}$  value for each automaton which

<sup>1</sup>with environmental noise present then this had the effect of modulating the information received ( $X$ ) at each receiving membrane automaton and therefore the probabilities would be dependent on the value of the environmental noise.

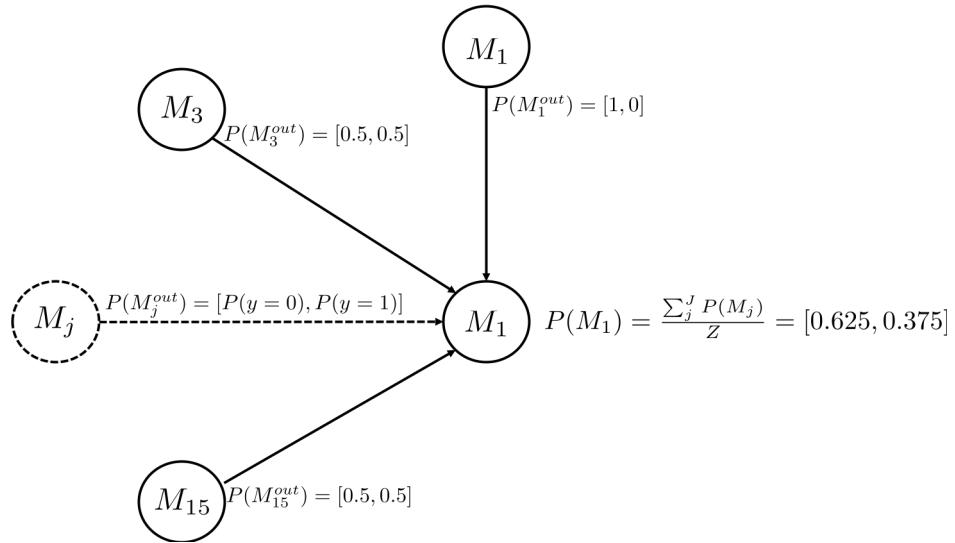


Figure 8.1: An illustrated example of the calculation of  $P_{max}^{active}$  for the membrane automaton  $M_1$ . Each membrane automaton  $M_j$  in the set  $M_J = \{M_1, M_3, \dots, M_{15}\}$  transmits information to  $M_1$  (it also transmitted to itself) in the form of a two-element probability distribution ( $P(M_j) = [P(y=0), P(y=1)] = 1$ ). The input function  $P(M_1)$  is the cumulative probability distribution of all inputs. In this example the weightings on each edge are assumed to be equal and therefore  $P_{max}^{active} = \max(P(M_1)) = 0.625$ . Under changing conditions the edge weightings modulate the information received by  $M_1$  that can lead to fluctuating values of  $P_{max}^{active}$  which subsequently effects the activation behaviour of the receiving automaton.  $Z$  is a normalising factor.

took into consideration the probability of mono input automata receiving out-of-scope information from dual output automata.

Figure 8.1 illustrates how the input probability distribution ( $P(M_i)$ ) was calculated for each membrane automaton. As can be seen the cumulative inputs from each incoming edge was normalised to give a two-element probability distribution. This distribution simply captures the information that has been collected at the membrane automaton's inputs. To determine whether the membrane activates required this input probability distribution ( $X$ ) to be filtered to the information processing domain of the receiving automaton ( $\tau$ ) (as per equation 3.9) to give  $X' = [0.625, 0.375] \times [1, 0]^T = [0.625, 0]$  where  $T$  was the transpose of the vector  $\tau$ . As such at  $t = 1$  there was a 62.5% chance that membrane automaton  $M_1$  would activate.

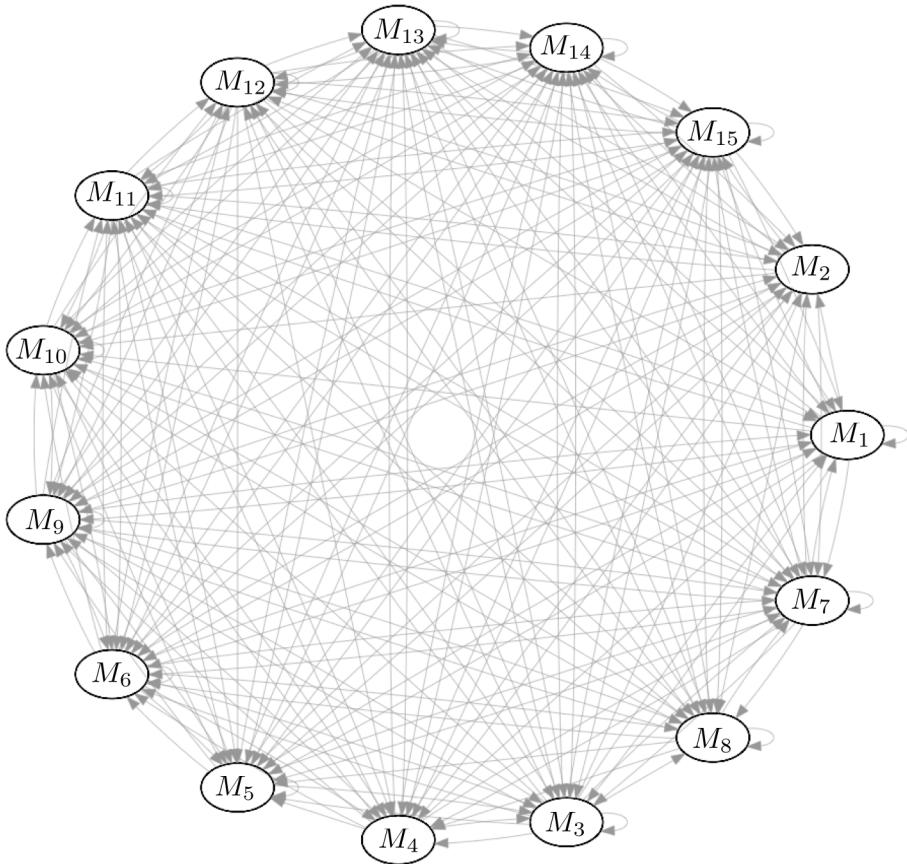


Figure 8.2: The topology of the membrane automata network where the directed edges indicate the flow of transfer of information between the source automaton ( $M_a$ ) to a target ( $M_b$ ) automaton from the interaction relationship  $T_b \circ T_a = T_c$  i.e. automaton  $M_a$  emitted information which was received by  $M_b$  that then subsequently processed that information according to its internal structure. This was a highly connected network with an average in-degree of 13.8 and an average out-degree of 13.8 giving a 1:1 ratio that indicated a highly symmetrical structure of 207 edges. As each membrane automaton was highly connected this created competition within the membrane network in the form of multiple source automata interfering in each others attempts to influence the activation of a target automaton.

### 8.3 The effect of a membrane on a self-producing population

Simulations of the computation niche model were run for  $1 \times 10^5$  iterations<sup>2</sup> with the membrane network initialised as described in section 8.2 and the internal population

<sup>2</sup>The computation niche model performed a synchronous update of the internal population, compared to an asynchronous update which was used in the information niche model, and this required significantly less iterations to generate a steady-state population. The decision to use a synchronous approach was based on the need to ensure that the stochastic processes of the computation niche were using the most complete and up-to-date information at all times.

initialised to a uniform distribution of 90,000 automata across the 15 different one-state automata types operating under well-mixed conditions.

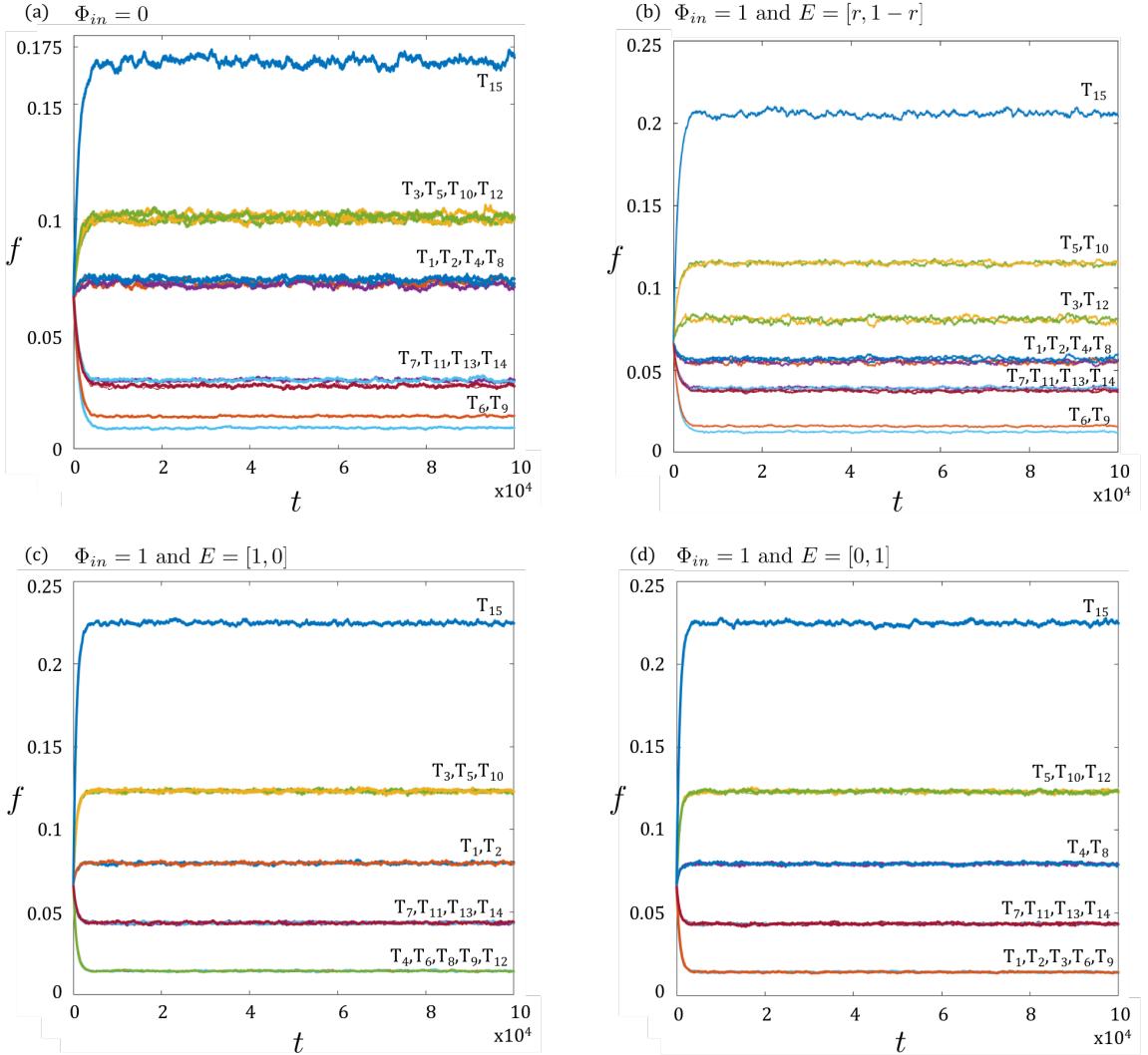


Figure 8.3: The steady-state population structure of the computation niche model after  $1 \times 10^5$  iterations with and without environmental noise: (a) the steady-state population with no environmental noise ( $\Phi = 0$ ) was very similar to the one-state information niche 1D population structure; (b) a constant environmental noise that switches randomly from '0' and '1' led (where the randomly generated number  $r \leq 0.5$  indicated the generation of the '0' symbol and  $r > 0.5$  generated a '1' symbol) to a significant drop in the concentration of six automata (that were all mono-channel input) to generate a new steady-state structure; (c) a constant '0' was emitted as environmental noise and this led to the drop in concentration of all automata that could only process '1' symbols; (d) a constant '1' was emitted as environmental noise and this led to a reduction in those automata that could only process '0' symbols. For (b)-(d) the environmental aperture was set to  $\Phi = 1$  hence membrane automata were only processing environmental information.

Four environmental settings were simulated: (a) with no environmental noise meaning

that information flow over the membrane were effected by the membrane itself and changes in population structure, (b) the environment randomly generated 0's and 1's from a uniform probability distribution, (c) the environment only generated the symbol '0', and (d) the environment only generated the symbol '1'. For one simulation setting the environment aperture  $\Phi$  was set to  $\Phi = 0$  indicating that membrane automaton activity was determined solely from information received from other membrane automata. For the remaining three simulation settings the environment aperture  $\Phi$  was set to  $\Phi = 1$  which meant that the calculation to determine whether a membrane automaton was activated was determined solely by the information it received from the environment. A more in-depth examination of various values for the environmental aperture were also examined (see section 8.8). Sections 8.3.1-8.3.3 interpret the results of the population dynamics shown in Figures 8.3a-d.

### 8.3.1 The effect of a membrane on production dynamics in the absence of environmental noise

A computation niche consisting of 90,000 one-state population automata and 15 one-state membrane automata were simulated for  $1 \times 10^5$  with  $\Phi_{in} = 0$ . Figure 8.3a shows the results of simulating the computation niche in the absence of environmental noise. The processing in the membrane network and the production of new automata were determined entirely by the flow of information (i) within the membrane network, (ii) from the membrane to the internal population, and (iii) changes in population structure reflected in the weightings of the membrane network edges. The simulation was run for  $1 \times 10^5$  iterations and the results (see Figure 8.3a) showed that the internal population had evolved to a steady-state structure characterised by fast growth (1off), slow growth (4off), no growth (4off) and fast decay (6off) automata respectively. These proportions were similar to those of niche 1D (see Chapter 4) and confirms that the computation niche model is producing the expected behaviour of a one-state automata population under well-mixed conditions. The reason why niche 1D was reproduced rather than niche 1A was examined in detail and the results are described in Appendix 12.4.

On average the membrane automata were active 64.6% of the time:

group	membrane automata	time active
A	$M_1, M_2, M_3, M_4, M_8, M_{12}$	67%
B	$M_5, M_6, M_7, M_9, M_{10}, M_{11}, M_{13}, M_{14}, M_{15}$	63%

Table 8.3: Examination of the activity within the membrane showed that seven membrane automata were active for 67% of the simulation and nine were active for 63% of the time.

The production of population automata for each of these activity groupings were:

group	automata produced ( $f$ )	total $f$
A	$T_1(4), T_2(4), T_3(4), T_4(4), T_8(4), T_{12}(4)$	0.49
B	$T_5(13), T_6(2), T_7(6), T_9(2), T_{10}(13), T_{11}(6), T_{13}(6), T_{14}(6), T_{15}(27)$	0.51

Table 8.4: Examination of the activity within the membrane showed that seven membrane automata were active for 67% of the simulation and nine were active for 63% of the time. Examining these groups separately showed that their activation only activates those parts of the interaction network that produce themselves in the internal population.

Several observations were made:

- the interaction matrix ( $G$ ) for these two groups were strongly connected components i.e. each member of the group was produced by other members of the group exclusively. The final frequency distribution (total  $f$  in Table 8.4) showed an even split in the population between the two groups and yet group A consisted of 50% less membrane automata than group B. This suggests a link between the activity of a membrane automaton and the success (or not) of the production of its equivalent population automaton.
- the membrane matrix ( $M$ ) revealed that the group A automata had less incoming edges than those in group B ( $k_{in} = 12$  compared to  $k_{in} = 15$  respectively).
- the weightings on the membrane network showed that the group A edge weightings were lower than the group B network weightings. In general terms the higher the weighting on an edge the more that the information communicated over that edge influenced the activation behaviour of the receiving (target) automaton. In this case the effect of the edge weightings were counterintuitive - the lower weighted edges in group A were activating their receiving automats more frequently. This disparity can be explained as follows: the weightings signify the 'amplitude' of the information being sent over that edge, and not the fit between the range of information that can be sent over that edge and the domain of the automaton receiving it. Hence, membrane automata that could alternate between emitting a '0' or a '1' (so-called dual output automata) would sometimes emit information that was of no value to the receiving node e.g. automaton  $T_6$  emitted a '0' or a '1' over its outgoing edges to all other automata in the membrane network and for those automata that can only receive one of those symbols there were occasions where no information was received as it could not 'read' all the information emitted by  $T_6$ . This negating effect of information on the receiving automaton was not restricted to mono input channel

automata. Given that dual input channel automata could receive information from all other membrane automata there were occasions where they would receive competing information e.g. a '0' over one edge and a '1' over another edge. Such competition between information had the effect of interference that had the effect of decreasing the input probability distribution which subsequently decreased the probability of the automaton surpassing its activation threshold. Dual symbol output automata had this effect on all automata in the network and the difference between the activity of automata in group *A* compared to group *B* was simply because they had less incoming connections to other automata in the membrane which translated into less interference (from competing information) at their inputs. This suggested that simpler automata were less effected by competing information by virtue of their lower information processing properties i.e. they were less susceptible to 'noise' from the other membrane automata.

### 8.3.2 The effect of constant random environmental noise on production dynamics

A computation niche consisting of 90,000 one-state population automata and 15 one-state membrane automata were simulated for  $1 \times 10^5$  with  $\Phi_{in} = 1$  and  $E = [r, 1 - r]$  where  $r$  was a real number in the range  $0 \leq r \leq 1$  randomly generated on each iteration. As such, the environmental input to a membrane automaton was a probability distribution and not an absolute value of '0' or '1'. The time-series of the frequency distribution of the population automata is shown in Figure 8.3b.

The structure of the steady-state population was similar to that produced by the computation niche under endogenous information flow only. However there was a noticeable reduction in the production of the automata  $T_1, T_2, T_3, T_4, T_8$  and  $T_{12}$ . These automata shared the characteristic of being mono channel input automata i.e. they could only receive one type of symbol (either a '0' or a '1'). Given that the generation of environmental noise was sampled from a uniform distribution there were times where environmental information was weighted towards the extremes (e.g.  $e = 0$  or  $e = 1$ ) which, for mono channel receivers, was detrimental as they were very unlikely to activate - if at all. Whilst this was not a phenomenon exclusive to these automata - the membrane automata in group *B* were receiving the same environmental information - the *B* group automata could benefit from the full range of environmental information as they were dual channel input automata.

The following table shows a comparison of the *ratio of activity* of each membrane automata when the population was isolated from the environment (with  $\Phi = 0$ ) and when it

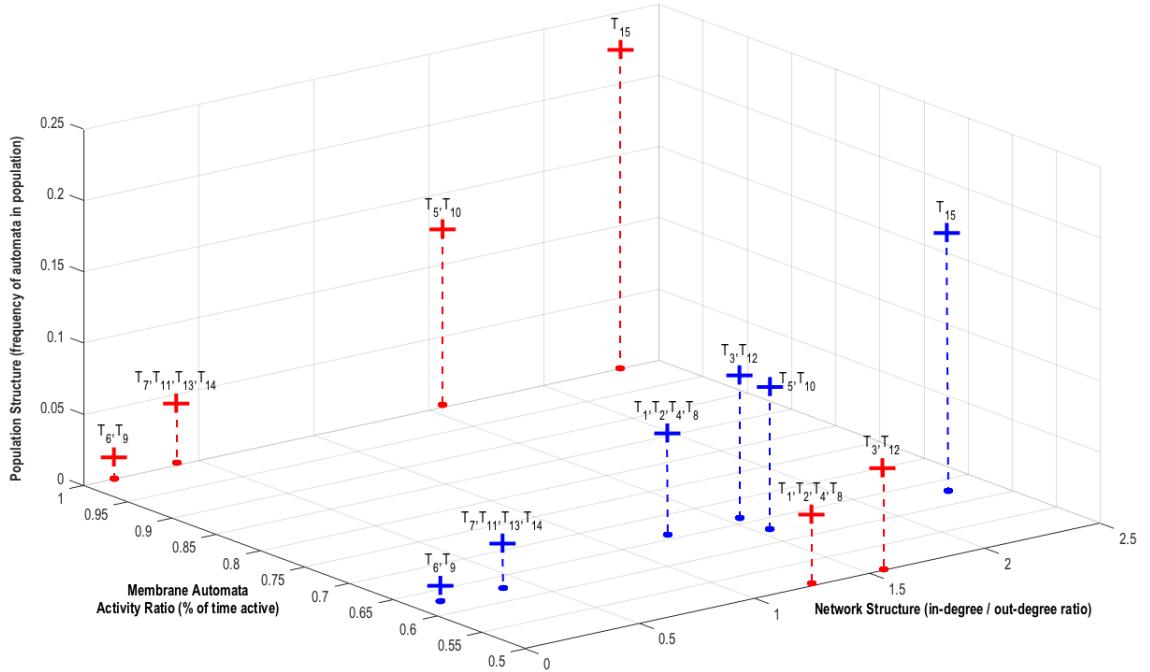


Figure 8.4: Comparison of the behaviour and structure of the internal population with (red) and without (blue) environmental noise effecting the membrane automata. Environmental noise had the most effect on the activity of membrane automata - in the absence of any environmental noise the activity range of membrane automata were tightly grouped in the range 63% to 67% of the time, compared to the range 50% to 100% of automata active over the duration of the simulation due to environmental noise. Such a difference in membrane behaviour resulted in a different population structure with the automata  $\{T_5, T_6, T_7, T_9, T_{10}, T_{11}, T_{13}, T_{14}, T_{15}\}$  increasing in concentration and the automata  $\{T_1, T_2, T_3, T_4, T_8, T_{12}\}$  decreasing in concentration.

was receiving randomly generated environmental information (with  $\Phi = 1$  and  $E = [r, 1-r]$ ):

automata	$\Phi = 0$	$\Phi = 1$	difference
set A	0.33/0.67	0.42/0.58	$\pm 0.09$
set B	0.37/0.63	0.34/0.66	$\pm 0.03$

Table 8.5: Comparison of the activity of membrane automata under isolated ( $\Phi = 0$ ) and random environmental noise ( $\Phi = 1$  and  $E = [r, 1-r]$ ) conditions showed a significant reduction in the activity of the group A membrane automata in the presence of environmental noise due to the limited processing of the mono-symbol input automata. The group B automata were also slightly inhibited however this did not significantly effect the production of those automata in the population.

As can be seen, the presence of environmental information reduced the activity of the automata in set A and increased the activity of the automata in set B. This indicated that the mono input channel automata (group A) were more sensitive to changes in environmental information. The converse was that the dual input channel membrane automata (group B) were less effected by the environment and, indeed, benefited as they

were able to process a wider range of inputs and, as such, their activity levels increased. The additional uncertainty introduced by the presence of environmental noise disrupted the normal operation of the membrane to the detriment of the simpler automata from group *A* and to the benefit of the more complex information processing automata of group *B*.

### 8.3.3 The effect of constant environmental noise of fixed value on production dynamics

Two simulations were run of a computation niche consisting of 90,000 one-state population automata and 15 one-state membrane automata for  $1 \times 10^5$  iterations with  $\Phi_{in} = 1$  and  $E = [1, 0]$  and  $E = [0, 1]$  respectively. Such values for  $E$  indicated that the probability of the environment transmitting a '0' symbol or a '1' symbol was certain. The time-series of the frequency distribution of the population automata with environmental noise at the fixed value of '0' is shown in Figure 8.3c and at the fixed value of '1' is shown in Figure 8.3d.

Environmental noise as '0': as can be seen there was a significant reduction in the population of the automata  $T_4, T_8$  and  $T_{12}$  all of which could only process a '1' symbol. As such, these automata were not activated during the simulation whilst all other automata were constantly active.

Environmental noise as '1': likewise, only those membrane automata that can process a '1' symbol were active during the simulation. As such, those automata that could not process '1' ( $T_1, T_2, T_3$ ) were not activated.

In both simulations the inactive membrane automata were also poorly produced in the internal population. Examination of the interaction matrix showed that under normal conditions (i.e. in the absence of environmental noise) the automata  $T_1, T_2, T_3, T_4, T_8$  and  $T_{12}$  were heavily involved in their own production either as self-replicators  $T_1, T_8$  or in interactions with each other. However, due to the inactive nature of these membrane automata under constant environmental noise of a fixed value, the number of interactions in the population that could produce them decreased drastically from 60 interactions producing 15 each of  $T_1, T_2, T_4, T_8$  to just 8 interactions producing two of each, and from 42 interactions producing 21 each of  $T_3$  and  $T_{12}$  to just 4 interactions producing two of each. The constant environmental noise of a fixed value decimates the interaction network for those membrane automata that remain inactive due to their mono-symbolic input channels.

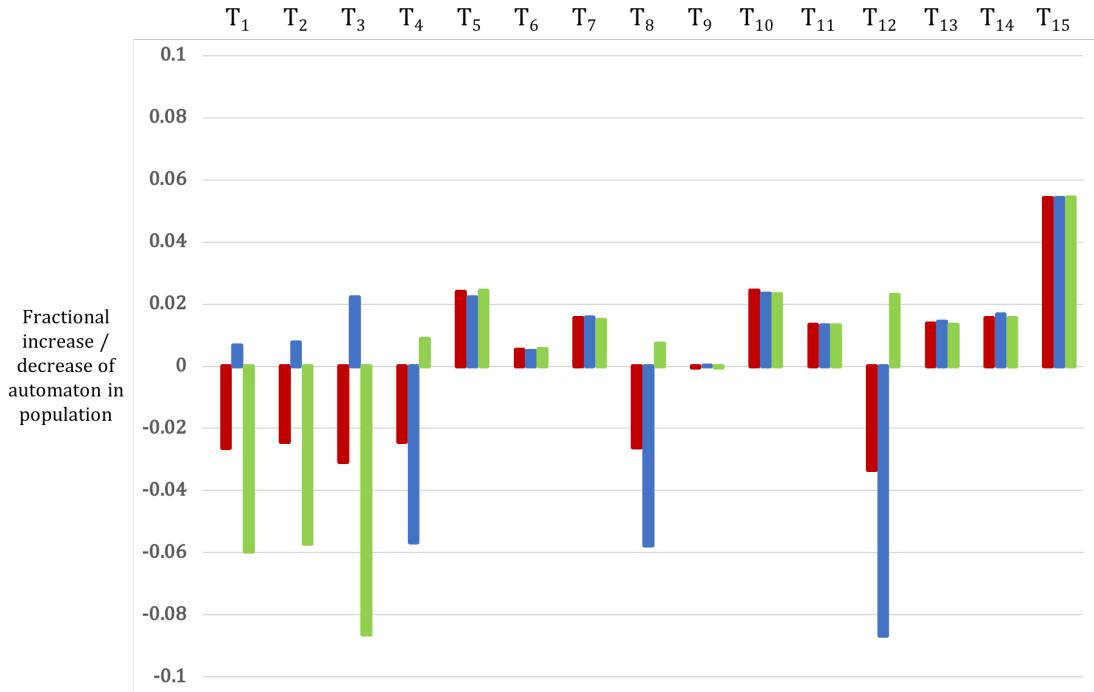


Figure 8.5: Changes in the final frequency of each automaton type as a result of changes in environmental noise. The baseline (at zero) is the frequency distribution of the population in the complete absence of environmental noise. The +/- fractional change in frequency of each automaton is shown in the presence of random environmental noise (red), fixed '0' environmental noise (blue), and fixed '1' environmental noise (green). Those automata with minimal changes across all three environmental noise settings were deemed to be more robust to environmental noise. Group A automata (mono-symbol input) are T<sub>1</sub>, T<sub>2</sub>, T<sub>3</sub>, T<sub>4</sub>, T<sub>8</sub>, T<sub>12</sub> and the remainder are Group B automata (dual-symbol inputs).

Figure 8.5 shows the fractional change in the frequency of each population automaton for each of the three environmental noise conditions examined and illustrates that the automata in the computation niche responded in three different ways to environmental noise: (i) the production of T<sub>6</sub> and T<sub>9</sub> were relatively unperturbed with minimal changes to their level of concentration in the population, (ii) the production of T<sub>5</sub>, T<sub>7</sub>, T<sub>10</sub>, T<sub>11</sub>, T<sub>13</sub>, T<sub>14</sub>, T<sub>15</sub> benefited from the presence of environmental noise by successfully occupying a higher proportion of the population, and (iii) the production of T<sub>1</sub>, T<sub>2</sub>, T<sub>3</sub>, T<sub>4</sub>, T<sub>8</sub> and T<sub>10</sub> were heavily influenced by the prevailing environmental information that under random or fixed value conditions led to some automata (T<sub>3</sub>, T<sub>12</sub>) losing over 8% of the population to other automata. Those automata in (i) and (ii) were part of group B (dual-symbol input automata) and those in (iii) were part of group A (mono-symbol input automata) thus indicating that automata with a wider 'language' were more robust to the presence of environmental noise.

### 8.3.4 Examining the information processing capacity automata were more sensitive to environmental noise

There was an association between the information processing capacity (see section 3.5.5) of a membrane automata and its sensitivity to environmental noise:

Partition	$\rho(T_i)$	automata	% activity change	edges (e)	interactions
1	1 bit	$T_1, T_2, T_4, T_8$	9% reduction	1	24
2	1.6 bits	$T_3, T_5^*, T_{10}^*, T_{12}$	9% reduction	2	27
3	2 bits	$T_6, T_9$ $T_7, T_{11}, T_{13}, T_{14}$ $T_{15}$	3% increase	2 3 4	30

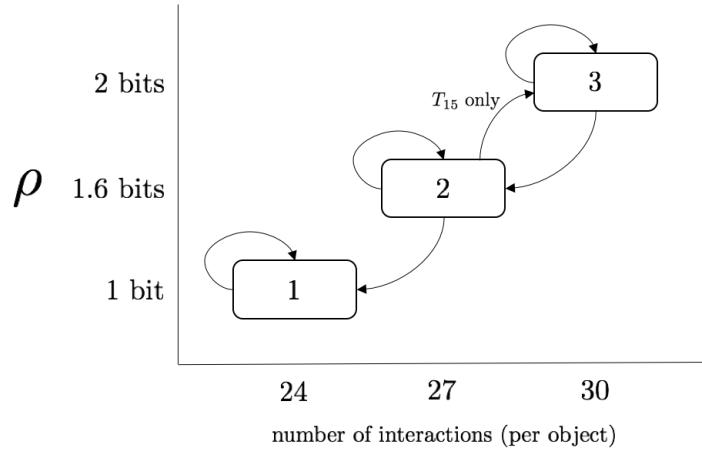


Figure 8.6: Partition map showing the flow of production of new automata between the partitions. In general, production flows either downwards to partitions of lower information processing capacity ( $\rho$ ) or horizontally within a partition. In only two cases -  $T_5 \circ T_3 = T_{15}$  and  $T_{12} \circ T_{10} = T_{15}$  from partition 2 - did production flow upwards to a higher partition due to the multiplicative effect of the functional composition of two automata.

Analysis of the behaviour of objects within and across these partitions revealed that interactions were adhering to the following condition:

Condition: If  $\rho(T_a) > \rho(T_b)$  then  $\rho(T_c) \leq \rho(T_a)$

$T_a, T_b$  automata could not create a  $T_c$  automaton of greater information processing capacity than the interacting automaton with the highest  $\rho$ . The only exception to this was in the production of  $T_{15}$ . It was not always the case that the  $T_c$  automaton would inherit the information processing capacity of the  $T_a, T_b$  automaton with the highest  $\rho$ .

Conversely, higher  $\rho$  automata could create an automaton with a lower  $\rho$ . This indicated that the production of automata flowed in two directions: downwards e.g. from partition 3 to all other partitions and from partition 2 down to partition 1, and (b) horizontally within a partition.

There was no upward flow of production between partitions with the exception of partition 2 automata to  $T_{15}$  in partition 3. This was due to the multiplicative nature of producing a new automaton e.g. the functional composition of two automata with each having only one edge ( $e$ ) can only create a new automaton with a maximum of  $e_{max} = 1 \times 1 = 1$  transitions,  $e_{max} = 2 \times 1 = 2$  and  $e_{max} = 1 \times 2 = 2$  transitions and  $e_{max} = 2 \times 2 = 4$  transitions and this latter case was how  $T_{15}$  could be constructed from partition 2 automata (which were all two transition automata).

Furthermore, automata with three transitions could not be created by 1-transition or 2-transition automata. This explains why the automata in partition 3 (with the exception of  $T_{15}$  which was a 4-edge automaton) performed so poorly in replication. They were only produced from horizontal production flows within their partition and they also participated in downward production flows which benefitted objects in the lower  $\rho$  partitions which was not reciprocated. To summarise, production flow occurred where (a) the complexity of either  $T_a$  or  $T_b$  was equal to that of the  $T_c$  except where (b) the multiplicative effect of functional composition led to the creation of more information processing capacity and this was only possible when both  $T_a$  and  $T_b$  consisted of at least 2 transitions each.

The information processing capacity ( $\rho$ ) measure was only applicable to examination of individual states of an automata as it was a measure of the scope of interactions that an automata can undertake at any time (if you like, it's interaction potential). As such, its usefulness in analysing multi-state automata was very limited as the information processing capacity was determined by the present state of the automaton. In multi-state automata the information processing capacity of the membrane automata varied dependent on its present state and the alphabet that could be processed whilst in that state.

### **8.3.5 The effect of intermittent environmental noise on production dynamics**

To further understand the relationship between the environment and population structure 11 simulations were run under various environmental conditions. Starting with constant environmental noise of '0' the population was evolved with the environment aperture set to  $\Phi = 0.5$  and the frequency distribution of each automaton was noted after  $1 \times 10^5$  iterations. This was repeated for each increment of  $E$  from  $(1, 0)$  in 0.1 increments to  $(0, 1)$ . The results

are shown in figure 8.7.

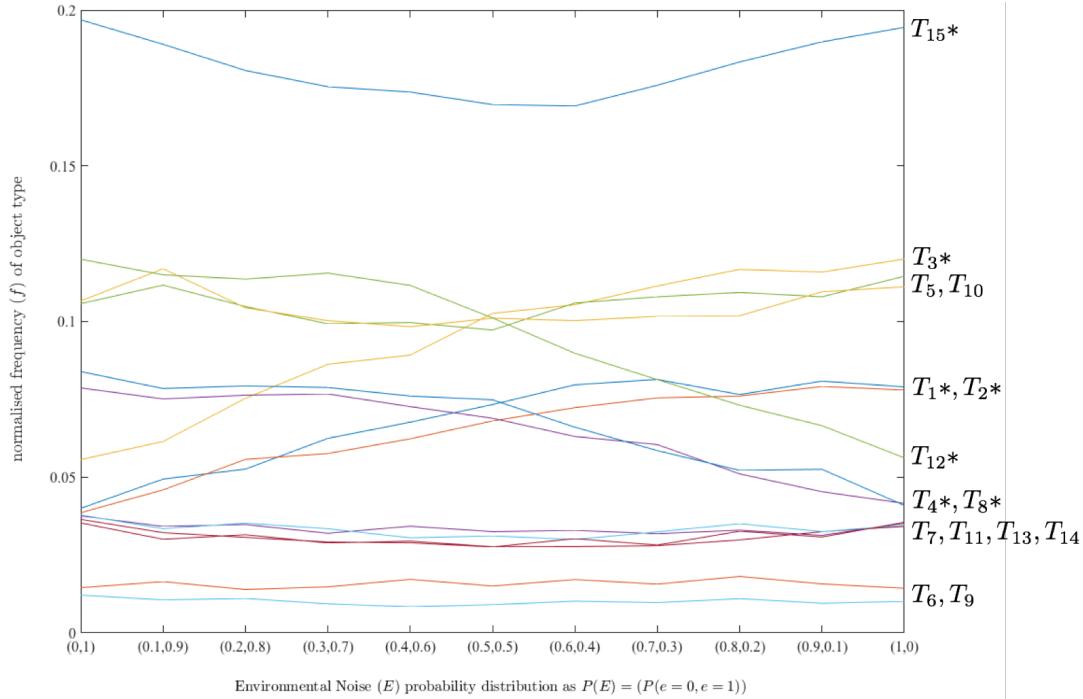


Figure 8.7: The final frequency distribution of automata types for eleven different environmental settings incrementing from  $P(E) = (0, 1) \rightarrow P(E) = (1, 0)$  and with the environmental aperture set at  $\Phi = 0.5$ . The production of seven automata (indicated by \*) were more sensitive to changes in environmental information. The  $x$  axis indicates the environmental information setting used for that simulation run and the  $y$  axis indicates the final frequency distribution of the population automata after  $1^5$  iterations. The environmental setting of  $P(E) = (0.5, 0.5)$  was the closest match to the computation niche that forms in the absence of environmental noise.

The reference point at  $P(E) = (0.5, 0.5)$  - which is the midpoint of the  $x$  axis - was where the population's frequency distribution most closely aligned to the structure of the computation niche in the absence of environmental noise. Production of some automata were sensitive to changes in the environment e.g.  $T_3$  benefitted from an environment where  $P(E) \rightarrow (0, 1)$  but fared less well where  $P(E) \rightarrow (1, 0)$ . This was a direct result of environmental information *amplifying* or *inhibiting* the information that was received by each membrane automaton. Depending on the processing that occurred at each automaton the same environmental information could *amplify* the activation of an automaton whilst simultaneously *inhibiting* the activation of another. For example, with  $P(E) = (1, 0)$  the node  $T_1$  - which only accepted a '0' symbol - was more likely to activate than  $T_2$  - which could only accept '1' symbols. This was because of the summation of inputs to each automaton surpassing (or not) the activation threshold. As such, environmental information could

reduce the activation threshold for a membrane automaton meaning that it was triggered more frequently, or it could increase the activation threshold thus reducing the chances of that automaton being activated.

### **8.3.6 Examining the intensity of environmental noise on production dynamics**

To examine the effect of the *intensity* of the flow of information from the environment on automaton production - the influx rate  $\Phi_{in}$  - the previous simulation (of examining the final frequency distribution of the population for different types of information from the environment) was repeated for various values of  $\Phi$  where  $0 \leq \Phi \leq 1$  in increments of 0.1. This required 121 simulations: 11 simulations for  $E$  from  $E = [1, 0] \rightarrow E = [0, 1]$  in 0.1 increments for each of 11 different values of  $\Phi$ . Each simulation was run for  $1 \times 10^5$  iterations. The results are shown in figure 8.8.

As to be expected when  $\Phi = 0$  (no environmental noise and where the niche was exclusively processing endogenous information) there was little difference between successive values of  $E$  because environmental information had no effect on population dynamics and the variation in frequency of population automata was due to the stochastic nature of the membrane activation process. With  $0 < \Phi \leq 1$  the scale of the variation that occurred in production increased as  $\Phi \rightarrow 1$  for those membrane automata that were more sensitive to environmental information e.g. the group A automata.

### **8.3.7 The effect of modulating environmental noise with emissions from the computation niche**

To examine the effect of emissions from the niche entering into and modulating the environment five simulations were run for various outflux rates of  $\Phi_{out} = \{0, 0.25, 0.5, 0.75, 1\}$  and with the rate of environmental noise into the niche set to  $\Phi_{in} = 1$  throughout. The time-series data of the environmental information was captured on each iteration of the simulation and this was used to generate a histogram with the value of each data point allocated into 1 of a 100 bins. This resulted in a distribution of the likely environmental information values observed during the simulation. The histogram values were normalised and the Shannon entropy of the resultant normalised frequency distribution was calculated:

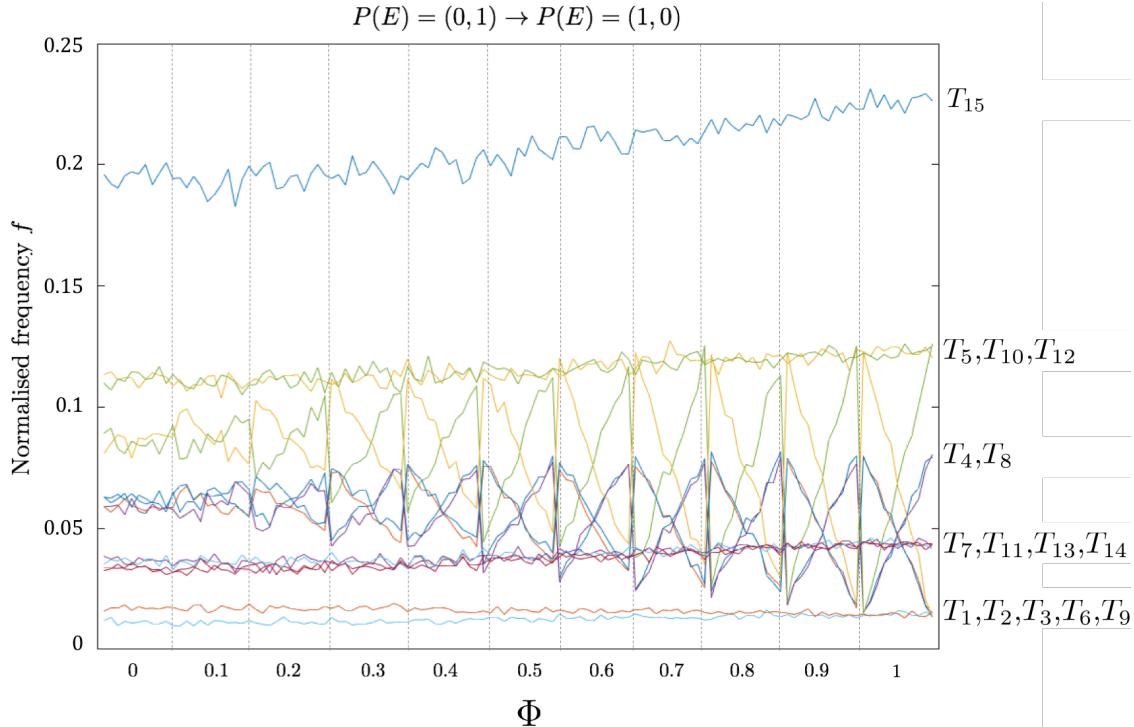


Figure 8.8: The level of structural change that was occurring within the niche was dependent on the rate of information flow into the niche from the environment. The  $y$  axis shows the frequency of occurrence of an automaton type at the end of the simulation. Each column - separated by a vertical dotted line - showed the results from 11 simulations for various environmental values for a given value of  $\Phi$  as indicated on the  $x$  axis. For example, for each of the 11 simulations for a given  $\Phi$  the environmental information was incremented from  $P(E) = [0, 1] \rightarrow P(E) = [0, 1]$  in 0.1 increments. For each simulation the computation niche was allowed to evolve for  $10^5$  iterations at which point the frequency of each automaton type was recorded. There were three types of observed changes in the structure of the niche. Some automata types were produced more frequently as  $\Phi \rightarrow 1$ , some automata types experienced drastic oscillations in their rate of production as a result of environmental information and an increasing value of  $\Phi$ . The rate of production of the two automaton types ( $T_6, T_9$ ) converged at  $\Phi = 1$ .

$\Phi_{out}$	$H_{env}$ (bits)
0	6.64
0.25	6.48
0.5	6.26
0.75	5.94
1	6.21

Table 8.6: The Shannon entropy of the environment ( $H_{env}$ ) for increasing rate of emissions from the computation niche ( $\Phi_{out}$ )

In general as the rate of niche emissions into the environment increased (as indicated by a higher value for  $\Phi_{out}$  in Table 8.6) the greater the reduction in the entropy of the

environment. However, there was an increase in environment entropy with  $\Phi_{out} = 1$  as the environment was now fully mirroring the structure of the niche which had a flatter distribution than the one seen in the environment with  $\Phi_{out} = 0.75$ . Several subsequent re-runs of the simulation in the range  $0.75 \leq \Phi_{out} \leq 1$  identified that there was a steady increase in environment entropy as  $\Phi_{out} \rightarrow 1$ . Hence, with  $\Phi_{out} = 0.75$  was the most effective at reducing the entropy of an environment that was randomly generating binary information. This was examined in further detail below (also see Figure 8.9).

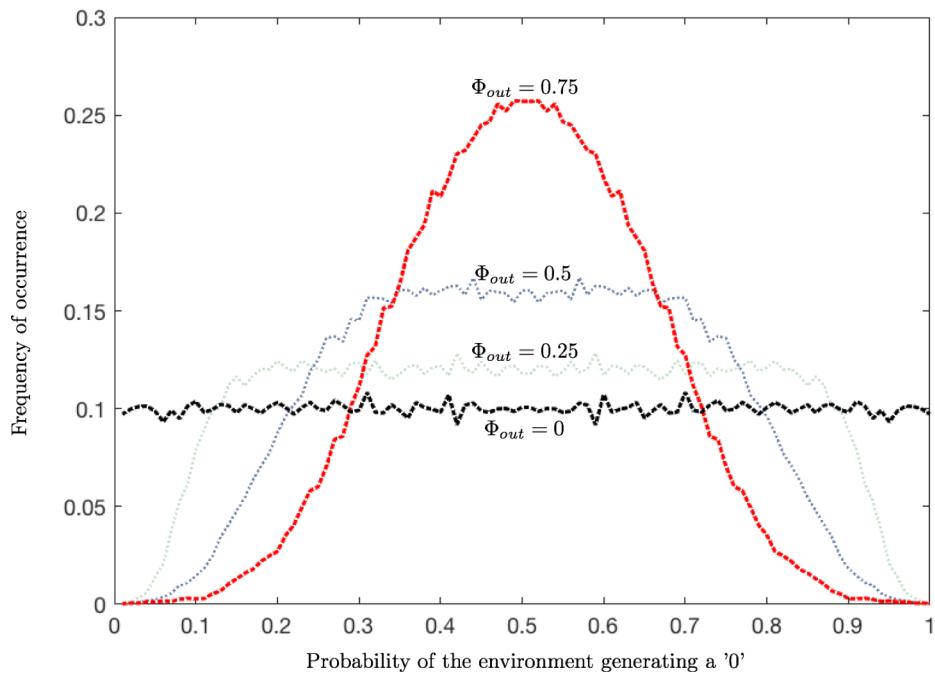


Figure 8.9: Histogram of the value of  $E$  throughout four different simulations with varying values of  $\Phi_{out}$ . The stronger the coupling of the computation niche to the environment the greater the reduction in the information entropy generated in the environment up to a maximum of  $\Phi_{out} = 0.75$ . Higher rates of outflux of niche emissions into the environment led to a subsequent increase in entropy due to the environment beginning to completely mirror the niche structure.

The emissions from the niche were decreasing the Shannon entropy of the environment thus reducing uncertainty about its next most likely transmission. Hence, the niche was ordering the environment which, given the cyclical nature of the computation niche model, meant that the behaviour of the membrane should also become more predictable. There was a noticeable effect on the population dynamics when environmental information was being modulated by emissions from the niche (see Figure 8.10) that were similar to that found when simulating the effect of random environmental noise on membrane activity

### **8.3. THE EFFECT OF A MEMBRANE ON A SELF-PRODUCING POPULATION**

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(see Figure 8.3b). Although there were slight changes in the structure of the population for various values of  $\Phi_{in,out}$ , the Shannon entropy of the frequency distribution of automata at  $t_{max}$  was  $\approx 3.6$  bits in all cases indicating that the identity of the computation niche was retained under the influence of environmental noise that was being modulated by emissions from the niche itself.

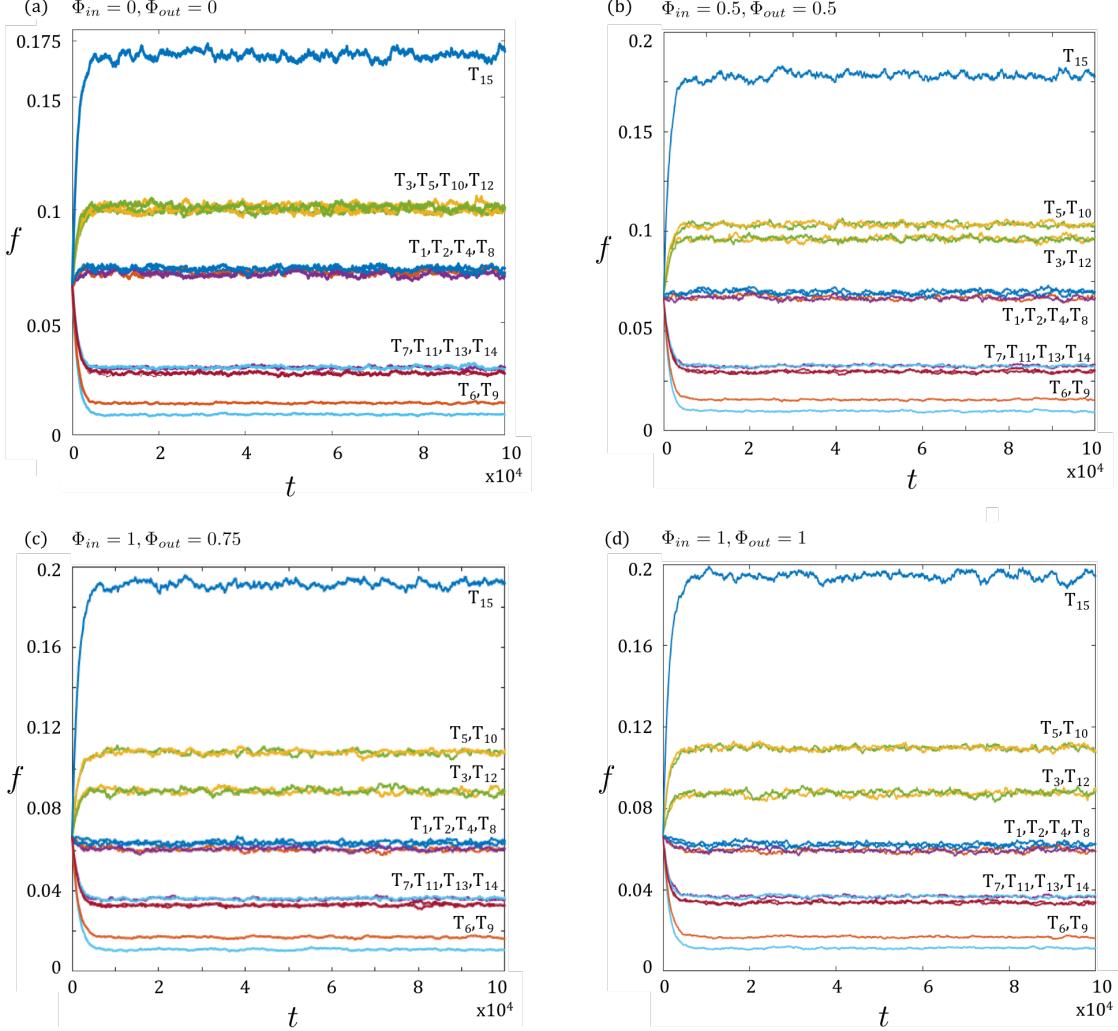


Figure 8.10: The time-series plots of the frequency distribution of the computation niche population over  $1 \times 10^5$  iterations for various  $\Phi_{in,out}$  values: (a) the nominal population structure of the computation niche under endogenous information flow conditions with  $\Phi_{in} = 0, \Phi_{out} = 0$ ; (b) the population structure where a partial exchange of information between the environment and the niche was occurring with  $\Phi_{in} = 0.5, \Phi_{out} = 0.5$  leading to some separation of the  $T_3, T_5, T_{10}, T_{12}$  concentrations with the reduction in number of the  $T_3, T_{12}$  automata due to their only processing single symbols (e.g. '0' or '1' but not both); (c) the population structure where information flow within the computation niche membrane was solely from environmental noise ( $\Phi_{in} = 1$ ) and with the environmental noise itself mostly influenced by the emissions from the niche ( $\Phi_{out} = 0.75$ ). As can be seen there was a greater reduction in the production of  $T_3, T_{12}$ ; (d) the population structure where the 'information coupling' between the niche and the environment is total i.e. the membrane of the niche solely processed environmental noise ( $\Phi_{in} = 1$ ) and emissions from the niche completely determined environmental noise ( $\Phi_{out} = 1$ ) thus creating a closed cycle of information flow. As can be seen there was a reduction in the production of  $T_3, T_{12}$ .

To examine the effect of various values for  $\Phi_{in,out}$  on the entropy of the niche emissions and environmental noise, 121 simulations were run for  $1 \times 10^5$  for values of  $\Phi_{in} =$

$\{0.1, 0.15, \dots, 0.95, 1\}$  and  $\Phi_{out} = \{0.1, 0.15, \dots, 0.95, 1\}$ . The history of the niche emissions and environmental noise during these simulations were used to estimate their entropy ( $H$ ). The results were mapped according to the value of  $\Phi_{in}, \Phi_{out}$  and  $H$  as can be seen in Figure 8.11a for the entropy of the environment and Figure 8.11b for the entropy of the niche emissions.

The environment entropy map showed a steep reduction in entropy as  $\Phi_{out} \rightarrow 0.75$  before increasing in entropy from  $0.75 < \Phi_{out} \leq 1$ . This was consistent with the earlier finding that demonstrated niche emissions reducing the entropy of the environment. There was one instance, with  $\Phi_{in} = 1, \Phi_{out} = 0.75$ , where there was a sudden reduction in entropy from 5.8 bits down to 5.6 bits.

The niche entropy map showed a shallower profile with entropy decreasing with  $\Phi_{in} \rightarrow 0$  which suggested that the intensity of environmental noise on the membrane ( $\Phi_{in}$ ) increased the uncertainty of the behaviour of the computation niche (as reflected in a higher entropy of its emissions). Similarly, there was a sudden drop in entropy at the exact same point as was observed in the environment entropy niche map ( $\Phi_{in} = 1, \Phi_{out} = 0.75$ ).

Figure 8.12 reproduced the data where  $\Phi_{in} = 1$  and  $0.05 \leq \Phi_{out} \leq 1$  were increasing in 0.05 intervals. Four states of the computation niche and environment were identified: (i) with  $H_E > H_N$  the environmental entropy decreased at a faster rate than the niche entropy was increasing in entropy; (ii) there was a crossover point at  $\Phi_{out} = 0.45$  where  $H_N > H_E$  at which the environment and niche entropies continued to decrease and increase respectively; (iii) with  $\Phi_{out} = 0.75$  there was a sudden decrease in both entropies to the extent that the entropy of the emissions from the niche were now lower than that of the environment; (iv) from  $\Phi = 0.8 \rightarrow 1$  the entropy of both returned to a value close to that prior to (iii), however, the environmental entropy began to increase and at  $\Phi_{out} = 1$  the entropy of both the niche and the environment were identical.

Whilst the environment entropy changed significantly for all values of  $\Phi_{out}$  the niche entropy remained relatively stable throughout (with the noted exception at  $\Phi_{out} = 0.75$ ). The niche entropy with  $\Phi_{out} = 0.05$  was 6.08 bits and with  $\Phi_{out} = 1$  was 6.15 bits compared to the environment entropy of 6.6 bits and 6.15 bits respectively. The matching entropies  $H_N = H_E$  with  $\Phi_{in} = 1, \Phi_{out} = 1$  was anticipated as the membrane automaton only received information from the environment and the environment exactly matched the emissions from the niche. The highest ratio of  $H_N/H_E$  was 1.03 with  $\Phi = 0.65$  and the lowest was 0.92 with  $\Phi = 0.05$ . According to Fernandez et al. [117] when  $H_N/H_E > 1$  then the system ( $N$ ) is acting autonomously within its environment ( $E$ ) and they suggest that this indicated an autopoietic system.

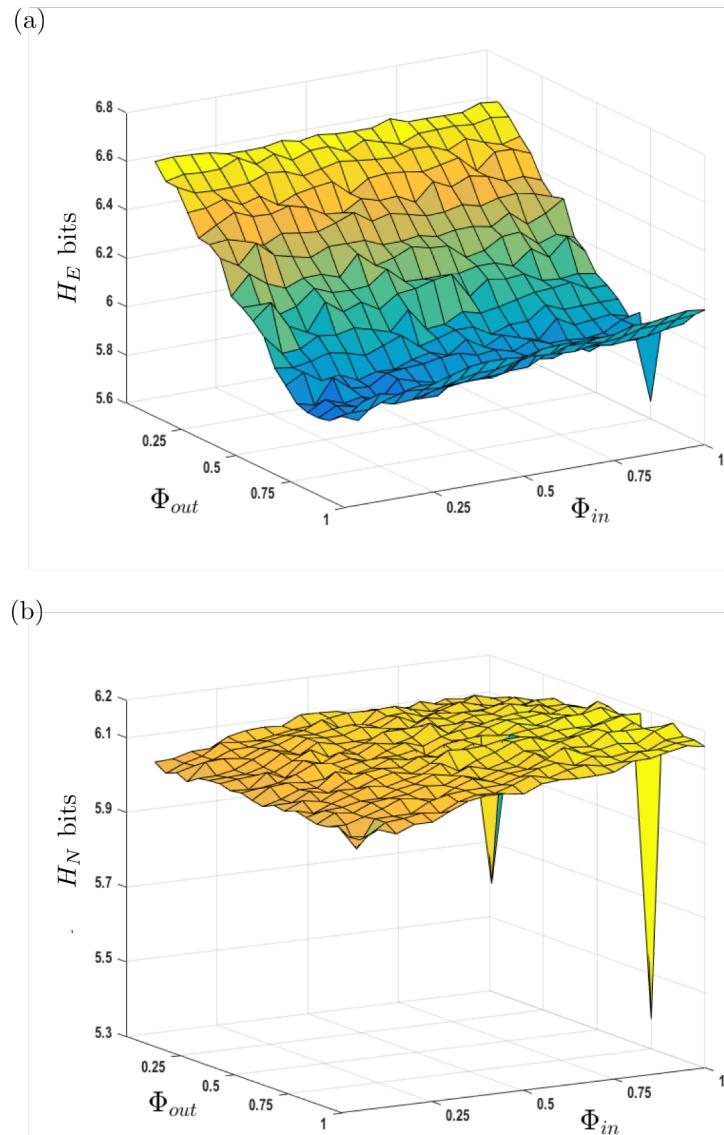


Figure 8.11: Maps of the environment and niche entropy measurements over 121 simulations for various values of  $\Phi_{in}, \Phi_{out}$ : (a) the environmental entropy map showed a consistent decrease in entropy across all values of  $0 \leq \Phi_{in} \leq 1$  and with  $0 \leq \Phi_{out} \leq 0.75$ . However, there was a steady increase in environment entropy in the range  $0.75 < \Phi_{out} \leq 1$ . The mean environment entropy was  $\bar{H}_E = 6.18$  bits with a maximum of  $H_E^{max} = 6.6$  bits and a minimum of  $H_E^{min} = 5.67$  bits; (b) the niche entropy map showing a shallower profile where the entropy steadily increased as  $\Phi_{in} \rightarrow 1$ . There was a significant dip in entropy to its lowest point at  $\Phi_{in} = 1, \Phi_{out} = 0.75$  which corresponded exactly with the minimum entropy point of environmental entropy. The mean niche entropy was  $\bar{H}_N = 6.1$  bits with a maximum of  $H_N^{max} = 6.2$  bits and a minimum of  $H_N^{min} = 5.38$  bits.

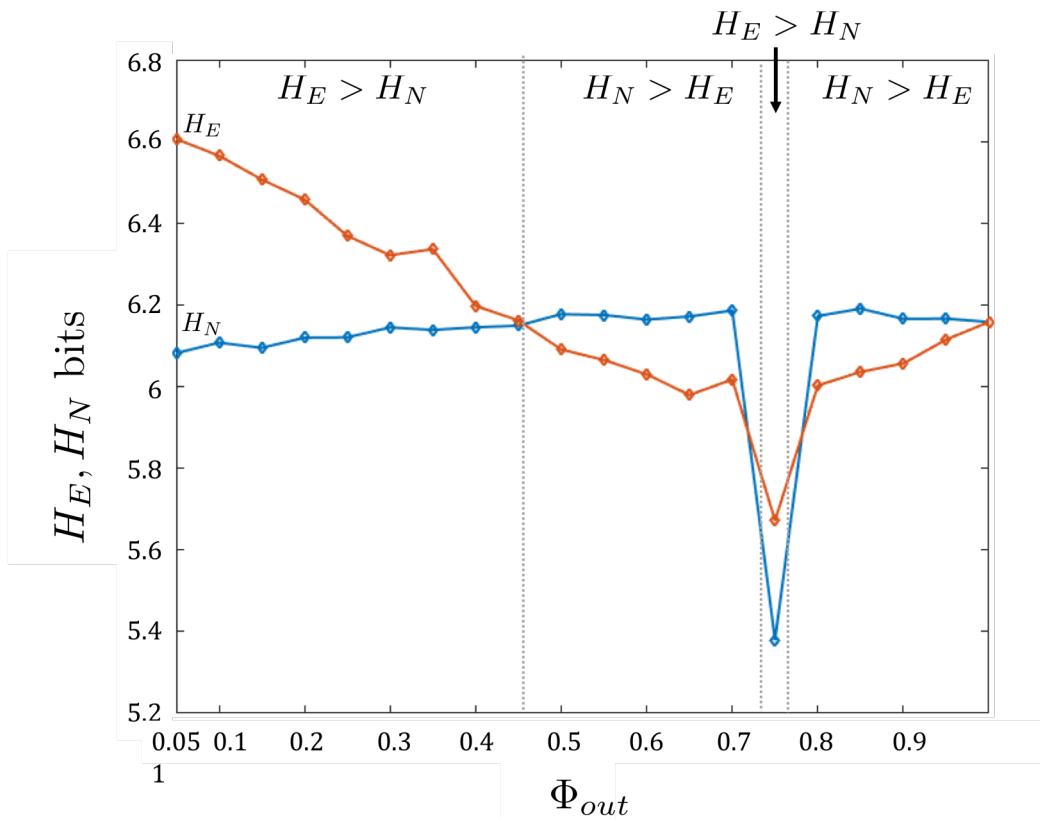


Figure 8.12: A graph comparing the changes in the Shannon entropy of emissions from the niche and the environment over 21 simulations for increasing values for  $\Phi_{out}$ . At  $\Phi \approx 0.75$  there was a distinct drop in the Shannon entropy of both niche and environment.

In summary, with an outflux of information from the niche at a rate  $\Phi = 0.75$  there is a simultaneous reduction in the entropy of both the niche and the environment. This may suggest that the coupling of niche and environment does have the effect of increasing the order of both. Further work is required to investigate what effect, if any, this increased structuring of information has on the general properties of the niche.

## 8.4 Analysis of the activity of the membrane

Analysis of the activation history of the membrane's automata showed the set of unique states that the membrane occupied. A state here is the unique configuration of membrane automata activation status (i.e. on or off) recorded in the 15-element vector  $\Psi$ . An algorithm was developed (see Chapter 3) to examine the time-series data of membrane automata activation status  $\bar{\Psi}$  which had been recorded on each iteration of the simulation. The algorithm identified each unique state that the membrane entered and how often it entered

that state during the simulation. This analysis was performed on the results from four simulations and the results are shown in Table 8.7.

$\Phi_{in}$	$E$	No. of Unique States ( $\Sigma$ )	Most Visited	Shannon Entropy ( $H(\Sigma)$ bits)
0	$\emptyset$	23,811	0.7% (683)	13.7
1	$[r, 1-r]$	22,386	6.3% (6,373)	11.9
1	$[1, 0]$	1	100%	0
1	$[0, 1]$	1	100 %	0

Table 8.7: The different states that the membrane can occupy for various environmental settings

For a simulation of the computation niche in the absence of environmental noise ( $\Phi_{in} = 0$ ) there were 23,811 unique states that the membrane occupied and in the presence of random environmental noise ( $\Phi = 1$  and  $E = r$ ) there were 22,386 unique states identified. These were very small when compared to the theoretical maximum number of states which was  $2^{15}$  and very large when compared to the number of states that the membrane occupied in the presence of fixed environmental noise. It was interesting to note that the presence of environmental noise increased the number of states that the membrane entered during the simulation and also the number of times that the membrane re-visited those states e.g. the membrane network spent 6.3% of its time re-visiting the same network state compared to the membrane network spending just 0.7% of its time re-visiting a prior state when there was no environmental noise. The Shannon entropy of the distribution of states ( $H(\Sigma)$ ) indicates that the presence of environmental noise is introducing more order into membrane activity ( $H(\Sigma_{E=r}) = 11.9$  bits) compared to the membrane acting completely under endogenous conditions ( $H(\Sigma_{E=\emptyset}) = 13.7$  bits). This is an interesting result as it suggests that the presence of random environmental noise increases the range and diversity of the activity of the membrane and yet simultaneously introduces a more structured and predictable pattern of behaviour from the membrane than compared to the membrane acting purely under an endogenous information flow (i.e. with no environmental noise). In the context of the membrane as a systems interface to a self-producing system this increased diversity and structured behaviour of the membrane could be important to the system adapting (through assimilation and accommodation processes) itself to changes in its environment. This is an observation that is worth exploring in future work.

By comparison in the presence of constant and fixed environmental noise ( $\Phi = 1$  and  $E = [1, 0]$ ) the membrane occupied and stayed in the same state throughout the simulation. In this recurring state all membrane automata that could process a '0' symbol were activated and all membrane automata that could not process this symbol were de-activated (the three membrane automata  $M_4, M_8, M_{12}$ ) throughout the simulation. Likewise, with

$\Phi = 1$  and  $E = [0, 1]$  the membrane occupied and stayed in the same recurring state but this time with all '1' symbol processing membrane automata activated and all membrane automata that could not process '1' de-activated (the membrane automata  $M_1, M_2, M_3$ ) throughout. This represented a complete lack of diversity in membrane activity which was reflected in a Shannon entropy of 0 bits.

On very rare occasions a simulation run of the computation niche in the absence of environmental noise would result in the membrane becoming completely deactivated. This subsequently led to the cessation of any production of new automata within the internal population and, hence, the system effectively 'died'. Examination of the status of the membrane automata immediately prior to this death state did not reveal any kind of unusual activity. One possible explanation is the extremely unlikely scenario whereby none of the membrane automata surpassed their activation threshold simply because the randomly generated number ( $r$ ) happened to be of a sufficiently high value for all fifteen membrane automata within the same time step. This should be a possible state, however unlikely, that the membrane could enter and did on only four occasions (in reality, several hundred simulations were run of the computation niche and the 'death state' was only observed on four occasions).

## 8.5 Cognition and the Computation Niche model

The computation niche model has demonstrated a cyclical and hierarchical process where a primitive form of learning occurs with the coupling between the membrane automata and the population automata reducing uncertainty about the future behaviour of the system based on its previous behaviour and that of the environment. The learning is stored as information in the weightings of the membrane network edges and simultaneously in the frequency distribution of the internal population. If such information represents an internal model of the system and its environment - as suggested by Robert Rosen [68],[85] and his concept of anticipatory systems - then the computation niche is a model that may be anticipating the next state of itself based on the past and present information. Such a system requires a continual renewal of the information storage and retrieval processes to maintain a steady-state distribution of information within the system. It appears that the computation niche model is able to simulate such a dynamical process. Recent developments in information theory such as transfer entropy [118] can be applied to the computation niche model, specifically, by treating certain stochastic processes as the source and destination processes in quantifying information flow. Indeed, analysing and quantifying a complex system as a computation process has been proposed by Lizier

et al. [119] and the application of such techniques to the computation niche model is recommended as future research work (see Chapter 10).

The coupling between the membrane and the environment demonstrates a basic form of structural coupling whereby the system is effecting its environment in a way that contributes to its own operation. This suggests that the operational limits of the computation niche model extends beyond the processes that are defined by the membrane/internal population as a unity. As such, the computation niche model could be a useful model for examining extended autopoiesis [17] whereby the assumption is that the operational limits of an autopoietic system includes external processes that it does not create but on which it is dependent.

## 8.6 Summary

This chapter has investigated the effect of a membrane on the population dynamics of an interacting population of self-producing automata. The main findings were:

- the membrane had a direct effect on the structure of the population by inhibiting parts of the interaction network of the internal population
- the relationship between the membrane and the internal population was cyclical with activation of membrane automata effecting the production of new automata in the interior which subsequently changed the weightings of the membrane network and which subsequently effected the information that was processed by the membrane
- environmental noise interfered with the normal operation of the membrane that, dependent on the processing behaviour of each automata, could inhibit or excite activation of a membrane automaton
- mono-symbolic membrane automata were more sensitive to environmental noise which led to their reduced activation in the presence of random environmental noise and their complete de-activation in the presence of constant environmental noise
- the greater the inhibition of the membrane the greater the change that occurred in the structure of the internal population
- emissions from the niche into the environment modulated environmental noise and which reduced the Shannon entropy of the environment

- fixed probability environmental noise had a noticeable effect on the membrane automata information processing and this led to a change in the population structure. With environmental noise constantly producing a '0' or a '1' this led to the largest disturbances to the niche. Conversely, environmental noise that flipped with equal probability between '0' and '1' had a more subtle effect on the population structure. In all cases the degree of disturbance was more pronounced as the rate at which the noise was being received into the membrane increased (i.e. as  $\Phi \rightarrow 1$ )
- a niche could 'die' when all membrane automata were de-activated which was extremely rare. In such instances the presence of environmental noise was required to resurrect the membrane automata. This observation revealed the critical importance that the environment had in perturbing a membrane to prevent it reaching a 'death state'.
- the computation niche model could be used to model related concepts of autopoiesis such as extended autopoiesis [17], Rosen's anticipatory systems [85] and in understanding how computation occurs in complex systems [119].



CHAPTER  
**9**

## RESULTS VI - NOVELTY IN A MULTI-STATE COMPUTATION NICHE

### 9.1 Introduction

Chapters 4-8 explored the emergence of information and computation niches from one-state and two-state interacting automata. Whilst the results are non-trivial the effect of novel automaton types through endogenous growth was not examined. Interactions between one-state automata can only ever produce other one-state automata, and given the constraint that all automata must belong to the special class of finite state transducers called  $\epsilon$ -machines ( $T$ ), this constrained the total number of possible one-state types to 15 (see Chapter 3). By contrast, interacting automata with two or more states ( $|Q| \geq 2$ ) could generate a new automaton that had up to  $|Q|^2$  states. That new automaton may then interact with other multi-state automata to create another new automaton with  $|Q| \times |Q|^2$  states. Each new (novel) automaton produced by multi-state automata interactions introduced a new information processing function into the population. However, for the reasons discussed in Chapter 5 the interacting populations were restricted to producing two-state automata only. This chapter now extends the computation niche model to allow uninhibited interactions between multi-state automata to allow the open-ended evolution of automata types to be investigated. Any effect that increasing the structural complexity ( $C_\mu(T)$ ) of the population may have on niche dynamics was also examined.

The questions that were being examined with the open-ended evolution simulations

were:

1. How does novelty arise in an automata population?

The ability for interacting automata with  $|Q| > 1$  was trivial and this was described in chapter 3. What are the population dynamics of an uninhibited multi-state automata population?

2. What was the effect of novelty?

In a population that initially consisted of automata that could self-replicate and where some mutual production was occurring, how did novelty affect population dynamics?

3. How does novelty compare to self-replication as a competitive strategy?

Due to a constant population size the generation of new automata displaced incumbent automata (some of which were self-replicators and some novel automata). Simultaneously, self-replicators were reproducing themselves which also displaced other incumbent automata. Given the synchronous update nature of the computation niche model all possible productions were carried out within a single time step. Data on changes in the frequency of self-replicating automata and novel automata were recorded during the simulation.

4. What can novelty tell us about the evolution of self-producing populations?

As has been seen with the information niche and computation niche models with a one-state population there were a finite number of steady-state organisations that persist (aka. a niche). These niches could not evolve in the Darwinian sense of the word and, as such, they have been described as pre-evolutionary models. To evolve required the ability for the population to generate types of automata that were different to themselves and to do so in an unrestricted manner i.e. without any constraints on the type of automata that could be produced. An environment with limited space and limited resources created competitive pressures that acted as a form of constraint on the type of automata that could persist. This interplay between creating new automata types and the ability of those types to persist was investigated.

## 9.2 Simulation Setup

The open-ended simulation used the computation niche model described in Chapter 8 and the ability to generate multi-state automata with no constraints was added to the model. For the reasons explained in Chapter 8 the synchronous update of the population was more appropriate as examining the rate of novelty generation in the population required that all possible interactions, and therefore productions, were considered at each time step. By comparison, the asynchronous update of the population only produced one new automaton on each iteration of the simulation and this would omit a significant number of other possible interactions. Hence, at the end of each iteration of the simulation all possible interactions were performed and all valid productions of new or existing automata types were accounted for. This represented the maximum development, or progression, of the population given its current composition and the completion of one full update of the population on each iteration of the simulation was referred to as a *generation* of the population.

The environmental condition experienced by the population was that of a well-mixed environment ( $c = 0, v = 0, \Phi = 0$ ). Given the primary interest here of examining the generation of novelty within a population, factors such as environmental perturbations or noise were not considered. The population size was fixed at 99,950 automata and consisted of 129 one-state and two-state automata that were selected as they were all self-replicators and also able to interact with each other to produce new automata types. This initial population was the seed from which novelty could be generated.

### 9.2.1 Generating and characterising the seeding population

It was essential that the initial population of automata (at  $t = 0$ ) had the potential to generate new automaton types beyond the initial set of automata whilst also being able to reproduce itself to a degree and thus act as a competitor to novel automata. The following criteria defined the requirements for selecting the automata that would form the initial generation:

1. The selection of automata types to use in the initial population was guided by the assumption that before the ability to generate novelty existed that the most likely types of entities that would prevail would be self-replicators. Furthermore, these self-replicators would have the potential to interact with other self-replicators and therefore had the potential to generate novel automata types

2. one-state automata were insufficient on their own as a seeding generation as they could not generate automata types that had more states than themselves. Therefore, at least two automata consisting of two or more states were required in addition to self-replicating one-state automata for constituting the seed population
3. The initial population should have the minimum complexity required to kick-start the generation of new automaton types (novel automata) whilst simultaneously not introducing any bias into the selection of that seed population
4. The initial population should include interactions that do not generate novelty e.g. self-replication or interactions that re-produce the automata within the seed population This ensured that the competitive interplay of re-production of existing automata against novelty could be examined

The seeding generation of automata met the above criteria and consisted of all one-state and two-state self-replicating automata. The presence of the one-state self-replicating automata satisfied conditions 1 and 3, and the two-state self-replicating automata satisfied conditions 1,2 and 4. The presence of all self-replicating automata ensured that no bias had been introduced into selecting the initial population (which satisfied condition 3). The seeding population was generated from examining the interaction networks for a one-state automata population ( $G_1$ ) and a two-state automata population ( $G_2$ ) of self-replicating automata. Those automata that were identified as self-replicators were added to the initial generation ( $T_s$ ). The algorithm for generating the seed set is shown in figure 9.1.

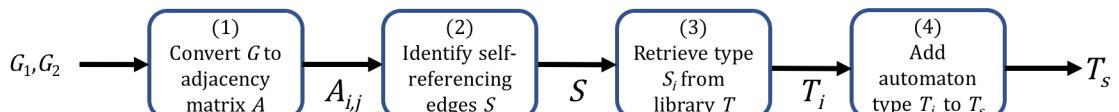


Figure 9.1: The seed population was derived from all one-state and two-state self-replicating automata of which there were 10 one-state and 119 two-state automata for a total seed population of 129 automata types

The seed consisted of 10 one-state automata and 119 two-state automata. The average structural complexity was  $C_\mu(T) = 0.87$  bits and the interaction network complexity was  $C_\mu(G) = 12.98$  bits. There were 7,978 closed productions (excluding self-replications) and 5,677 novel productions that generated automata that were outside of the seed set. Figure 9.2 shows the results of simulating the population dynamics of the seed population where the production of new automata were prohibited. As can be seen the seed population evolved to a steady-state computation niche with no loss of any of its automata. This simulation provided an important insight to the dynamics of the seed population in the

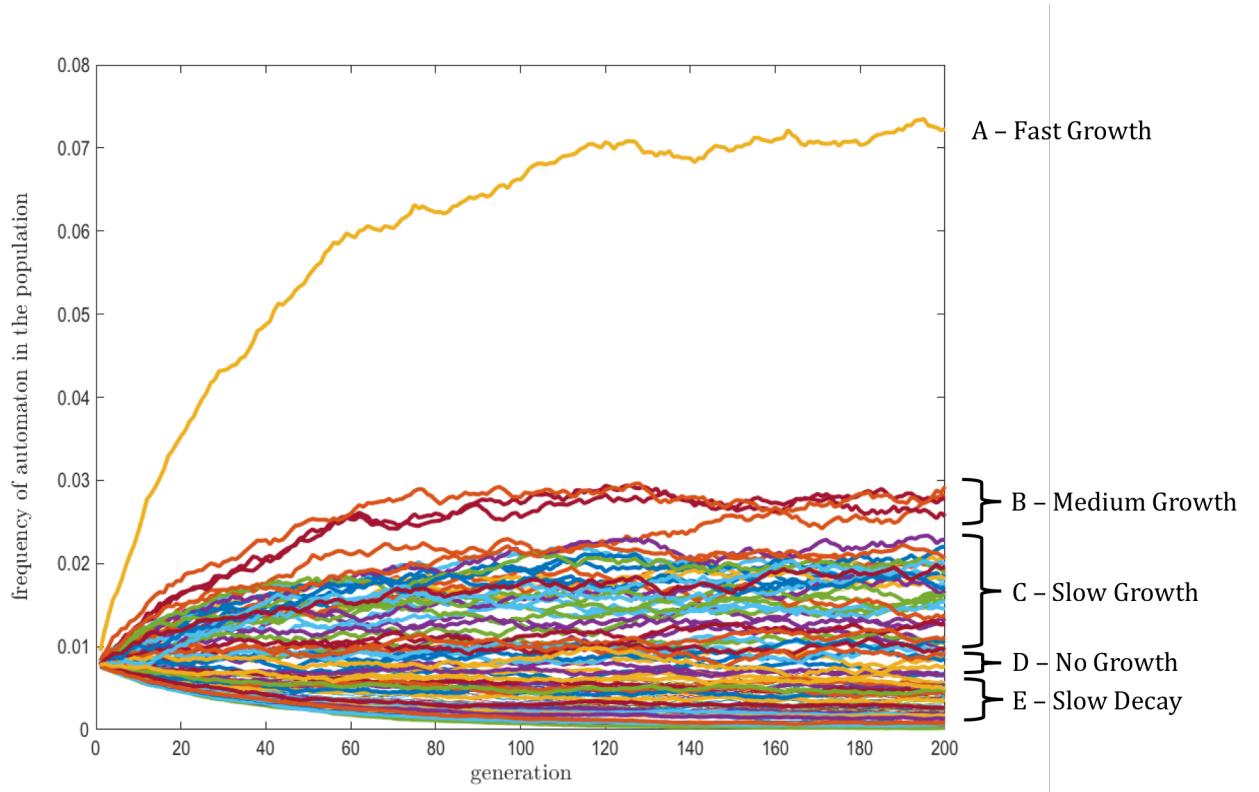


Figure 9.2: The interaction and production dynamics of the seed population over 200 generations where the production of novel automata was prohibited. The seed population had structured itself into four categories of automata: (A) Fast Growth - consisting of a single one-state automaton ( $S_{10}$ ) that accounted for 7.2% of the population, (B) Medium Growth - consisting of four two-state automata ( $S_{23}, S_{28}, S_{35}, S_{37}$ ) that collectively accounted for 11.2% of the population, (C) Slow Growth - consisting of 34 automata (four one-state and 30 two-state automata respectively) that accounted for 53.3% of the population, (D) No Growth - consisted of three two-state automata ( $S_{38}, S_{57}, S_{94}$ ) occupying 2.5% of the population, and (E) Slow Decay - consisted of the remainder of the seed population with five one-state automata and 82 two-state automata that occupied 25.8% of the population

absence of novelty which then provided a baseline for comparing to the effect of novelty on this same population.

### 9.2.2 Setting up the simulation

The simulation was initialised with an equal number ( 775) of each of the 129 automata types of the seed population which were allowed to interact under well-mixed conditions. Interactions between automata proceeded via. cascade composition, minimisation and then validated as an automaton that satisfied the criteria for an  $\epsilon$ -machine (see chapter 3). Any new automaton type ( $T_c$ ) generated from this process was added to the population by:

increasing the length of the frequency distribution vector  $f$  by  $f + 1$  to generate a new index ( $f + 1$ ) that became the unique identifier ( $k$ ) for that automaton type in the population and the membrane. The new automaton type was added to the set of all automaton types ( $T_k$ ) and the interaction that generated the automaton was added to the interaction network ( $G_{i,j} = k$ ) where  $i,j$  represented the interacting automata  $T_a, T_b$ . A membrane automaton ( $M_k$ ) was added to the membrane network and the  $M_x$  (incoming) and  $M_y$  (outgoing) edges to/from  $M_k$  were added according to  $G_k$ . This process was repeated for all valid productions of novel automata at time  $t$ . The normalised frequency distribution and the edge weightings in the membrane network were re-calculated at the end of the time step and after all valid productions had been completed. The new automata were available to participate in interactions at the next time step ( $t + 1$ ) of the simulation subject to their being activated within the membrane network (as per the normal operation of the computation niche model).

The population was initialised with the seed automata consisting of 129 self-replicators. The simulation was set to run for 50 generations and the following data was collected at the end of each generational cycle:

### **9.3 The generation and effect of novelty within a computation niche**

Figure 9.3 shows the effect of novel automata being generated from the evolving population which initially contained only the seed population. As can be seen the endogenous growth of new types of automata has a significant impact on the seed population with 85 seed automata going extinct (three one-state automata and 82 two-state automata) from the Slow Decay category with only two automatons remaining at the 50<sup>TH</sup> generation. The novel automata have grown to occupy 84% of the population by the end of the simulation.

Data Acquired	Method/Measure	Explanation
Average Structural Complexity	$mean(C_\mu(T))$ bits	The internal structure of each automaton could be quantified from estimating its statistical complexity [36] which was referred to as its structural complexity. The average structural complexity of all automata provided a quantitative measure of changes within the population
Interaction Network Complexity	$C_\mu(G)$ bits	The interaction network complexity provided a quantitative measure of the information required to describe all interactions that could occur and the likelihood with which each production could occur. An interaction network complexity that was increasing could signify two important changes: a population that was becoming increasingly diverse and/or a population that was becoming increasingly uniform
Changes in frequency distribution	$f$	The proportion of each automaton in the population was captured at each time step which revealed whether an automaton was increasing or decreasing in number
Min, Max, Mean and Standard Deviation	$min(Q), max(Q), mean(Q), std(Q)$	The statistical profile of each generation was examined: automaton with the least number of states ( $min(Q)$ ), the most number of states ( $max(Q)$ ), the average number of states ( $mean(Q)$ ) and the standard deviation of the states of automata in the population. This provided a general indication of the composition of the population at that time
Number of Automata Types	$ T $	A count of all unique automaton types in the population at time $t$

Table 9.1: The list of quantitative measurements that were used to characterise the effect of endogenous growth of novel automata on the seed population

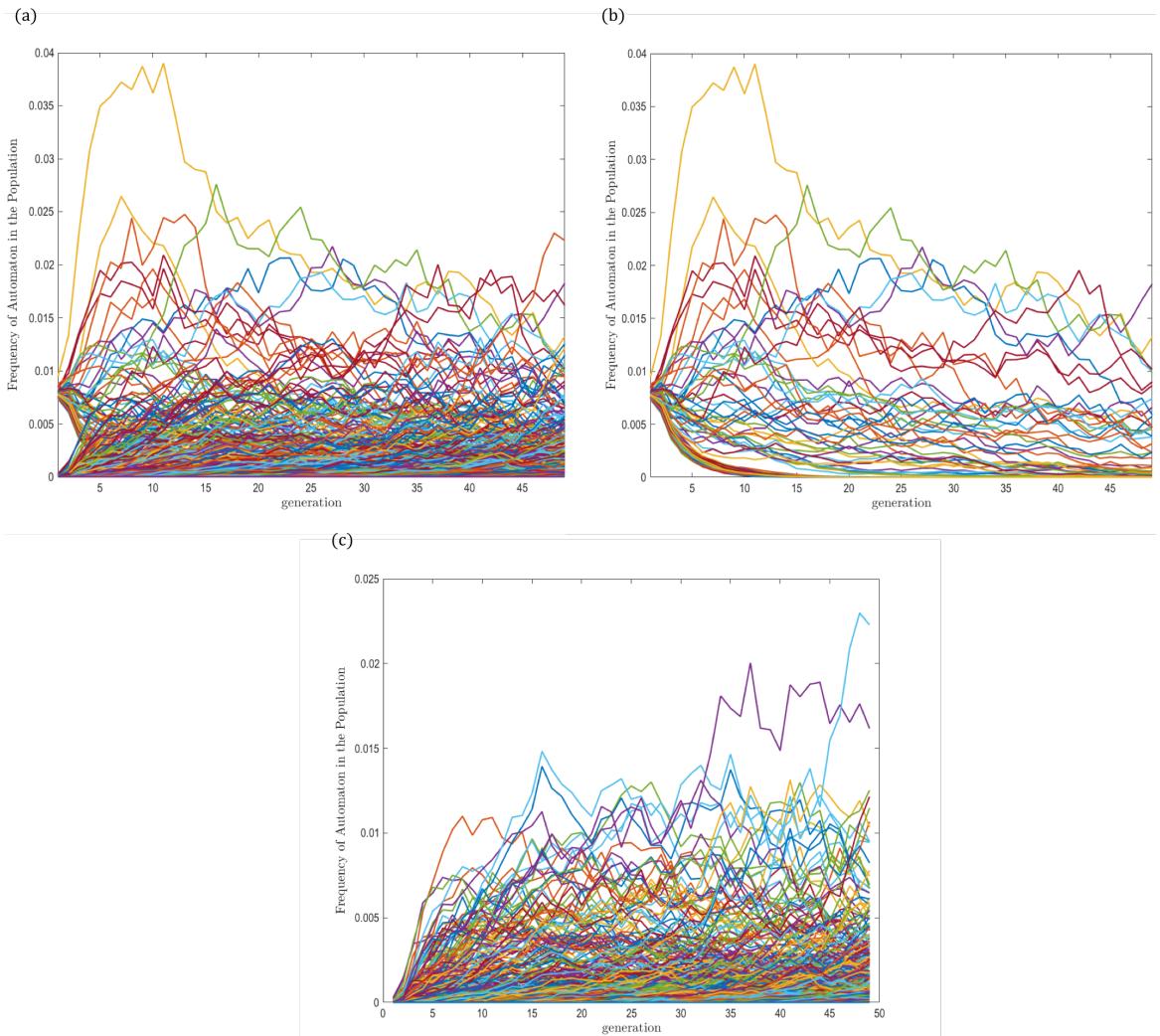


Figure 9.3: The results from simulating the population dynamics over 50 generations leading to the introduction of new (novel) automata that displaced the seed population: (a) the dynamics of the seed population only (the novel automata dynamics have been omitted) which should be compared to figure 9.2, (b) the dynamics of the novel automata only which appeared from generation 1, and (c) the combined results of (a) and (b) showing the effect of open-ended novelty generation on a seed population

### 9.3. THE GENERATION AND EFFECT OF NOVELTY WITHIN A COMPUTATION NICHE

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Original Category	Original Frequency at Generation 50	Frequency at Generation 50 under Novel Dynamics
A - Fast Growth	7.2%	1.32%
B - Medium Growth	11.2%	2.36%
C - Slow Growth	53.5%	11.65%
D - No Growth	2.5%	0.6%
E - Slow Decay	25.8%	0.0006 %

Table 9.2: Comparison of the seed population at the end of 50 generations *in the absence* of the generation of novel automata vs. the seed population in the presence of novel automata. The structure of the seed population was disrupted leading to a significant reduction in the number of seed automata down to just 15.93% and the extinction of 82 of the 129 automata that were originally present at  $t = 0$ .

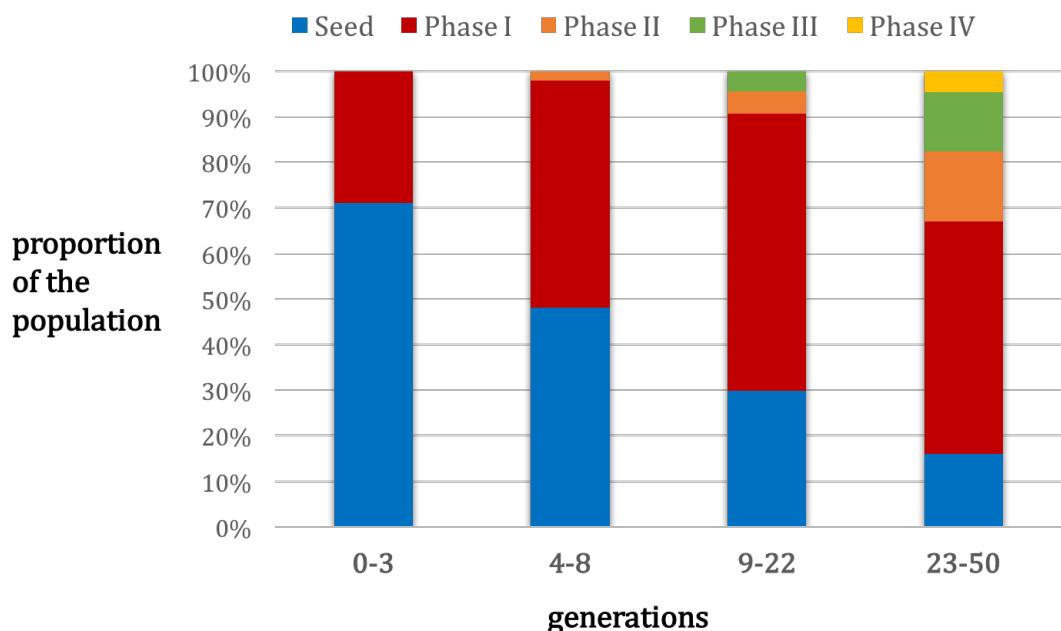


Figure 9.4: A graph comparing the relative concentration of the automata present at certain generations split into the generation in which the automata was introduced to the population. As can be seen the seed population (blue) decayed as the simulation proceeded. The novel automata that were introduced in Phase I (1-3 shown in red) actually increased in number over three generational phases and decayed at a slower rate than the seed population. Subsequent novel automata introduced in Phase II (orange) and Phase III (green) increased in concentration but at a much slower rate than the novel automata introduced in Phase I.

Examination of the population dynamics identified four phases that the automata progressed through and these were characterised as: diversification, competition, penetration, and saturation.

#### I. Diversification (generations 1-3):

The first transition of the population is dominated by an explosion of new automata types with 7,322 being introduced in just three generations. This endogenous growth of novel automata immediately displaces the incumbent automata from the initial population which experiences a reduction of their proportion in the population from an average of xxx to an average of yy. The interaction network also grows in size with 7,732 new nodes and a minimum of edges added. This is accompanied by a moderate increase in the interaction network complexity (from 13.25 to 13.77 bits) and a significant increase in the structural complexity of the population (from 1.38 bits to 1.93 bits). Even though this phase is the shortest it experiences the most significant rate of growth and increase in complexity of all the phases.

## II. Competition (generations 4-8):

The second transition is characterised with increased competition between incumbent automata and novel automata. The novel automata are establishing themselves in the population and increasing the range and number of their interactions with other automata. This is displacing more of the incumbent automata which see their relative proportions continue to decrease over this period. The growth of the interaction network is introducing more structure into the population which is leading to a reduction in the uncertainty over which automata will be produced. The reduction in the interaction network complexity (from 13.69 to 13.15 bits) supports this observation. As the majority of productions are of existing automata this leads to a significant decline in the rate at which novel automata are produced (570 novel automata introduced over five generations compared to the previous phase of 7,322 novel automata within just three generations).

## III. Penetration (generations 9-22):

The third transition is defined by the continued growth and establishment of existing automata that increases their overall proportions within the population. The continued rise in frequency of these automata with the simultaneous decrease in the frequency of the seed automata introduces more uniformity into the distribution of automata within the population. This is commensurate with the sharp increase in the interaction network complexity (from 13.18 to 14.51 bits). This internal consolidation of existing automata is also supported by the

### 9.3. THE GENERATION AND EFFECT OF NOVELTY WITHIN A COMPUTATION NICHE

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significant reduction in the rate of novel automata being produced over this period (an average of 72 new automata per generation).

#### IV. Saturation (generations 23-50):

The final phase is characterised by the rate of change of the population reducing significantly. This phase is similar to the previous phase - increased penetration and consolidation within the existing population at the expense of new automata being produced - except that the inter-generational changes are significantly smaller. For example, the production rate of novel automata has reduced from 72 per generation to just 42 per generation in this phase. The rate of change within the interaction network also reduces as fewer new automata types are being added to the population. Indeed, the interaction network complexity (from 14.57 to 15.71 bits) see's a significant slow down with an increase of 0.04 bits per generation compared to 0.17, 0.1 and 0.07 bits for the phases I-III respectively.

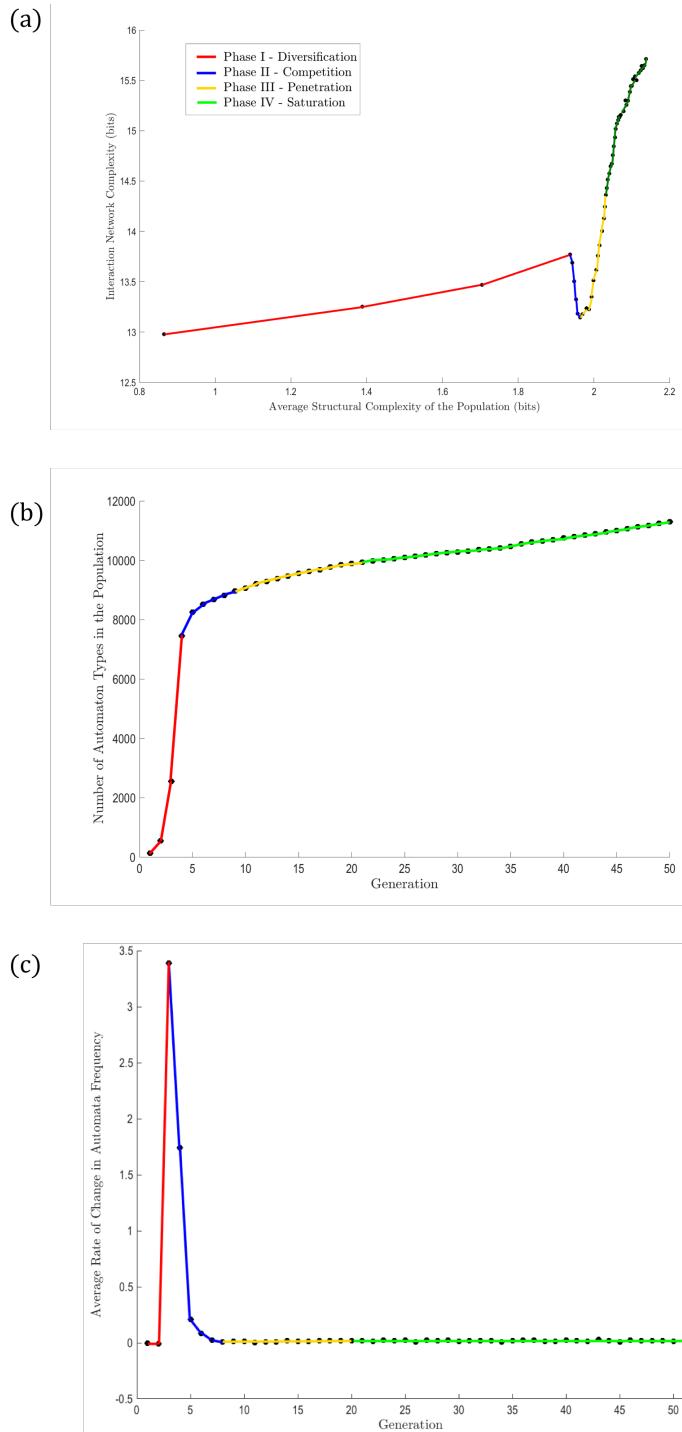


Figure 9.5: Changes in the population over 50 generations could be classified into four distinct phases I - Diversification, II - Competition, III - Penetration and IV - Saturation : (a) the Interaction Network Complexity ( $C_\mu(G)$ ) vs. the Average Structural Complexity of the Population ( $C_\mu(T)$ ) over the 50 generations, (b) the Number of Automata Types in the population at the end of each generation, and (c) the Average Rate of Change in Automata Frequency in the population indicating that an initial and significant re-structuring of the population was followed by a drastic levelling off of the rate of novelty and the emergence of a steadier and more incremental introduction of novel automata

#### 9.4. ANALYSIS OF THE EFFECT OF NOVELTY ON POPULATION DYNAMICS

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Description	Generation	Average $C_\mu(T)$ (bits)	$Q_{min}$	$Q_{max}$	$Q_{mean}$
Diversification	1-3	1.38 to 1.93 0.55	1	8	3.75
Increased Competition	4-8	1.94 to 1.96 0.02	1	12	4.5
Penetration	9-22	1.97 to 2.03 0.06	1	17	4.8
Saturation	23-50	2.04 to 2.13 0.09	1	34	5.3

Table 9.3: Comparison of the Average Structural Complexity of the Population  $C_\mu(T)$  and the automaton with the least number of states ( $Q_{min}$ ), the maximum number of states ( $Q_{max}$ ) and the mean number of states ( $Q_{mean}$ ) in the population for each of the four dynamic phases

Description	Generation	$C_\mu(G)$	Rate of Change in $C_\mu(G)$ per Generation
Diversification	1-3	13.25 to 13.77 0.52	0.17 bits/gen
Increased Competition	4-8	13.69 to 13.15 -0.54	0.1 bits/gen
Penetration	9-22	13.18 to 14.51 1.33	0.09 bits/gen
Saturation	23-50	14.57 to 15.71 1.14	0.04 bits/gen

Table 9.4: Comparison of the Interaction Network Complexity ( $C_\mu(G)$ ) and how much it changed (Rate of Change) across the four phases of the population

Description	Generation	No. of Types	Average Rate of Change
Diversification	1-3	129 to 7,451 7,322	2,440/gen
Increased Competition	4-8	8,253 to 8,823 570	114/gen
Penetration	9-22	8,968 to 9,977 1,009	72/gen
Saturation	23-50	10,010 to 11,302 1,292	46/gen

Table 9.5: Comparison of the composition of the population by the number of unique types and the rate at which new automata were being introduced within each dynamic phase.

## 9.4 Analysis of the effect of novelty on population dynamics

### 9.4.1 Properties of the population

The interaction network complexity ( $C_\mu(G)$ ) of the seed population at  $t = 0$  was 12.98 bits and underwent a very modest reduction to 12.82 bits when dynamics were driven under closed conditions (i.e. novel automata were forbidden) and significantly reduced to 8.33 bits in the presence of increased competition from novel automata being produced and introduced into the population. The average structural complexity ( $C_\mu(T)$ ) of the seed population at  $t = 0$  was 0.87 bits which was retained under closed conditions and increased to 0.9 bits in the presence of competing novel automata indicating that automata with a

lower structural complexity were, on average, less competitive and were more likely to go extinct.

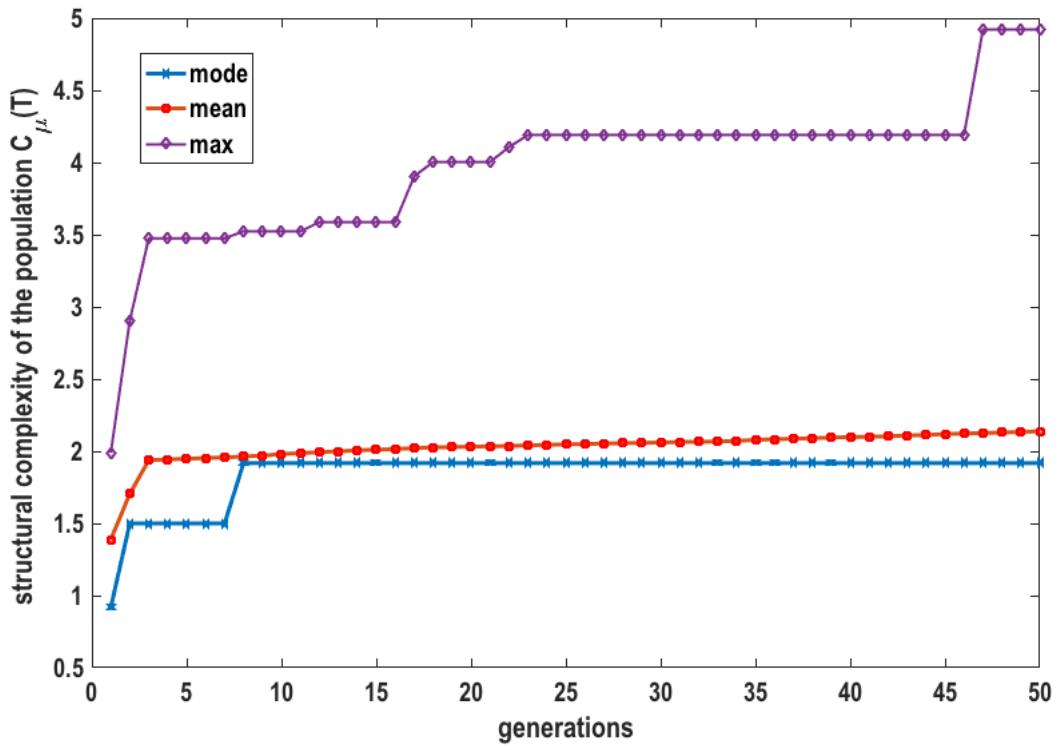


Figure 9.6: Comparison of the mean, mode and the maximum structural complexity present in the automata population at each generation. Whilst the population is still generating increasingly complex automata the mean is only incrementally increasing whilst the overall mode of the population is locked in from the 8th generation. These estimates are consistent with what is expected from a 'passive evolution' process [3].

## 9.5 Summary

This chapter has examined the introduction of novel automata into an existing population. The key findings are:

- An interacting seed population that consisted of 129 self-replicating and network-replicating one-state and two-state automata interacting under the constraint that novel types of automata were forbidden, self-organised into a steady-state organisation structured into five clusters: A - Fast Growth automata (1 off), B - Medium Growth (4 off), C - Slow Growth (34 off), D - No Growth (3 off) and E - Slow Decay (82 off)

- The same simulation was re-run but now with novel automata able to be produced and this resulted in the population failing to self-organise into a distinct, invariant organisation and instead transitioned through four phases: Diversification, Competition, Penetration and Saturation. After an initial explosion of novel automata (the Diversification phase) and within three generations of the population, the growth rate of novel automata types rapidly plateaued as internal competition came to dominate (the Competition phase) leading to the establishment of novel automata as the dominant types in the population (the Penetration phase) prior to a gradual slowing down of both the level of competition within the population and the rate at which novel automata were being produced (Saturation phase)
- The initial (seed) population was devastated by the endogenous growth of novel automata and its size was reduced from occupying 100% of the population to just 16% at the 50<sup>TH</sup> generation and with 82 of the original 129 automata going extinct
- Novelty removed any existing structure within the population and, in the presence of continuous novelty, prevented the establishment of any discernible structure. This was demonstrated by comparing the dynamics of the seed population with and without novel automata. In the former a steady-state emerged - a niche - whilst in the latter this structuration of the population was prevented. This was entirely due to the displacement of incumbent automata with novel automata. This was similar to the observed behaviour of a constant influx of automata as seen in the information niche results (see Chapter 4). Whilst the origin of these disruptive automata was different - an inflow of new automata from an exogenous source compared to the endogenous growth in the case of the simulations discussed in this chapter - they both demonstrate the disruptive effect that automata that are not produced from the existing interaction network have on the dynamics and structure of the population.
- The disruptive effect of novelty raises questions about the mechanism by which it can be suppressed - possibly through some regulatory feedback mechanism - to allow a steady-state structure of the population to emerge. There was a tension between diversification and consolidation in the population. A system that could intrinsically and periodically move between these two extremes could be demonstrative of a form of organisation that can operate in a 'window of viability' [120],[121]. The simulation of a system to demonstrate such viable behaviour could be the focus of future work.



CHAPTER

# 10

## DISCUSSION

Chapters 4 - 9 presented the results from simulating the emergence and dynamics of information niches and computation niches under various environmental conditions and perturbations. This chapter summarises those results and evaluates the findings in light of the research questions posed in Chapter 1 and discusses them with reference to related works in the literature.

### 10.1 Summary of Simulation Results

Chapter 4 presented the results of simulating a population of one-state automata interacting and evolving over a large number of iterations. The emergence of different information niches for various environmental conditions were identified and the information content of each niche was measured. This revealed that the ability for the population to transform its structure in response to environmental perturbations was contingent on its present structure and the nature of the perturbation both of which determined the amount of information within the population at that time. It was shown that the 'fitness landscape' that was sculpted by the environment was not traversable by the population if there was an insufficient amount of information that was required to undergo the necessary structural transformations. This is an original contribution to the field of autopoiesis.

This chapter also revealed that there were initially a very large number of production networks that were competing with each other to survive. Such inter-network competition was in addition to, and related to, inter-automata competition whereby the extinction of

an automaton type could lead to the collapse of all networks that were dependent on it. Conversely, automata that were produced by several different networks tended to persist due to the inherent redundancy with which it could be produced within the population. Further analysis of these networks revealed that the most competitive networks had four properties: (i) they were strongly connected indicating that each automaton in the network was produced at least once by other automata in the same network, (ii) that these networks were dynamically stable over time with no loss of any of their constituent automata, (iii) they were hierarchical with larger networks decomposable to irreducible elementary networks which acted as the building blocks for larger networks, and (iv) collectively the surviving networks had redundancy i.e. each automaton in the network could be produced from more than one (and typically several) different networks. These results were comparable to those discovered by Crutchfield & Gornerup [35] with two key distinctions: the discovery that the quantified information content of a niche can explain the transformation of the population structure to different niches within the environment, and (ii) the explicit definition of an information niche as a population that has transformed itself in response to changing environmental conditions to reach a new steady-state. Crutchfield & Gornerup's equivalent structures were called *meta machines* and whilst this is an accurate description of the composition and relationships of the population (a machine of machines) it does not capture the important observation that different population structures form under different environmental conditions *nor* does it capture the equally important observation that each steady-state structure has a unique measure of information. As such, referring to these steady-state structures as information niches adds a necessary biological/evolutionary context to appreciating the similarities of the dynamics and self-organising behaviour of these systems to biological behaviour. Another closely related work is that of Fontana's algorithmic chemistry which demonstrated similar structures emerging from an initially disordered state. In his work Fontana describes the emergence of Level 0 (self-replication) and Level 1 (networked replication) organisations - with the latter being a self-maintaining organisation - that are equivalent to Crutchfield & Gornerup's  $\epsilon$ -machine and meta-machines respectively. Fontana's Level 1 organisation is similar to an information niche however, as was the case with the Crutchfield & Gornerup work, there is no explicit consideration of how Level 1 organisations behave under varying environmental conditions. As such, the information niche model offers a more powerful explanatory narrative than either of these two models for how autopoietic systems form under a range of environmental conditions.

Chapter 5 presented the results for simulating a population of two-state automata interacting and evolving over a large number of iterations. This led to the emergence

of different two-state information niches for various environmental conditions. The two-state automata population was significantly more diverse (1,873 unique automata types compared to 15 automata types in a one-state population) and this led to more complex population dynamics with competition now occurring at the automata, network and the niche level. Under well-mixed environmental conditions with automata production driven entirely from endogenous automata the formation of two competing niches emerged and after a period of co-existence an abrupt event (a 'punctuated equilibrium') occurs that leads to the demise of one of the niches. By comparison, in the presence of environmental perturbations those same competing niches were now able to co-habit and co-exist within the same space. Finally, under conditions of non-diffusivity and where production of automata was dominated by local interactions only then two new competing mechanisms emerged that defined new population dynamics (the summary of Chapter 6 examines these mechanisms in detail). There does not appear to be any published work that has achieved similar results nor interpretations. The work of Gornerup & Crutchfield [122] examined the population dynamics in an open-ended model where multi-state  $\epsilon$ -machines could be generated and, whilst that particular work is more related to my work on open-ended novelty (more on this shortly) what is relevant here is that their results do not demonstrate nor do they discuss the emergence of novel forms of competition and competitive strategies between networks of interacting automata. As far as the author is aware the demonstration of the relationship between the increased diversity of the population and an increase in the range and type of competitive dynamics that emerge under varying environmental conditions is a new finding in the field of autopoiesis.

Chapter 6 presented findings on the spatial patterns that emerged on the lattice environment from the one-state and two-state simulations of the information niche model. It was observed that interesting spatial configurations emerged only under environmental conditions of zero mobility of automata (i.e. no diffusive mixing). The one-state niche that emerged under such conditions was characterised as two competing domains of one-state automata separated by a dynamic and continually produced boundary consisting of two other types of automata. This reproduced similar results in unpublished work by Piantadosi & Crutchfield [108] however my explanation of the behaviour of the boundary differs from theirs. Where they have incorporated specific terminology such as general replicators, spatial replicators and membrane replicators to describe the dynamics observed. Whilst I acknowledge the attraction of categorising the automata in this way I deemed that they were unnecessary and inaccurate. For example, they define a spatial replicator as an automaton that forms the spatial domains and are 'self-maintaining' which is not accurate. For example, the  $T_2$  and  $T_4$  automata types that constitute the domains - and in

their language are spatial replicators - are not self-maintaining because  $T_2 \circ T_2 = \emptyset$  and  $T_4 \circ T_4 = \emptyset$ . There is no renewal of automata within domains and, in effect, the automata that constitute the domains have precipitated - the inner part of domains are static. On this basis the notion of a spatial replicator that they have introduced does not concur with what is observed in the mechanics of domain and boundary dynamics. The only dynamic aspect of a domain is at its boundary where domain growth occurs through the outward growth of the boundary which is a function of the interactions between four different automata. Competitive dynamics therefore played out at the immediate interface of domains and boundaries and competition between domains was characterised by the seizure of part of a competing domain through a two-step mechanism of (a) growth of the boundary into a competing domain (as a random occurrence during the continual maintenance of the boundary) and, (b) the replication of the other domain into the 'hole' left by the boundary automaton. This 'protected outgrowth' mechanism proved to be a major survival strategy for the four participating automata with the remaining eleven automata types going extinct. There is no description or explanation of such competitive dynamics in Piantadosi & Crutchfield's work.

Simulation of a two-state population under low-diffusivity conditions resulted in similar spatial patterns with domains consisting of a single type of automaton that had grown outwards until they met other domains. However, there was no evidence of boundary-type automata. Instead the domains were in direct contact with other domains. Examination of the underlying dynamics revealed that two competitive strategies had emerged within the population: (a) a 'mutual maintenance' strategy where a subset of automata were co-operating to continually produce each other at their interface thus maintaining their immediate areas of contact, and (b) a 'replicate and lock-in' strategy that was significantly more aggressive in outward growth of a domain whereby in an interaction with other domains these type of automata would only produce themselves. Hence, not only did this allow for the transformation of neighbouring automata into themselves it also meant that there were very few automata that could perform the reverse i.e. interact with one of these self-replicating domains in a way whereby any new automata that are produced were different from one of the automata included in the interaction. This mechanism was termed 'replicate and lock-in' which was a more aggressive form of the 'protected outgrowth' strategy observed in the one-state population. The results and analysis on two-state automata under low-diffusivity conditions is a new contribution to the literature.

Chapter 7 simulated two populations - a one-state population and a two-state population - interacting either through co-location within the same space or by the transfer of automata from the two-state population into the one-state population. The simulation of

a one-state niche (1A) and a two-state niche (2B) was also executed. The main findings were that: (a) the one-state niche was able to take advantage of the presence of a large number of new automata types that did not originate from within its own niche and this led to its original automata types being produced in higher numbers. Indeed, whilst the presence of the two-state automata led to structural changes within the one-state niche the organisation (and hence its identity) of the one-state niche remained invariant. The two-state niches also retained their identity however their concentrations in a shared space was significantly reduced as the one-state niche automata increased in concentration and dominated the space. Hence, the two-state niches were able to survive and retain their identity however they did so as a smaller proportion of a more diverse population; and, (b) in the case where the one-state and two-state niches were located in separate environments but with a transfer of automata from the latter into the former, the two-state niche was reproduced in the one-state niche environment. It was observed that the method of sampling from the two-state automata niche to determine the automaton type to be transferred into the one-state niche reproduced the population structure of the donating niche i.e. the frequency distribution determined the probability distribution which over many iterations reproduced the frequency distribution of the donating population in the receiving population albeit at a smaller scale.

Chapter 8 simulated the computation niche model under a wide range of environmental conditions. With a one-state population the expected structure for a well-mixed environment was reproduced as per the information niche model thus confirming the accuracy and consistency of the results in the presence of an information processing systems interface. The membrane had a demonstrable effect on the production dynamics of the internal population which led to changes in the population structure. This, in turn, had an effect on the behaviour of the membrane as the weights on the membrane network were directly correlated to the population structure e.g. the more populous an automaton in the population the higher the weighting on the outgoing edges of its membrane-equivalent automaton. However, there was a change in the population dynamics with a membrane: no automata go extinct in the computation niche model. This was examined <sup>1</sup> and was not due - as was first suspected - to the population update occurring synchronously on each time-step rather than asynchronously i.e. any 'activated' automata in the population were deemed to interact on that same time-step whereas in the information niche model only one automaton can be produced per time step. This was examined in detail and explained in Appendix 12.4 with the conclusion that the production process in the

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<sup>1</sup>the computation niche model was re-configured to only update one automaton per time-step and several repeated simulations were run under the same conditions as the original simulation

computation niche model was partially sampling the population (due to the membrane inhibiting some population automata types) whereas the information niche model was fully sampling the population on each time step. This partial sampling had the effect of boosting the production rate of less competitive automata at the expense of the more competitive automata. The consequence of this was that previously poorly performing automata (e.g.  $T_6, T_9$ ) were retained in the population. This is potentially an important insight to the role of a biological membrane as it suggests that a process for regulating internal reactions to maximise the survival chances of all constituent components. Such a function increases the ability of the niche (aka. the biological cell) to retain sufficient information that would be required to maintain its identity under a wide range of environmental conditions. This simple insight may aid in our understanding of why compartmented structures tend to be omnipresent in living systems. This warrants further investigation and is recommended in future work.

Another key finding from simulation of the computation niche model was that automata that were too simple (e.g. that could only process one type of symbol) were not robust to extreme fluctuations in environmental information leading to their long-term deactivation in the membrane and subsequent dis-engagement of the equivalent automata in participating in interactions in the internal population. This was shown to be detrimental to their competitiveness. Finally, emissions from the niche into the environment had the effect of modulating the environmental noise that was subsequently received into the niche via. the membrane. This led to a moderate change in population structure which was demonstrative of structural coupling between a self-producing system and its environment via. an exchange of information.

Chapter 9 examined the effect of the unrestricted production of novel automata solely from interactions within a seed population of 129 self-replicating one-state and two-state automata. One-state and two-state self-replicators were chosen as the seed population as their ability to reproduce themselves whilst also interacting with other automata to generate novel automata would create a competitive survival pressure i.e. whether self-replication would outcompete novelty generation. The generation of novel automata occurred so rapidly that the population underwent significant diversification in just a few generations that the self-replicating automata were quickly displaced. Indeed, there was a runaway effect where too much novelty was introduced into the population and this prevented the establishment of any kind of structure within the population. Eventually the population became saturated with no discernible structure. As such, the conclusion was that novelty destroyed structure when left unregulated and that this may indicate a critical requirement for any kind of autopoietic system emerging from simple beginnings -

an ability to regulate novelty and diversity. In studying this finding the observation was made that there appears to be a 'window of viability' [121],[120] for self-producing systems i.e. not too simple and not too diverse. This is discussed later in this chapter.

## 10.2 Evaluation of Results

This project has sought to examine whether autopoietic systems can form from minimal and unstructured beginnings and, if so, the nature of and the properties of such a pathway. This has been achieved with the demonstration of the formation of autopoietic systems that occupy a niche within a given environment. These niches persist through a continual process of production (autopoiesis) that assimilate and accommodate (cognition) environmental perturbations through structural transformations. Each of the original research aims will now be evaluated in light of the research findings.

### 10.2.1 Can autopoietic systems form from simple, unstructured beginnings?

*Autopoietic systems that were maintaining a non-physical boundary formed from simple, unstructured beginnings.*

The formation of so-called proto-autopoietic networks emerge from a highly competitive environment and they exhibit specific properties that yield a survival advantage. Perturbing these systems revealed a degree of robustness and an ability to maintain the system's identity over time. Maturana & Varela's strict criteria for autopoiesis - that the boundary generated by the network of interactions must be physical<sup>2</sup> - is not fulfilled by these results. However, given (i) the present and contested view that systems can be autopoietic if they are maintaining a non-physical boundary and, (ii) these systems demonstrate an autopoietic process (self-producing and able to recover from perturbations) and a cognitive process (structural coupling and adaption to the environment) these systems are deemed autopoietic on the condition that they are maintaining a non-physical boundary.

*McMullin's heuristic test was passed.*

In an attempt to make progress on the contested issue of whether an autopoietic system must be maintaining a physical boundary, Barry McMullin's heuristic test [33] states that if a system can maintain its own identity in a shared space with other systems then it can

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<sup>2</sup>the continued contestation of whether autopoietic boundaries must be physical remains an ongoing issue within the field

be deemed to be maintaining a non-physical boundary. This test was applied to the results of the simulations on interacting niches (see Chapter 7) where the co-habitation of the same space by one-state and two-state automata niches was clearly demonstrated thus, on the condition that McMullin's heuristic test is deemed a credible and qualitative indicator of autopoiesis, then we can deduce that these systems are autopoietic.

*Spatial patterns emerged under extreme environmental conditions but they were not autopoietic.*

It is generally held that the formation of a boundary - or a compartment - is a critical step towards increasing biological complexity [123]. Information niches demonstrated non-trivial spatial patterning on the lattice in one-state and two-state automata populations under non-diffusive conditions. In the one-state population clearly defined domains and boundaries were evident with the boundary dynamically maintained by just four one-state automata. These domains were competing and ultimately led to the dominance of one domain leading to a homogenous structure. Boundary formation had occurred directly as a result of a competitive process and led to the success and persistence of the boundary and domain automata co-operating in that process. Compartmentation not only occurred in the most simple system (a one-state population) under a selective pressure but its formation was necessary for the survival and persistence of the entities which had constructed it i.e. the competition as to which domain/boundary pair could replicate the fastest was dependent on the continued production of those pairs. This is a clear demonstration of the basic autopoietic process in practice. The formation of domain and boundaries in some populations under certain conditions confer a significant competitive advantage on those automata that cooperate to form such relationships. The boundary automata acted as an interface between a domain and the rest of the population and, in the simulations, it was seen that the growth of the boundary by encroaching into a neighbouring domain allowed its host domain to grow into the space recently vacated by the boundary. Hence, this protected outgrowth of a domain was an important survival advantage as it reduced the diversity of the population and, subsequently, competition. The spatial patterns formed by boundary and domain automata were similar to those seen in chemical reactions whereby there is a phase separation of a mixture from one phase into two phases known as spinodal decomposition [124]. The emergent topological structure was reminiscent of the patterns that emerge in reaction diffusion systems exhibiting a Turing instability in morphogenetic systems [125]. Models of these systems have taken on a number of different forms [126] such as predator-prey [127] and activator-inhibitor [128] systems. In my simulations the environment has acted as the morphogen - an agent (normally a

chemical but in this case a change in conditions) that causes morphogenesis - by severely restricting the movement of automata so that only local interactions were possible. This changed the accessibility that automata had to the full diversity of the population. The resultant competitive automata were those that thrived on local interactions which was a function of the mutually producing networks that they formed and that were reinforced by the spatial formation of domains and boundaries.

In the two-state population domains were evident however they lacked the dynamic boundary structures evident in the one-state population. Instead the domains were immediately adjacent to each other. Three novel, competing mechanisms were identified that emerged through the spontaneous affinity of a subset of automata based on their intrinsic information processing properties. The role of the boundary was important to the growth of a domain in the one-state niche as it translated between two incompatible regions. This effect was missing from a two-state population where domains did form but, in the absence of any boundary-forming automata, the population effectively reached a state of stasis where no domains were able to grow as there were no possible interactions between surrounding domains.

### **10.2.2 If they exist, what pathways emerged and what were their properties?**

*Hierarchical, strongly connected networks were a signature feature*

A population of automata self-organised into production networks which, in a one-state population, consisted of 7,831 different networks which was reduced to just 29 networks once the population reached a steady-state. Competition between networks proceeded with their constituent members growing or decaying in quantity dependent on the nature of the network itself. For example, networks that were cyclic, redundant, hierarchical and dynamically stable were significantly more competitive than other networks. These highly competitive networks consisted of automata that were more readily produced and formed mutually producing relationships with other similar automata. The importance of cyclical, mutually producing networks itself was not a new result and has been discussed extensively by numerous prominent researchers such as Tibor Ganti [40], Eigen & Schuster [41], and Stuart Kauffman [69] whose work on such networks has been studied in depth by Hordijk & Steel [96],[39]. However, what none of these other works identified - or, at least, explicitly stated - was the quantification of the properties of competing networks. Neither did they introduce the notion that these networks were competing with other networks and that there were certain qualities which, due to their constituent components, meant

that some networks were more competitive than others. For example, Kauffman proposed that autocatalytic networks will arise given enough time and diversity [?] and Eigen & Schuster described what was required for a hypercycle to exist but neither were able to describe what actually emerged under competitive conditions and nor what the properties of those self-organised networks were. However, more recent research on the evolvability of autocatalytic networks [102], complex network formation [129], and measuring the degree of hierarchy in a complex network [130] are recognising the competing nature of the growth and persistence of such networks. In particular, the proposition that the formation of hierarchical, self-maintaining and enduring networks is a signature component of all biological organisms [131] complements my research findings. Nevertheless, there remains a gap in the literature for addressing the notion that biological networks must have formed from simpler networks that had to compete to survive. Furthermore, a quantitative analysis of the properties of competing networks does not appear to have been explicitly examined within the context of autopoesis and my contribution here was recently published [47].

The behaviour of 'networks of networks' are claimed to be markedly different to the behaviour of single networks [132] and this rapidly growing area of research has implications for a wide range of subject areas [133]. The characteristics of networks that out-compete other networks has been examined [134] and that measuring the eigenvector centrality of competing networks was an indication of success of that network. Cooperation of networks has also been examined [135]. The examination of the structure of networks in Chapter 4 could be extended to measure the eigenvector centrality of each sub-network. This could be implemented by extending the network detection algorithm to include an estimation of the eigenvector centrality of each network detected. This would simply be a case of calculating the sum of the eigenvector centrality measure of each node. If measured for each network these measurements could be used to identify critical dependencies between networks. Such an investigation could form the basis for future work (see Chapter 11).

#### *The information content of a niche*

Two measures of information - the Shannon entropy of the frequency distribution of automata and the interaction network complexity - were estimated for each steady-state that the population evolved to. This revealed variations in the amount of information contained within the population at each steady-state and - given the structurally deterministic nature of the system - this had a contingent effect on the ability of the population to adapt to changes in the environment. For example, a population in a state that contained low levels of information was not able to 'climb' to states that required higher information content.

To do so required an influx of information in the form of randomly added automata from the environment which acted as an exogenous source of diversification of the population.

Chapter 4 demonstrated how the full range of environmental conditions (given by  $c, v, \Phi$ ) created a 'fitness' landscape in which the automata population evolved. Each steady-state configuration of the population was called an 'information niche' to denote two factors: (i) that the information required to re-produce each steady-state configuration could be estimated using Shannon entropy, and (ii) that each steady-state of the population occupied a position in the fitness landscape that was created by the environment. In a one-state population six niches were identified. Each information niche could be seen as a 'local optima' [136] within a rugged landscape where the vertical axis was defined as the production threshold (the measure that I have introduced in this project which is calculated as the Shannon entropy of the information required to re-produce the niche) and the population traversing across the landscape in response to changes in environmental conditions. The actual mechanism that drove the transformation of the population from one niche to another was the accessibility of information. For example, in a well-mixed environment with some influx of external automata from the environment all possible automata interactions for a one-state population were possible. The diversity and proximity of the population under such conditions resulted in an ergodic process of production where all possible productions were examined given a sufficient amount of time (this is one reason why the simulations were run for a minimum of  $10^6$  iterations). Given that a more diverse population required more information then the production threshold to reproduce that population would also be higher. Hence, a rate of influx of automata from the environment was promoting information generation in the niche. By comparison, a low mobility environment with no influx of external automata severely restricted the accessibility of automata to the full diversity of other automata with which to interact. This resulted in interactions between automata being restricted to those that are locally available only and such a non-ergodic process eventually led to the extinction of the majority of automata from the population. As such, access to information within the context of continual self-production of the system was about the diversity and accessibility of automata for interactions and this bounded the structural transformations that were possible within the population in response to given environmental conditions. This led to the interesting observation that the population could only evolve to a niche if it already contained at least as much information as was required to describe that new niche. If the population did not have sufficient information to describe that new niche (e.g. the new niche contained automaton types that did not already exist in the population) then

additional information could only be generated through some influx of external automata. Hence, the environment created multiple attractors within an information landscape and in which several different forms of autopoietic system (niches) could emerge.

*The population consistently and repeatedly evolved to steady-state niches as defined by the environment*

A similar initial population evolving under similar environmental conditions would evolve to a steady-state niche that was similar to previous simulation results. The results were highly repeatable indicating that the information and computation niche models were deterministic for the same initial conditions and with fixed environmental conditions. Any structural variations between simulation runs were a result of the inherent stochasticity of the 'select and replace' mechanism of exchanging existing automata with new automata used in both models. The repeatable and consistent pathways that emerged on each simulation indicated the presence of an attractor. The environment defined these attractors of which there were four across the spectrum of environmental conditions in the information niche model. Even when perturbed the structural values of the population of automata (i.e. their respective proportions in the population) stayed close to the attractor values. A dynamical analysis of the information and computation niche model may yield further insight into the nature of these attractors.

*The defining features of these self-producing systems were simplicity, diversity and robustness*

Chapter 8 demonstrated the effect of environmental noise on the behaviour of the membrane. Examination of the behaviour of each membrane automaton node showed that those automata that could only process a single symbol (e.g. a 0 or a 1) were more sensitive to changes in environmental noise. This sensitivity was particularly acute where the environmental noise was at a constant value and, in some cases, this led to the long-term deactivation of some membrane automata with a subsequent catastrophic impact on that automaton type in the population. Random noise tended to have the effect of maximising the activity of the membrane automata over successive time steps. This basic observation suggested that there was a minimum level of complexity at which robustness to environmental noise became effective. In the case of an automata population this level of complexity was met when all states of an automaton could process both '0' and '1' symbols. Of course, the intensity of environmental noise (which increased as  $\Phi_{in} \rightarrow 1$ ) would convey the degree of causal influence of those symbols on the information processing that occurred in each membrane automaton and which, subsequently, determined whether its

activation threshold had been met. This raised the interesting question of whether there was a minimum level of complexity required in each class of multi-state automaton (e.g. two-state, etc.) that was robust to environmental noise.

In a population consisting of several possible niches the niche that consisted of simpler automata (e.g. one-state) were able to maintain its identity and structure whereas more complex niches (e.g. two-state) were not able to maintain their identities. This was due to the production advantage that lower complexity automata benefit from as interactions between automata tended to more often produce lower complexity automata. This advantage is driven by the need for new automata to meet the strict criteria of an  $\epsilon$ -machine i.e. the automaton must be minimised and this could have quite a drastic effect on reducing the number of states of the newly produced automaton. This observation appears to align with the idea that the most dominant species in evolutionary history happen to be the smallest [137] whilst it also appears to diverge from the generally held view that evolution moves from simple to more complex organisms [138] but this would be incorrect. Simpler automata, whilst they tended to dominate diverse, multi-state populations, they did not drive out all other types of automata. In fact, it was observed that two-state niches were being reproduced and sustained in a population dominated by one-state automata. In addition, simpler automata network together to form more complex population dynamics and from this can emerge more sophisticated processes to support more complex automata. Whilst this was not investigated rigorously during this project the notion of an information or computation niche providing a resilient platform for the development of more complex processes, structures and automata is entirely consistent with the arrow of evolution from simple to complex.

The membrane automata had an important modulating and buffering effect between the environment and the population automata. The modulation of environmental noise caused by information emitted from the membrane altered the noise that was subsequently received from the environment. The buffering effect of the membrane minimised the impact on the interactions between population automata when environmental noise was present. Instead the membrane automata processed the environmental noise and whilst this could lead to changes in the production dynamics of population automata it did not interfere with the interactions between automata. The effect that the environment had on the population was therefore indirect i.e. environmental noise could deactivate membrane automata which in turn inhibited the corresponding population automata from interacting. Environmental noise did not directly affect the interaction network in any way. The effect of the membrane on the population is starkly illustrated in the rare event

where the membrane entered a state of complete de-activation which, in the absence of environmental noise, became a permanent state leading to the death of the niche entirely. It is interesting to note that environmental noise was the only causal source that could re-activate a non-active membrane. The ability for a relationship between the membrane and the internal population to delimit the processes that make up an autopoietic system has previously been refuted by Virgo et al. [17] and instead they have proposed the concept of 'extended autopoiesis'. The emergent roles of the environment, the membrane (boundary) and the internal population that I have observed in the computation niche supports the extended autopoiesis argument. Indeed, the 'operational limits' of the computation niche has to include processes in the environment (in this case the generation and transmission of information to the autopoietic system) to ensure the long-term survival and robustness of a self-producing population.

### 10.2.3 If they exist, why and how do these pathways form?

*Competition was a fundamental mechanism that occurred at multiple levels*

Pathways self-organised through a process of competition with 'fitter' entities being produced more often thus ensuring their survival. The environment defined the fitness landscape which altered the conditions required to be competitive. The critical mechanism driving the emergence of the underlying networks of production was competition initially between interacting automata to survive in their constrained environment which, as the population evolved, extended to competition between networks and eventually between different niches. Those automata that, by virtue of their composition and interactive behaviour, formed mutually producing relationships with other automata benefited from a collective ability to endure. Redundancy within such networks ensured a degree of robustness to environmental perturbations. None of these properties were 'designed in' nor present under the initial conditions. Chapters 4 and 7 concluded that simpler automata were more readily produced compared to more complex automata. The reason was straightforward: the likelihood of two highly complex automata interacting to produce a more complex automata was much less likely than two simpler complex automata interacting to produce a simpler automata. As explained previously this was due to the requirement for all new automata to meet the criteria for an  $\epsilon$ -machine which required the minimisation of the newly produced automata. Newly produced automata that were very complex were less likely to stay in the same form after minimisation compared to an automata that was already of a very low complexity e.g. a one-state automaton could not be minimised and hence would stay as a one-state automaton whereas a multi-state automaton had a chance

of being minimised to consisting of fewer states). Or, to put it another way, there were more interactions that produced simpler automata than that produce more complex automata. To compound this issue the lack of more complex automata being produced further reduced the chances of other similarly complex automata being reproduced. As such, being a simple form of automata conferred a significant survival advantage through a higher rate of production compared to more complex automata. This finding confirms similar findings and conclusions from Gornerup & Crutchfield [122] and was also analogous to empirical evidence from the real world with the domination of prokaryotes [137].

More complex automata populations generated more complex competitive dynamics. For example, in a well-mixed two-state population two competing networks of automata emerged and it was only through chance that one of those networks came to dominate the population through a punctuated equilibrium event. This repeatable occurrence of two niches competing and eventually leading to the demise of one of those niches had an analog in ecology and the competitive exclusion principle [139].

The membrane was a noisy environment with intrinsic (information transfer between membrane automata) and extrinsic (incoming environmental information) sources of noise competing to activate a membrane automaton. As such, competition in the membrane proceeded via communication channels seeking to maximise their signal-to-noise ratio. As explained in Chapter 8 each membrane automaton acted as an information source within the membrane by being connected to all other membrane automata which could receive some or all of the information that the source automaton could emit. A membrane for a one-state population was highly connected and, as such, each automaton node within the membrane network had at least nine incoming edges (receiving channels) which were integrated into a single two-point probability distribution that potentially triggered the automaton to activate and emit information over its outgoing edges (transmit channels). The integration of incoming information was a competition between the various information sources with weak incoming signals (i.e. from an edge with a low weighting that was sending binary information that was marginal when compared to all other symbols being received at the receiving automaton's input e.g. a '0' is emitted when all other competing channels are emitting a '1') failing to have a significant effect on the subsequent behaviour of the receiving membrane automaton as it would be less likely to surpass the randomly determined threshold. Concurrently, each membrane automata was also receiving information from the environment that acted as a another competitive communications channel. This kind of analysis of the dynamics of the membrane network as information is transferred, processed and modified lends itself to network information theory [140] which was

developed to quantify and understand systems where there were multiple, concurrent information sources and receivers. Adoption of network information theory to the study of the computation niche membrane dynamics is recommended for future work.

Environmental noise had a significant effect on the activity of membrane automata which tended to be to the benefit of automata that had more computational capacity i.e. they could process '0' and '1' symbols rather than one or the other. The environment (as an extrinsic information source) was competing with intrinsic noise in the membrane whilst simultaneously emissions from the niche modulated environmental information. The noisy environment of the membrane - with automata activating and transmitting simultaneously and that led to changes in the production of new automata - has an interesting analogy to gene expression noise and the effect it had on cellular behaviour [141], [142]. Indeed, the quantification of gene expression noise in those models treated the total noise as the sum of the intrinsic and extrinsic noise which was consistent with how this was handled in the computation niche.

The environment had a two fold effect on the competitive process in the niche. The first factor - the global parameters  $c, v, \Phi$  - had a significant effect on the competitiveness of individual automata and production networks as all automata were effected simultaneously. For example, the automata that were highly successful in a well-mixed environment were not at all as effective in a low mobility environment. The environment effectively created a fitness landscape [136] which via. competition within the niche, led to the population transforming its structure until a new steady-state was reached. The second factor - environmental noise affecting operation of membrane automata - had a dramatic effect on the flow of information within the membrane which subsequently effected the production of automata by promoting the production of automata that had a higher information processing capacity.

In some instances the environment acted to stabilise population dynamics by introducing variation into the population that had the effect of reducing the rate of production of highly competitive automaton networks. For example, the co-existence of two two-state competing networks was only present when there was an influx of randomly generated automata from the environment that prevented the punctuated equilibrium event from occurring. This interesting observation - of a stochastic process (the environment) having a stabilising effect on a population and that allowed for the co-existence of competing entities [143] - has been observed in population growth models [144], ecological niches [145], and climate change studies [146]. Indeed, the theory of coexistence [147] has shown that environmental variation can buffer inferior competitors against the competitive exclusion principle [139].

*The environment triggers changes in the population*

Chapters 4 and 5 showed the effect of the environment on the behaviour of a population of automata. The simulations examined population dynamics under fixed and intermittent conditions and with and without disturbances in the form of material or information influx. The notion of a fitness landscape was introduced in the paper that was reproduced in Chapter 4 and the population progresses around this landscape via structural transformations resulting from changes in the underlying production of automata. The production dynamics were driven by the interaction network and the current concentration of each automata in the population. This combination determined the probability with which each automaton type would be produced. The environment conditions affected these probabilities in three ways: (i) inhibition (or not) of interactions due to restriction of movement of automata, (ii) inhibition or amplification of interactions due to signalling changes from the membrane, and (iii) the introduction of new automata from exogenous or endogenous sources.

Under fixed environmental conditions it was shown in Chapter 4 that the simpler the automaton (as measured by its structural complexity) the more easily it could be reproduced and, conversely, the chances of reproducing a more complex automaton (with increasing structural complexity) were reduced when they co-existed with simpler automata. Changes to the environment that affected mobility and the influx of new automata did not appear to change this relationship. However, under intermittent and fluctuating environmental noise the more complex automaton in the population fair better as they have the greater information processing capacity required to handle more uncertainty e.g. a more complex automaton may be in a state with the ability to receive a '0' or a '1' symbol meaning that it could continue to interact with other automata whereas that same environmental noise was inhibiting the activity of other automata that were in a state with only one input possibility (e.g. they could accept a '0' or a '1' but not both).

In general, environmental conditions and environmental noise led to different effects in the information niche and computation niche models. The environmental conditions of the information niche model had a global effect on all population automata by (a) impacting on the availability of automata to interact with each other due to changes in diffusivity (spatial mixing) of automata on the lattice, and (b) by acting as an exogenous source of diversification of the population with the influx of automata from outside the population. By comparison, the environmental noise of the computation niche model had (c) a local effect of activating or deactivating specific automata in the membrane which indirectly inhibited specific automaton types in the population thus altering specific parts of the interaction network, (d) maintaining or decreasing the interaction network complexity of

the population, and (e) on the rare occasions where it occurred environmental noise can increase the interaction network complexity by re-activating a 'dead' membrane leading to the production of automata in the population (but only where those automata were still present in the population). The possibility of combining global environmental conditions with localised environmental noise into a single model is a potential area for future work.

#### *Computing the attractor in the environment*

A population of interacting automata continually re-produced itself through interactions with other automata in the population. The basis of this interaction was a successful functional composition requiring the output from one automaton to be the same as the input of the receiving automaton. The new automaton then displaced an incumbent automaton. Given that each automaton represented a unique function - it transformed the information it received by mapping an input to an output - the growth or decay in the quantity of those functions in the population was an indication of how 'fit' those functions were to the current environment. As the population evolved all possible functions and organisations of those functions were explored - the underlying model and algorithm represented an ergodic process - and the resultant steady-state structure of the population represented the 'solution' that was the best fit of the population to the environment (the niche). In other words, a population of interacting automata computed the attractor in a given environment through a de-centralised and concurrent process of reproducing fitter functions.

The composition and structure of each steady-state population was measured by the Shannon entropy of the number and type of each automaton. Measuring each population in this way revealed that in some cases the population was unable to traverse the fitness landscape where the information required to describe the population at a different niche was not contained in the population and nor was new information being added from the environment. Information was therefore a measure of the complexity of each steady-state population across a range of environmental conditions.

The information niche could therefore be seen holistically as an integrating function between various information sources and factors (see Figure 10.1). The circular logic depicted in this diagram is reminiscent of the model of a minimal autopoietic system [8], the system logic of a protocell [1] and the logic of social autopoiesis [19].

#### *Complexity begets complexity*

The computation niche simulations demonstrated that emissions from the niche had the effect of reducing the information entropy of the environment and that the degree to which

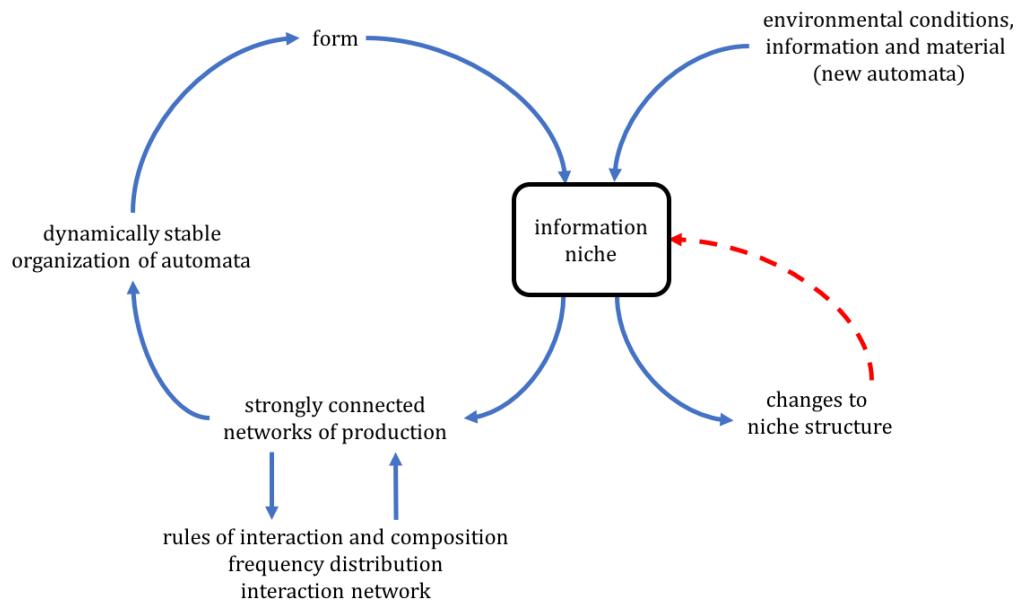


Figure 10.1: The information niche served as a nexus as it was responsive to external factors such as changes in environmental conditions, information content and input dynamics, as well as to internal changes in structure

it did this was a function of the rate of outflux of information from the niche  $\Phi_{out}$ . The reduction in entropy of the environment due to modulation with niche emissions was found to be maximal with  $\Phi_{out} \approx 0.75$  which matched a normal probability distribution profile. Above this value and the normal distribution profile began to flatten thus increasing the information entropy. Conversely, the environment had a marginal effect on the complexity of the niche. This was consistent with Ashby's Law of Requisite Variety [148] which states that the regulatory mechanism of a system must be at least as complex as the system it was regulating and "the larger the variety of actions available to control a system, the larger the variety of perturbations it is able to compensate [for]" and "the greater the variety within a system, the greater its ability to reduce variety in its environment through regulation" [148].

Given the need for operational closure of an autopoietic system this required the system to be sufficiently complex to achieve closure but only from the integrated nature of its constituent parts (or, if you like, its unity). If the environment was significantly increasing the complexity of the niche then this would indicate the absence of any operational closure of the system and would be more indicative of an allopoietic system i.e. the processes in the environment were partly, if not wholly, producing and regulating the behaviour of the niche. The information entropy of the membrane was increased when environmental noise

was present. Conversely, the environment's information entropy was reduced when the membrane was emitting information. The relationship between the membrane and the environment was examined by calculating the f-complexity (see Chapter 8) which showed that whilst the environment does increase the complexity of the membrane's activity it was by a very modest amount (an increase of 2%) on the complexity that was generated by the membrane itself. In other words, the information entropy in the membrane was generated primarily by the switching on/off behaviour of the membrane automata. The ratio of the f-Complexity of the niche to the f-Complexity of the environment showed that the former was generating more of its own complexity than it was receiving from the environment. Fernandez et al. [117] suggest that this indicates that the system was autopoietic rather than allopoietic.

*The rate of novelty needs to be regulated from the outset*

The open-ended production simulation described in Chapter 9 demonstrated an explosion in the diversity of the population progressing through four phases: I - diversification, II - increased competition, III - consolidation, IV - saturation. As the population evolved through these phases the rate at which new types of automata (novel automata) were produced reduced drastically. Examination of the mode of the population across all fifty generations showed that by the 8th generation the mode of the population was locked in at 1.92 bits and this was characteristic of a 'passive evolution' process [3]. The average structural complexity of the population increased gradually to 2.13 bits and this also concurred with other simulations of passive evolution [149].

There was no clear structure within the population and the interaction network complexity was very high compared to the seed population which had already established itself as a niche prior to the introduction of novel automata. This was partly understandable due to the significant diversity of the population however it was more than that. The majority of automata were of a very similar frequency in the population (concentration) and this uniformity meant that competition was very intense in the population. Such 'saturation' of the population has been proposed as one reason why dinosaurs became extinct [150].

There was a significant decline in the seed population with a consequent growth in the number of new automata. The niche that the seed population would ordinarily evolve to does not get reproduced. The intensity of competition generated from the diverse automata types created from endogenous novelty rapidly displaced the generations of automata that created that diversity. The population may be cycling through generational waves with the rise and fall of the seed population being replaced by a second wave of automata produced

entirely through novelty. More research and investigation is required here and this will be the subject of future work.

Whilst this investigation into open-ended evolution and the production of *de novo* automata has revealed interesting findings the model itself is fairly limited in that it only allows one form of novelty to occur i.e. new automaton types. The model does not, for example, allow for new species of automata to emerge (e.g. those that process a different alphabet other than binary), or changes to the population itself (e.g. growth or reduction in the size of the population). Such changes would be in the form of 'genotype' variation at the automata level and 'phenotype' variation at the population level. At a more fundamental level the model does not allow the mechanics of the self-producing system to evolve e.g. the rules of interaction, the interacting units themselves and as such the organisation - in the Maturana & Varela sense - of the system.

In summary, the rapid diversification of the population through endogenous production of novel automata prevented any persistent networks of production to form which would have been required for the onset of proto-autopoietic and eventually autopoietic behaviour. This strongly suggests that real-world autopoietic systems must have some regulatory mechanism that acts to limit or prevent runaway diversification of its constituent population of interacting entities.

#### **10.2.4 What contribution does this make to the theory of autopoiesis?**

*Demonstrates that autopoietic processes emerged from undefined beginnings*

The simulation results demonstrated the fundamental processes of autopoiesis and cognition emerging from the networks of interactions that formed from a simple population of entities that compete at multiple levels to survive. The underlying population of interacting automata increased in structure over time and reached a steady-state. Such stable configurations provided an enduring and resilient state from which more complex populations could form without loss of the underlying networks of production (e.g. Chapter 7 demonstrated that one-state and two-state niches co-existed within the same space). The possibility for increasing the complexity of the underlying networks of production whilst retaining several concurrent autopoietic identities, within the same space, was analogous to Oparin's 'increasing complexity of an autonomous chemical system' [49]. What was not observed was the spontaneous formation of an ideal chemistry of very few components that efficiently produced a minimal autopoietic system. The simulation of the information niche model under conditions of low diffusivity led to the emergence of a small (four automata) population that was demonstrating spatial pattern formation of domains and boundaries on

the lattice. However, this result was deemed to not be autopoietic as the domain automata were not being maintained and the observed behaviour was partly an effect of how the information niche model was designed.

*The criteria for a physical boundary is overstated*

The contested issue of whether a physical boundary is a necessity for a system to be deemed autopoietic (as per Varela's criteria, see Chapter 2) was not upheld by this research. Indeed, the opposite was found with co-occurring autopoietic systems that were co-habiting the same space and retaining and maintaining their separate identities without the need for a physical boundary were frequently observed. This is further evidence in favour of a 'non-physical' interpretation of autopoiesis that was originally pioneered by Luhmann [?] and that has more recently been elaborated on with the notion of extended autopoiesis that redefines our understanding of the operational limits - and therefore the scope of what is included in the operational closure of an autopoietic system - to include processes that may be physically outside of the autopoietic unit but that are depended on by processes physically within the unit.

### **10.2.5 What contribution does this make to the origin of life?**

*These research findings are consistent with Oparin's view*

Oparin proposed that the origin of life arose through the increase in the complexity of 'autonomous chemical systems' to the point at which they resemble biological behaviour (i.e. a metabolism) [49]. Complexity here is synonymous with order and persistence which has been demonstrated in this work both qualitatively (e.g. the recurring spatial patterns and networks of production) and quantitatively (e.g. the frequency distribution of automata and the information content of a steady-state population using Shannon entropy). As such, this work reinforces Oparin's view in a similar way that Fontana's algorithmic chemistry does with demonstrating the emergence of viable self-producing structures from simple, unstructured beginnings.

### **10.2.6 Can autopoietic theory contribute more to evolutionary biology?**

*Autopoiesis and Darwinian evolution*

Autopoiesis and Darwinian evolution could be complementary in three ways: (i) Darwinian evolution does not account for the origin of life as, ontologically, it does not set out a description of what a living system actually is; Darwinian evolution is a phenomenological theory based on empirical observations [31]. By comparison, autopoiesis does define what

a living system is and, as such, potentially offers an important theoretical basis for Darwinian evolution; and (ii) Darwinism is dependent on the transfer of information between generations of organisms and this is dependent on templated replication for the processes of variation, heredity and reproduction to occur. However, this is dependent on the presence of sophisticated molecular machinery such as DNA and proteins. What processes may have existed prior to the emergence of such biochemistry? What possible pathways are there from the inception of a living system to the interwoven complexity of the biology which is now referred to as the modern synthesis [151]? This is where autopoiesis has an explanatory power that potentially reaches further back in time and to simpler chemical environments that gave rise to the first living systems. Whilst the concept of autopoiesis has been demonstrated with a toy chemistry consisting of three chemical entities, these approaches assumed the occurrence of an infinitesimally improbable event that happened to endure. This is an unsatisfactory approach and what is required, and what has yet to be examined in the context of autopoiesis, is how a primitive autopoeitic system may have emerged and endured from simple, random beginnings, and (iii) competition is the universal mechanism by which the steady-state populations in the information niche and computation niche simulations have formed. Natural selection is also a competitive process. As such, both theories have a common process - competition - that could be understood as extending on a continuum from chemical competition through competing networks to competing autopoeitic units and so on to competing species and beyond that to competing ideas and norms in a social context. In this way one could argue that natural selection process of Darwinian evolution is present even in a minimal, non-genetic system such as the proto-autopoietic populations studied here. The conceptual gap between autopoeitic theory and evolutionary theory is therefore arguably non-existent and instead there may exist a continuum on the pathway from simple, competing networks through to abiogenesis and onwards to multicellularity and larger organisms. The fundamental mechanism that drives this continuum is competition that occurs at multiple levels (individual, network, niche) as new, emergent properties are formed which themselves contribute to the competitive dynamics. I am not aware of any literature in the field of autopoiesis that has made such a fundamental link between autopoiesis and Darwinian evolution based on the idea that they share a common mechanism - competition - that binds them at a theoretical level.

#### *A 'window of viability' exists*

The results of the one-state information niche model (chapter 4) and the one-state computation niche model (chapter 8) demonstrated the importance of a system's ability to modulate its interface with its environment. Too little exposure to the environment and the system

became too simplified (e.g. the significant reduction in the diversity of the population due to extinction of the majority of automata types caused by low mobility environmental conditions) leading to a lack of information, and too much and it was impossible for any kind of system identity to form (e.g. a very high influx of externally generated automata). There was a 'window of viability' [121]<sup>3</sup>, a 'Goldilocks zone', of the possible state space (or, the fitness landscape defined by the environment) characterised by more moderate exchanges with the environment. It may be that autopoietic systems happen to be able to maintain themselves in this window of viability. Indeed, cognition is the process by which this could be achieved i.e. accommodation of changes in the environment by alteration of the autopoietic network. Those forms of organisation that are self-producing but not sufficiently cognitive are less competitive and do not endure. This was seen in Chapter 4 with the finding that there were 7,821 possible networks and yet only 29 persisted. Such competition between networks led to the survival of those networks that supported the production of a plastic structure that could retain its identity under environmental perturbations. The vast majority of networks which could not achieve this - because they were not mutually producing, dynamically stable or strongly connected - did not survive. Furthermore, very simple populations of automata (e.g. one-state) were unable to generate novelty and therefore could not evolve. The presence of multi-state automata (e.g.  $\geq$  two-state) were necessary for the production of novel automata. As such, there is a minimal level of complexity that a population must have, or that it can develop, to allow the production of novelty. Such an ability may be important to how such systems may maintain themselves within a 'window of viability'. As has previously been explained, novelty cannot proceed unchecked and the role of a systems interface (boundary, membrane) may be the key to ensure that just the right amount of diversity is maintained within the population.

*Elementary networks are the 'fragments' required for reproduction and heredity*

As described in Chapter 4 elementary networks were self-producing, dynamically stable networks that were irreducible (i.e. the removal of one automaton from the network would mean the network ceased to exist). Elementary networks benefit from having the attribute of dynamic stability. As such, under constant environmental conditions these networks were persistent and provided an important foundation for the creation of more complex networks of production thus creating a hierarchy of networks. They were the building blocks

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<sup>3</sup>The 'window of viability' is a phrase coined by Ulanowicz and colleagues [121] to define a limited state space where a system maximises its sustainability which they show tends to reside where the system is sufficiently diverse whilst simultaneously being sufficiently efficient. Diversity introduces important redundancy into the system thus allowing it to respond to shocks and perturbations from its environment. Efficiency ensures that the system is able to effectively use resources to maintain itself.

of the larger networks that were required to achieve operational closure of the system. It was shown (see Chapter 4) that a one-state niche was re-produced from a 'seed' of just three elementary networks which cooperated to produce two larger, intermediate networks which themselves cooperated to generate the network that produced and maintained the niche. As such, elementary networks were 'packets of information' that were important in the reproduction of a niche as observed in the reproduction of a niche through the randomly selected transfer of individual automata from one niche to another (see Chapter 7). Hence this was a simple demonstration of the reproduction of an autopoietic system that "... takes place whenever a unity.... undergoes a fracture that separates fragments with individual structures realizing the same organization that characterized the original one" [13].

I hypothesise that these 'fragments' are in fact elementary networks. Chapter 7 demonstrates that self-producing systems are able to reproduce themselves from 'fragments' of their own organisation. There is a related idea in the literature that autocatalytic networks compete and form irreducible 'autocatalytic cores' [100] that act as 'units of evolution' in large molecular networks. However, as discussed by the authors, their work did not specifically address heredity nor autopoiesis.

### **10.2.7 How can a better understanding of the pathways to autopoiesis assist with the design of protocell experiments?**

*Signposting possible processes and architectures for pre-Darwinian protocells*

Chapter 2 cited that one of the challenges to protocell research was designing experiments whereby a minimal protocell (e.g. a vesicle) can evolve through a series of pre-biotic transitions towards more mature and sophisticated cellular structures. Such 'protocells as units of prebiotic evolution' [60] need to have the capacity to expand and grow in functionality whilst achieving integration of that functionality. One of the challenges for designing experiments with both an evolutionary trajectory and an organisational trajectory is in 'how far-from-equilibrium chemical assemblies that involve low-molecular-weight species... divide with regularity, [and] explore an ample range of - sufficiently robust - phenotypes, and have potential to set up mechanisms for increasingly reliable heredity' [60]. In more abstract terms, how can very simple entities self-organise into repeatable structures that are sufficiently robust that they can retain their identity and reproduce themselves (heredity) without loss of that identity even of themselves or their replicant. Such an ability has been demonstrated throughout all of the results generated during this project. As such, the notion of an information niche as a dynamically stable strongly connected network of mutually producing entities that form distinct organisational steady

states under various environmental conditions provides a guiding framework for designing chemistry experiments that seek to achieve such properties.

*Designing in competition and diversity*

Autopoietic forms of organisation are strongly dependent on the structure of the emergent network which itself is contingent on the diversity of the population and the environmental conditions that are present. It is recommended that experimental researchers consider the system-level relationships between all entities in the design of protocell experiments especially with a view to 'designing in' competition between those entities.

### 10.3 Summary

This chapter has discussed the results generated during this project with respect to the contribution that this makes to the theory of autopoiesis. This was done through analysis of the research findings and comparison to the literature where appropriate. The progress that this project has made in answering the original research questions that were posed in Chapter 1 were evaluated and this also identified where future work on this topic could be taken.

## CONCLUSION

### 11.1 Summary of Research Findings

This thesis has sought to answer the question of whether autopoietic systems can emerge from simple, unstructured beginnings. The conclusion is that autopoietic systems do emerge quite readily across a wide range of environmental conditions.

Two computational models were developed to address this question - the information niche model and the computation niche model - which reproduced a population of finite state automata interacting and producing new automata within a finite space coupled to an environment. A wide variety of simulations of the models were run under various conditions related to diffusive mixing and the rate of influx of new material and information for a large number of iterations. The results were analysed using quantitative techniques from information theory (Shannon's entropy, Interaction Network Complexity and Structural Complexity) and network theory (graph construction, degree distribution). The models and simulations were implemented in MATLAB and executed on a local computer and occasionally on the University of Bristol's supercomputer BlueCrystal. All of the results were analysed for structural changes to the population and characterisation of the underlying networks of production.

*Autopoietic systems form from simple, unstructured beginnings.* Simulation results consistently demonstrated that an initially uniform and unstructured population evolves to a steady state structure - a niche - that persists even in the presence of environmental

perturbations. The processes of autopoiesis and cognition emerged routinely and repeatedly across different simulation runs. The limitation of this result is that a physical boundary was not demonstrated. Historically the criteria for an autopoietic system has prescribed that the boundary created by an autopoietic process must be physical. However, and as discussed throughout this project, there is a growing consensus that an insistence on a physical boundary is too limiting and that non-physical boundaries (e.g. as evidenced by a system that is able to maintain its organisational identity in the presence of environmental changes) also satisfy the boundary criteria.

*Operationally closed networks of production emerged.* These structured populations were continually produced from a hierarchical, strongly connected and dynamically stable production network that was formed from the interaction affinity that existed between the interacting automata. Such networks were shown to persist based on their ability to produce the components which constituted the network itself. These networks produced all of the components required to continually re-generate the network. Hence, these are operationally closed systems which is the hallmark of an autopoietic system. Such networks formed readily and repeatedly across simulation runs with the exception of extreme environmental conditions that inhibited all interactions and endogenous production within the population.

*The environment sculpts the landscape that the autopoietic system transforms itself to occupy a niche.* It was evident that the range of environmental conditions that were being simulated were creating a 'fitness landscape' which drove the structural transformation of the population from one steady-state structure to another. Each niche represented a steady-state organisation that was operationally closed and that was structurally coupled to the prevailing conditions of the environment.

*The structure of autopoietic systems can be quantified.* Quantitative measurements of the steady state structure of the automata population provided an estimate of the information content present in each niche. Comparison of these measurements for one-state and two-state niches revealed one of the main findings of this project: a niche could only transform its own structure to another niche in the environmental landscape if either it (a) already contained enough information, or (b) the changing environmental conditions generated the necessary information required to generate the structure of the destination niche. This is a new result in the field of autopoiesis and provides a practical approach to quantifying autopoietic structures.

*New methods were developed to fully examine the constructive processes that were occurring.* To fully explore the nature of the proto-autopoietic networks that emerged and competed two new methods were developed: (i) an algorithm to detect strongly connected networks in an evolving population of interacting automata, and (ii) a numerical simulation implementation of a differential equation to determine the dynamic stability of a network. The development of these methods was necessary to identify the general properties of the proto-autopoietic networks that emerged.

*Elementary networks enable reproduction and heredity.* Each niche consists of a large network of networks that describe all possible interactions within the population. These networks are decomposable to so-called elementary networks that are irreducible, dynamically stable and strongly connected. They are the building blocks for the larger networks that are required to achieve operational closure of the autopoietic system. In simulations of the transfer of automata from one niche to another these elementary networks were reproduced in the receiving niche. Once present in the receiving population they ensured the continual production of their constituent parts thus forming a niche within a larger niche. Over time, and as more automata types are transferred into the receiving niche, more elementary networks are formed which, in turn, begin to combine into larger networks. This continues until the autopoietic network that formed the donating niche is reproduced in the receiving niche leading to the reproduction of the entirety of the donating niche in the receiving niche. This demonstrates the reproduction and heredity of autopoietic structures.

*A 'window of viability' exists.* The robustness of a niche is contingent on the composition of the population itself. There are two factors to consider: (a) if the population is too simple (both in terms of variety of automata types and the functional sophistication of those types) then - as demonstrated in this work - they are ineffective under constant environmental noise. More complex automata were more resilient; and (b) too much diversity in the population led to two issues: (i) more structurally complex automata (as measured by their number of states and number of transitions between those states) are more difficult to produce and, as such, were not produced at the same rate as simpler automata, and (ii) in the absence of any regulatory mechanism complex automata produce increasingly diverse and complex automata leading to saturation of the population which removes and inhibits any structural formation that has occurred or can occur. The primary reason is that the underlying networks of production are growing too fast and changing too frequently for any kind of recurring pattern of production to emerge. Due to these factors there is a 'window of viability' whereby the population is sufficiently diverse and sufficiently complex and the

processes of autopoiesis and cognition orchestrate the maintenance of the system within this window.

## 11.2 Concluding Statement

An unstructured population of finite state automata self-organise to steady state structures that are maintained by an operationally closed network that has the properties of mutual production, redundancy and dynamic stability. Such properties are required to enable the processes of autopoiesis and cognition and thus continually produce and maintain the population's identity within a changing environment. As these systems transform themselves to new steady-states in the presence of environmental conditions they are called niches. Niches satisfy all of the criteria for autopoiesis on the condition that a non-physical boundary is accepted.

## 11.3 Limitations of this research

Although this research has achieved its aims there were some unavoidable limitations as follows:

**Limited demonstration of cooperation** Cooperation between autopoietic sets has not been demonstrated. Interactions between autopoietic units was examined and this demonstrated the degree of robustness and reproducibility of autopoietic units however the emergence of a critical dependency between two separate systems was not observed e.g. one autopoietic system 'giving up' the ability to produce one or more automata on the grounds that it now receives it from a neighbouring autopoietic unit. The structural coupling between autopoietic units remains an active area of interest with potential insights into the origins of multicellularity and endosymbiosis.

**Physical accuracy.** The information niche and computation models do not accurately reproduce the physical behaviour of chemicals in a confined vessel e.g. the lack of any consideration of thermodynamics and the contingent effect that this may have had on population dynamics. However, as discussed in the Methodology chapter this was a deliberate design decision to minimise the complexity of the model. Model design priorities were given to determining the minimal number of features and mechanisms required to reproduce the dynamics and emergence of structured interacting populations.

**Scalability.** The computational cost of searching for all possible interactions within an open-ended model very quickly becomes prohibitive. For example, in a 3-state population there are 1.6 million unique processes (automata) representing  $2.75 \times 10^{12}$  possible interactions each of which would need to be examined for the potential for a successful interaction. Furthermore, to ensure the integrity of the population the results of each of those interactions would need to be minimised and examined for whether they satisfy the criteria of being an  $\epsilon$ -machine. So whilst prospect of examining a very large range of unique processes and their collective organisation is an exciting one this highlights a major constraint on not just the model used in this project but also for complexity science in general i.e. computationally analysing the bottom-up construction of an increasingly complex organisation as just one possible pathway amongst a very large number of competing pathways is a large and practical challenge in the field.

**No validation with experimental work.** Translating the insights gained from this research into a framework for designing experiments into bottom-up protocell fabrication would have provided an important opportunity to understand the opportunities and challenges of going from *in silico* to *in vitro* research. Importantly, the opportunity to test and revise the conclusions of this project based on real-world experimental results would have been invaluable.

## 11.4 Recommendations for Future Work

There are a wide range of possible avenues for further investigation into the emergence and evolution of autopoietic systems. I believe that the cultivation and development of the computation niche model - whilst retaining the ethos of minimality (i.e. the least functionality required to achieve a research aim) - should continue to yield insights into the nature of self-producing systems. In parallel, I also believe it is important to bridge the gap from computational study to experimental study. On both points I make the following recommendations for future work:

**Measure and analyse the information dynamics in a computation niche.** As discussed in the previous chapter the computation niche model can be understood as four inter-dependent stochastic processes. The information flow between these processes can be estimated using information-theoretic techniques such as transfer entropy [118] and active information storage [152] to quantify the computation that is occurring within the model. Existing literature [119] provides not only a framework for understanding computation in a complex system but also the open-source software - Java Information

Dynamics Toolkit (JIDT) - required to estimate information flow. Such work may yield insight to the causal structure of the niche. Given the hierarchical nature of the computation niche model this should also provide some insight into hierarchical causation [153] captured as bottom-up, same-level and top-down information flow. Work has already begun on incorporating information dynamics into the computation niche model for a one-state automata population.

**Model populations of niches.** Second-order autopoietic structures [13] have been suggested as the pathway from single autopoietic units to either meta-autopoietic units (interacting autopoietic systems that retain their own identity) or the integration of two autopoietic units into a unity (so called symbiosis). There are clear parallels here to the major transition from single cells to multicellularity [18]. The emergence of second-order autopoietic structures could be investigated by 'coarse-graining' the computation niche model such that each lattice site is occupied by a computation niche. Each computation niche should itself consist of a lattice occupied by individual automata (as per the current computation model). Neighbouring niches should be able to exchange automata and information with each other and their environment. Such a model would match that described by Maturana & Varela [83]. Whilst it is hoped that such a model would demonstrate co-operation between niches care would need to be taken not to 'design in' such a mechanism. From a pragmatic standpoint such a model would benefit from the implementation of parallel computing techniques to handle the inevitable increase in computational cost. Research on the transition to multicellularity/second-order autopoietic structures has received scant attention although it has recently been reported [154] that autopoietic principles have been applied successfully to explain how cells in a multicellular system handle environmental disturbances and self-maintenance (on this occasion it appears that an experimental finding can help to inform theoretical work).

**Incorporate energy considerations into the model.** Seminal work by Landauer [155] on the 'physics of information' examined the irreversibility and heat loss that occurs from information processing. In essence, the erasure of a bit of information must be accompanied by a corresponding entropy increase with the minimum possible amount of energy required to erase one bit of information - the Landauer limit - given by  $kT \ln 2$  where  $k$  is the Boltzmann constant,  $T$  is temperature and  $\ln 2$  is the natural logarithm of 2. The premise here is that an information processor generates heat (energy loss) as it manipulates information (e.g. receives a 0 and outputs a 1). As such, the addition of an information thermodynamics dimension to the computation niche model would (i) bring the model closer to a more rigorous and physical explanation of the emergence

of the dissipative structures on the pathway to autopoietic forms of organisation, and (ii) the energy cost of information processing [155] and information flow [156] could be studied under the general heading of information thermodynamics [157]. The extension of the information niche model to incorporate an energy representation would allow the information thermodynamics near and at steady-state configurations to be examined. In other words, the information thermodynamics of an autopoietic system could be estimated for the first time. Such a model could also be used to examine dissipation-driven adaptation [158].

## 11.5 Final Thoughts

Pathways to autopoiesis has been investigated using an abstract model of a population of interacting automata that self-organise to steady-state self-producing structures. These results are highly reproducible and the only occurrences where such structures did not form was under extreme environmental conditions. Hence, the formation of a mechanism to facilitate interactions between the system and environment is a necessity. It is worth stressing that these observations were obtained from a population that evolved from unstructured beginnings operating within a model with minimal assumptions that did not extend beyond how the automata interacted to produce new automata and the boundary conditions of their environment. All other properties - dynamically stable, hierarchical and strongly-connected networks with inherent redundancy - were emergent.

The theory of autopoiesis is undergoing something of a resurgence primarily due to increased efforts in synthetic biology and protocell research (where it has been adopted as a general framework for minimal cell architectures) but also, more recently, the surge in interest in artificial intelligence and the search for suitable models and architectures for achieving the goal of 'embodied AI' [159].

Whatever the future may hold for autopoietic theory a greater understanding of the pathways to their formation and the structures and processes that emerge on that journey can only assist with the application of the theory within and beyond its field of origin.



CHAPTER

# 12

## APPENDIX

### 12.1 Handling multi-state automata interactions

There are 3,508,129 possible interactions in a population of 1,873 unique 2-state automatons. For practical computational reasons the generation of the complete interaction network a priori to any simulation is required. For expedience the 2-state interaction network was generated by a parallel algorithm that was run on the University of Bristol's supercomputer - Blue Crystal. A single computation node on this supercomputer consists of 16 processor cores and so the task of generating the interaction network was packaged into 16 discrete packages of work of 116 automatons representing the  $T_b$  automaton for a given range of interactions (see Table 12.1).

After all parallel tasks have been completed the final interaction matrix ( $1873 \times 1873$ ) is constructed from the results of each run. The interaction matrix is then used as a lookup table during the simulation which considerably shortens the execution time.

Task	$T_b$ range	$T_a$ range
1	1 to 116	1 to 1873
2	117 to 233	1 to 1873
..	..	..
16	1740 to 1873	1 to 1873

Table 12.1: Parallelising the task of constructing the interaction network for a two-state automata population

Q	T	G	$O(ns \log n)$	Total Run Time	Cumulative G
1	15	225	-	-	225
2	1,873	$3.5 \times 10^6$	8	$2.8 \times 10^7$	$3.6 \times 10^6$
3	$1.6 \times 10^6$	$2.75 \times 10^{12}$	19	$5.2 \times 10^{13}$	$2.76 \times 10^{12}$

Table 12.2: The Hopcroft algorithm has a worst-case run time of  $O(n.s \log n)$  where  $s$  is the size of the alphabet (4) and  $n$  the number of states of the automaton

## 12.2 Handling open-ended novelty

The ability to support the open-ended generation of novelty (see chapter 9) in a computation niche places considerable demands on computational capacity that increases exponentially with growth in the average structural complexity of the niche. The following table illustrates the growth in the number of interactions that need to be evaluated in the process of constructing an interaction network for the population.

In an open-ended model (i.e. no restriction on the size and complexity of the automata that can be generated) it was impractical to re-construct the interaction network for each novel automaton type produced. Consequently, the general algorithm for the simulation was modified so that the interaction network was constructed in real-time rather than *a priori*.

## 12.3 Software implementation in MATLAB

All simulations and analysis were written in MATLAB (version: R2016b). The implementation of the Finitary Process Soup [35],[108] in MATLAB was written entirely by the author. The enhancements and extensions of the FPS model to what were subsequently called the Information Niche model and the Computation Niche model were also written entirely by the author. A dataset on the two-state interaction network was provided by Professor James Crutchfield at the University of California in Davis, United States to aid with the test and validation of my Hopcroft minimisation implementation routine. All information and network measures used in this project were also implemented by the author in MATLAB and the external software library, the Java Information Dynamics Toolkit (JIDT) [119], was used to verify the results that I obtained from my own implementation of Shannon entropy. Finally, the two papers [35],[108] and one internal report (a partially completed Masters report by a CSC student, Spencer Mathews) from the Complex Systems Group at the University of California at Davis (headed by Prof. Jim Crutchfield) were used to confirm some of the results in Chapters 4 (the structure of niche 1A), Chapter 5 (the

## 12.4. EXPLANATION OF THE DIFFERENCE BETWEEN THE INFORMATION NICHE AND COMPUTATION NICHE RESULTS FOR A ONE-STATE WELL-MIXED POPULATION

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competing nature of niches 2A and 2B) and Chapter 7 (the spatial lattice patterns formed by niche 1B).

The simulation software and documentation of how the information niche and computation niche model were implemented in MATLAB can be accessed via a Github open-source repository at <https://github.com/rjcarte/Pathways2Autopoiesis>.

### **12.4 Explanation of the difference between the Information Niche and Computation Niche results for a one-state well-mixed population**

*Why niche 1D is reproduced and not niche 1A* The niche that emerged in the one-state computation niche model with no environmental noise is structurally similar to information niche 1D (i.e. no automata go extinct). Given that the parameter settings for the computation niche model are for a well-mixed population why was niche 1A not produced? This was investigated by examining the effect of the activity of the membrane on population dynamics and the procedure for selecting the automata that will be produced and replaced on each iteration of the simulation.

**Activity of the membrane.** The randomly determined threshold of each membrane automaton may have been ‘perturbing’ population dynamics in a way that was analogous to an influx of external automata in the information niche model. To examine this the randomly determined threshold parameter ( $r$ ) was set to a constant value  $r = 0$ . With  $r = 0$  a membrane automaton would be active as long as it was receiving information from at least one of its incoming links. As such, all membrane automata were constantly active. This meant that all population automata were available to interact on every iteration of the simulation. Simulating this showed that the rate at which the decaying population automata were being produced was now reduced when compared to when  $r$  was randomly determined. However, the decaying population automata did not go extinct as per niche 1A. So, whilst the the membrane automaton activation threshold effected population dynamics it did not produce niche 1A.

**Asynchronous update mode of the population.** The computation niche model operates a synchronous update whereby all population automata that can be produced within a given iteration are produced and replace existing population automata. By comparison, the information niche model operates an asynchronous update whereby only one population automaton (randomly selected) was produced from the interaction between two randomly selected population automata. The computation niche model was adjusted to run

in asynchronous mode and this only has the effect of slowing down the rate at which the population evolves to a steady-state that is similar to niche 1D.

**Determining which population automata are produced.** Examination of the selection procedure used within the computation niche model showed that with  $r > 0$  the size of the population that is available for sampling varies over time due to the activity of the membrane. By comparison, the information niche model is sampling from a constant population size. Hence, the computation niche model led to partial sampling<sup>1</sup> of the population given that certain automata were not available for interactions (due to an inactive status of the equivalent membrane automaton). Over time this partial sampling of the population had the effect of equalising the frequency distribution of the population automata and, hence, from which the selection of automata that would interact were chosen. As such, lower frequency population automata were boosted in the rate at which they were selected for interacting whilst the rate at which higher frequency population automata were selected was reduced. On average this meant that the selection of an automaton to be produced in a given time step was taken from a more uniform distribution. This selection process had the effect of producing lower frequency population automata more frequently than would have been the case in the information niche model - see Figure 12.1 for the simulation results comparing the differences in how often each population automata was produced over  $4 \times 10^5$  iterations.

Hence, in the computation niche model the automata types that went extinct in the information niche model (due to being produced less) are now being produced often enough to remain in the population. Whilst this comparison of the two simulations was useful it did not explain why the computation niche model does not generate niche 1A.

A more detailed examination of the selection of automata to interact in the computation niche model showed that the synchronous mode of updating the population meant that the population didn't need to be sampled as all active population automata at a given time-step would interact with other active population automata to produce new automata. However, when the computation niche model was in asynchronous mode the sampling was of the list of automata that could be produced at that time-step rather than sampling the automata that were available to interact. This difference is important as they are sampling the population in different ways: sampling the list of automata that can be produced on a time-step (as per the computation niche) is actually selecting a single automaton ( $T_c$ ) from the partial interaction network  $\psi G$  whereas sampling the population to select the automata that would interact requires two automata to be selected ( $T_a, T_b$ ) from the

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<sup>1</sup>partial sampling is an acceptable feature of the computation niche model as it relates directly to the on/off switching activity of the membrane automata

#### 12.4. EXPLANATION OF THE DIFFERENCE BETWEEN THE INFORMATION NICHE AND COMPUTATION NICHE RESULTS FOR A ONE-STATE WELL-MIXED POPULATION

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frequency distribution  $f$ . Whilst this is not an issue with the synchronous update mode (as the assumption is that all interactions that can take place on a given time-step do occur) it does mean that sampling the interaction network with the computation niche in asynchronous mode (only one interaction can occur) will not produce the same results as the information niche (which runs in asynchronous mode). To test this a simulation was run with the computation niche in asynchronous mode and with the selection of automata that are produced replaced with the process for selecting two population automata to interact as per the information niche model. Furthermore, the activation threshold for membrane automata was set to  $r = 0$  (so they were always active thus the population was fully sampled on each time-step). The simulation result clearly showed the reproduction of niche 1A.

In summary, with the computation niche model in asynchronous mode, with membrane automata permanently active and with the selection of automata to be produced on each time step determined from the selection of two automata to interact (as per the information niche model) then niche 1A was produced with the computation niche model.

The motivation for the above investigation was to confirm that the computation niche model was capable of re-producing the niches 1A and 1D from the information niche model. This has been shown.

	<b>Information Niche</b>	<b>Computation Niche</b>	<b>Difference</b>
<b>T1</b>	29020	29054	34
<b>T2</b>	27383	29087	1704
<b>T3</b>	49035	40344	-8691
<b>T4</b>	28787	29191	404
<b>T5</b>	51138	40608	-10530
<b>T6</b>	325	3854	3529
<b>T7</b>	1165	11533	10368
<b>T8</b>	27146	28902	1756
<b>T9</b>	327	3843	3516
<b>T10</b>	47276	40596	-6680
<b>T11</b>	1144	11523	10379
<b>T12</b>	48166	40283	-7883
<b>T13</b>	1134	11754	10620
<b>T14</b>	1136	11611	10475
<b>T15</b>	86818	67817	-19001
Total	400000	400000	0

Figure 12.1: Comparison of the number of times each automaton was produced in a simulation over  $4 \times 10^5$  iterations under well-mixed conditions only. As can be seen in the 'Difference' column there is a significant increase in the production of the automata  $T_2, T_6, T_7, T_9, T_{11}, T_{13}, T_{14}$  balanced against a significant decrease in the production of the automata  $T_3, T_5, T_{10}, T_{12}, T_{15}$ . These changes were due to the partial sampling that occurs in the computation niche as a result of the membrane exciting or inhibiting different types of population automata.

## BIBLIOGRAPHY

- [1] S. Mann.  
Systems of creation: The emergence of life from nonliving matter.  
*Acc. Chem. Res.*, 45(12):2131–2141, 2012.
- [2] M. Bitbol and P.L. Luisi.  
Autopoiesis with or without cognition: defining life at its edge.  
*Journal of the Royal Society Interface*, 1:99–107, 2004.
- [3] Carroll S.B.  
Chance and necessity : the evolution of morphological complexity and diversity.  
*Nature*, 409:1102–1109, 2001.
- [4] A.I. Oparin.  
*The Origin of Life*.  
Macmillan, New York, 1938.
- [5] A.J. Dzieciol and S. Mann.  
Designs for life: Protocell models in the laboratory.  
*Chemical Society Review*, 41:79–85, 2012.
- [6] S. Rasmussen, M.A. Bedau, L. Chen, D. Deamer, D.C. Krakauer, N.H. Packard, and P.F. Stadler.  
*Protocells: Bridging Nonliving and Living Matter*.  
MIT Press, 2008.
- [7] Hermans T.M. Otto S. Taylor A.F. Ashkenasy, G.  
Systems chemistry.  
*Chemical Society Review*, 46:2543–2554, 2017.
- [8] P.L. Luisi.  
Autopoiesis: a review and a reappraisal.  
*Naturwissenschaften*, 90:49–59, 2003.

## BIBLIOGRAPHY

---

- [9] F.G. Varela, H.R. Maturana, and R. Uribe.  
Autopoiesis: The organization of living systems, its characterization and a model.  
*BioSystems*, 5, 1974.
- [10] M. Zeleny.  
*Autogenesis: On the Self-Organization of Life.*  
Elsevier North Holland, New York, 1981.
- [11] B. McMullin.  
Computational autopoiesis: The original algorithm.  
*Santa Fe Institute (SFI) Working Paper*, 1997.
- [12] P.L. Luisi.  
*The Emergence of Life: From Chemical Origins to Synthetic Biology.*  
Cambridge University Press, 2016.
- [13] H.R. Maturana and F.J. Varela.  
*Autopoiesis and Cognition: The Realization of the Living.*  
D. Reidel Publishing Company, Dordrecht, Holland, 1980.
- [14] P. Bourgine and J. Stewart.  
Autopoiesis and cognition.  
*Artificial Life*, 10:327–345, 2004.
- [15] Gershenson C and Heylighen F.  
When can we call a system self-organizing?  
In W. Banzhaf, T. Christaller, P. Dittrich, J.T. Kim, and J. Ziegler, editors, *Adaptation and Self-Organizing Systems*, 2003.
- [16] P. Razeto-Barry.  
Autopoiesis 40 years later. a review and a reformulation.  
*Orig Life Evol Biosph*, 42:543–567, 2012.
- [17] N. Virgo, M.D. Egbert, and T. Froese.  
The role of the spatial boundary in autopoiesis.  
In G. Kampis, I. Karsai, and E. Szathmary, editors, *ECAL 2009*, volume Part 1, pages 240–247. Springer-Verlag Berlin Heidelberg, 2011.
- [18] J. Maynard Smith and E. Szathmary.  
*The Major Transitions in Evolution.*  
Oxford University Press, Oxford, England, 1995.

- [19] N Luhmann.  
*Theory of Society, Volume 1.*  
Stanford University Press, 2012.
- [20] P.C. Chagas.  
Polyphony and embodiment: A critical approach to the theory of autopoiesis.  
*Transcultural Music Review*, 9, 2005.
- [21] S Blaschke.  
*The Autopoiesis of Organizational Knowledge, Learning and Memory*, pages 215–231.  
Bingley: Emerald, 2009.
- [22] J. Dewhurst.  
*Computing Mechanisms and Autopoietic Systems*, volume 375 of *Synthese Library*, chapter 2, pages 17–26.  
Springer International Publishing, Switzerland, 2016.
- [23] Abou-Zeid E.S.  
*An Autopoietic View of the Concept of 'Information System'*, volume 36 of *Information System Concepts: An Integrated Discipline Emerging*.  
Springer, Boston, MA, the international federation for information processing edition, 2000.
- [24] G Teubner.  
*Autopoietic Law - A New Approach to Law and Society*.  
Walter de Gruyter, Berlin, New York, 1988.
- [25] P. Schumacher.  
*The Autopoiesis of Architecture: A New Framework for Architecture, Volume 1*.  
Wiley, 1st edition, 2010.
- [26] Thompson E. Rosch E. Varela, F.J.  
*The Embodied Mind : Cognitive Science and Human Experience (Revised Edition)*.  
MIT Press, Cambridge, MA, 2016.
- [27] P. Stano and F. Mavelli.  
Protocell models in origin of life and synthetic biology.  
*Life*, 5(4):1700–1702, 2015.
- [28] Schatten M and Baca M.

- A critical review of autopoietic theory and its applications to living, social, organizational and information systems.  
*Drus. Istraz. Zagreb GOD.*, 19(4-5):837–852, 2010.
- [29] J.S. Podgorski.  
Humberto maturana's view on the theory of evolution. from autopoiesis to natural drift metaphor.  
*Ecological Questions*, 13:81–87, 2010.
- [30] A. Etxeberria.  
Autopoiesis and natural drift: Genetic information, reproduction, and evolution revisited.  
*Artificial Life*, 10:347–360, 2004.
- [31] J.M. Escobar.  
Autopoiesis and darwinism.  
*Synthese*, 185:53–72, 2012.
- [32] Uller T. Feldman M.W. Sterelny K. Muller G.B. Moczek A. Jablonka E. Odling-Smee J. Laland, K.N.  
The extended evolutionary synthesis: its structure, assumptions and predictions.  
*Proceedings of the Royal Society B*, 282(1813), 2015.
- [33] B. McMullin.  
Some remarks on autocatalysis and autopoiesis.  
Technical Report bmcm9901, Dublin City University, 1999.
- [34] M Mitchell.  
*Complexity - A Guided Tour*.  
Oxford University Press, 2009.
- [35] J.C. Crutchfield and O. Gornerup.  
Objects that make objects: the population dynamics of structural complexity.  
*Journal of the Royal Society Interface*, 3(7):345–349, 2006.
- [36] J.C. Crutchfield and K. Young.  
Inferring statistical complexity.  
*Physical Review Letters*, 63(2):105–108, 1989.
- [37] Y Jiang, B Travis, C Knutson, J Zhang, and P Weronski.

- Numerical Methods for Protocell Simulations*, chapter 19, pages 407–431.  
MIT Press, 2009.
- [38] F. Mavelli, E. Altamura, L. Cassidei, and P. Stano.  
Recent theoretical approaches to minimal artificial cells.  
*Entropy*, 16:2488–2511, 2014.
- [39] W. Hordijk, J. Hein, and M. Steel.  
Autocatalytic sets and the origin of life.  
*Entropy*, 12:1733–1742, 2010.
- [40] *Az élet principiuma*.  
Gondolat, Budapest, 1971.
- [41] M. Eigen and P. Schuster.  
Part a: Emergence of the hypercycle.  
*Naturwissenschaften*, 65:7–41, 1978.
- [42] F.G. Varela.  
*Autopoiesis and a Biology of Intentionality In: The Embodied Mind Cognitive Science and Human Experience*.  
MIT Press, 1991.
- [43] B. McMullin and F.J. Varela.  
Rediscovering computational autopoiesis.  
*SFI Working Paper*, (97-02-012), 1997.
- [44] W. Fontana.  
*Algorithmic Chemistry*, volume X.  
Addison-Wesley, 1991.
- [45] C.E. Shannon.  
A mathematical theory of communication.  
*Bell System Technical Journal*, 27:379–423, 1948.
- [46] M. Newman.  
*Networks: An Introduction*.  
Oxford University Press, 2010.
- [47] Wiesner K. Mann S. Carter, R.J.

## BIBLIOGRAPHY

---

- Emergence and dynamics of self-producing information niches as a step towards pre-evolutionary organization.  
*Royal Society Interface*, 15(138), 2018.
- [48] J. Hopcroft.  
An  $n \log n$  algorithm for minimizing states in a finite automaton.  
Technical report, Stanford University, 1971.
- [49] A.I. Oparin.  
The origin and development of life.  
*NASA TTF-488*, 1968.
- [50] Munteanu A. Rodriguez-Caso C. Macia J. Sole, R.V.  
Synthetic protocell biology: from reproduction to computation.  
*Philosophical Transactions of the Royal Society B*, 362(1486):1727–1739, 2007.
- [51] Assad-Garcia N.-Alperovich N. Yooseph S. Lewis M.R. Maruf M. Hutchison C.A. Smith H.O. Venter J.C. Glass, J.I.  
Essential genes of a minimal bacterial gene set.  
*Proc Natl Acad Sci USA*, 103:425–430, 2006.
- [52] Zhu-T.F. Szostak-J.W. Schrum, J.P.  
The origins of cellular life.  
*Cold Spring Hard Perspect Biol.*, 2(9), 2010.
- [53] R.F. Ludlow and S. Otto.  
Systems chemistry.  
*Chemical Society Review*, 37(1):101–108, 2008.
- [54] Green-D.C. Ross Anderson J.L. Binks B.P. Mann S. Li, M.  
In vitro gene expression and enzyme catalysis in bio-inorganic protocells.  
*Chemical Science*, 2:1739–1745, 2011.
- [55] Li-M. Green D.C. Williams D.S. Patil A.J. Mann S. Huang, X.  
Interfacial assembly of protein-polymer nano-conjugates into stimulus-responsive biomimetic protocells.  
*Nature Communications*, 4(2239), 2013.
- [56] D. Segre, D. Ben-Eli, and D. Lancet.

- Compositional genomes: Prebiotic information transfer in mutually catalytic noncovalent assemblies.  
*Proc. Natl. Acad. Sci.*, pages 219–230, 2000.
- [57] H.J. Morowitz, B. Heinz, and D.W. Deamer.  
The chemical logic of a minimum protocell.  
*Orig Life Evol Biosph*, 18(3):281–287, 1988.
- [58] L.E. Orgel.  
Molecular replication.  
*Nature*, 358:203–209, 1992.
- [59] P. Andras and C. Andras.  
The origins of life - the 'protein interaction world' hypothesis.  
*Medical Hypotheses*, 64:678–688, 2005.
- [60] Murillo-Sanchez S. Ruiz-Mirazo K. Shirt-Ediss, B.  
Framing major prebiotic transitions as stages of protocell development: three challenges for origins-of-life research.  
*Beilstein Journal of Organic Chemistry*, 13:1388–1395, 2017.
- [61] J.W. Sadownik and S. Otto.  
*Encyclopedia of Astrobiology*, chapter Systems Chemistry, pages 90–98.  
Springer Berlin Heidelberg, 2015.
- [62] S.M. Manson.  
Simplifying complexity: A review of complexity theory.  
*Geoforum*, 32(3):405–414, 2001.
- [63] Swadling J.B.-Wattis J.A. Greenwell-H.C. Coveney, P.V.  
Theory, modelling and simulation in origins of life studies.  
*Chemical Society Review*, 41(16):5430–5446, 2012.
- [64] T.S. Hofer.  
From macromolecules to electrons - grand challenges in theoretical and computational chemistry.  
*Frontiers in Chemistry*, 1(6), 2013.
- [65] G.M. Whitesides and R.F. Ismagilov.  
Complexity in chemistry.  
*Science*, 284(5411):89–92, 1999.

- [66] Ribeiro A. Niiranen, S., editor.  
*Information Processing and Biological Systems*, volume 11.  
Springer-Verlag Berlin Heidelberg, 2011.
- [67] Briones-C. de le Escosura A. Ruiz-Mirazo, K.  
Prebiotic systems chemistry: new perspectives for the origins of life.  
*Chemical Reviews*, 114(1):285–366, 2014.
- [68] R. Rosen.  
*Dynamical Systems Theory in Biology*.  
Wiley Interscience, New York, 1970.
- [69] S.A. Kauffman.  
Autocatalytic sets of proteins.  
*Journal of Theoretical Biology*, 119:1–24, 1985.
- [70] T. Ganti.  
*Chemoton Theory. Volume 1: Theoretical Foundations of Fluid Machineries. Volume 2: Theory of Living Systems*.  
Kluwer Academic, 2003.
- [71] J. Griesemer.  
The enduring value of ganti’s chemoton model and life criteria: heuristic pursuit of exact theoretical biology.  
*Journal of Theoretical Biology*, 381:23–28, 2015.
- [72] S. Beer.  
*Cybernetics and Management*.  
The English Universities Press Ltd., 1959.
- [73] E. Schwarz.  
Toward a holistic cybernetics. from science through epistemology to being.  
*Cybernetics and Human Knowing*, 4(1):17–49, 1997.
- [74] P Dittrich and P Speroni di Fenizio.  
Chemical organisation theory.  
In M Al-Rubeai and M Fussenegger, editors, *Systems Biology*, volume 5 of *Cell Engineering*. Springer Press, Dordrecht, Holland, February 2007.
- [75] B. Poerksen.

- The Certainty of Uncertainty: Dialogues Introducing Constructivism.*  
Imprint Academic, 2004.
- [76] P. Bourgine and F.J. Varela.  
Introduction: Towards a practice of autonomous systems.  
In F.J. Varela and P. Bourgine, editors, *Proceedings of ECAL 1*. MIT Press, 1992.
- [77] M. Wheeler.  
Autopoiesis, enactivism and the extended mind.  
In S. Bullock, editor, *Proc. ALIFE XI*, page 819. MIT Press, 2008.
- [78] R. Vanderstraeten.  
The autopoiesis of social systems.  
*Constructivist Foundations*, 9(2):181–183, 2014.
- [79] Williams D.S.-Perriman A.W. Mann S. Koga, S.  
Peptide-nucleotide microdroplets as a step towards a membrane-free protocell model.  
*Nature Chemistry*, 3:720–724, 2011.
- [80] Spruit E.-Hansen M.K. Dubuc E. Groen J. Chokkalingam V. Piruska A. Heus H.A.  
Huck W.T.S. Sokolova, E.  
Enhanced transcription rates in membrane-free protocells formed by coacervation of  
cell lysate.  
*PNAS*, 110(29):11692–11697, 2012.
- [81] Fothergill J.-Bretherton J. Tian L. Patil A.J. Davis S.A. Mann S. Kumar, B.V.V.S.  
Chloroplast-containing coacervate micro-droplets as a step towards photosyntheti-  
cally active membrane-free protocells.  
*Chemical Communications*, 29:3594–3597, 2018.
- [82] Wikipedia contributors.  
Aqueous two-phase system.
- [83] H.R. Maturana and F.J. Varela.  
*The Tree of Knowledge: The Biological Roots of Human Understanding*.  
Shambhala Publications, 1987.
- [84] J. Mingers.  
*Self-Producing Systems: Implications and Applications of Autopoiesis*.  
Plenum Press, New York, 1995.

## BIBLIOGRAPHY

---

- [85] R. Rosen.  
Autobiographical reminiscences of robert rosen.  
*Axiomathes*, 16(1-2):1–23, 2006.
- [86] W. Banzhaf and L. Yamamoto.  
*Artificial Chemistries*.  
The MIT Press, 2015.
- [87] R Rosen.  
*Life Itself: A Comprehensive Inquiry Into the Nature, Origin and Fabrication of Life*.  
Columbia University Press, 2005.
- [88] Marin G.-Mpodozis J. Letelier, J.C.  
Autopoietic and (m,r) systems.  
*Journal of Theoretical Biology*, 222:261–272, 2002.
- [89] D.M. Dubois and S.C. Homlberg.  
Anticipatory artificial autopoiesis.  
*Cybernetics and Systems*, 1, 2010.
- [90] O. Wolkenhauer and J.H. Hofmeyr.  
An abstract cell model that describes the self-organization of cell function in living systems.  
*Journal of Theoretical Biology*, 246(3):461–476, 2007.
- [91] T. Nomura.  
Category theoretical distinctiono between autopoiesis and (m,r) systems.  
In Rocha L.M.-Costa E. Inman H. Coutinho A. Costa, F.A., editor, *Advances in Artificial Life*, 9th European Conference, ECAL 2007, Lisbon, pages 463–474, 2007.
- [92] G. Nicolis and I. Prigogine.  
*Self-organization in Non-Equilibrium Systems: From Dissipative Structures to Order through Fluctuations*.  
Wiley-Interscience (London), 1977.
- [93] D. Farmer, S.A. Kauffman, and N. Packard.  
Autocatalytic replication of polymers.  
*Physics*, 22D:50–67, 1986.

- [94] JC Cavadore.  
*Polycondensation d'alpha-amino acids en milieu aqueux.*  
PhD thesis, Universite des Sciences et Techniques du Languedoc Academie de Montpellier, 1971.
- [95] S.W. Fox and K Dose.  
*Molecular Evolution and the Origin of Life.*  
W.H. Freeman and Co, 1977.
- [96] W. Hordijk and M. Steel.  
Detecting autocatalytic, self-sustaining sets in chemical reaction systems.  
*Journal of Theoretical Biology*, 227:451–461, 2004.
- [97] P. Erdos and A. Renyi.  
On the evolution of random graphs.  
*Pub. Math. Ins. of Hungarian Academy of Sciences*, 5:17–61, 1960.
- [98] S.A. Kauffman.  
*The Origins of Order.*  
Oxford University Press, 1993.
- [99] D Segre, D Lancet, O Kedem, and Y Pilpel.  
Graded autocatalysis replication domain (gard): kinetic analysis of self-replication in mutually catalytic sets.  
*Origins of Life and the Biosphere*, 28:501–514, 1996.
- [100] V. Vasas, E. Szathmary, and M. Santos.  
Lack of evolvability in self-sustaining autocatalytic networks constrains metabolism-first scenarios for the origin of life.  
*PNAS*, 107(4):1470–1475, 2010.
- [101] O. Markovitch and D. Lancet.  
Excess mutual catalysis is required for effective evolvability.  
*Artificial Life*, 18:243–266, 2012.
- [102] V. Vasas, C. Fernando, M. Santos, S. Kauffman, and E. Szathmary.  
Evolution before genes.  
*Biology Direct*, 7(1), 2012.
- [103] Letelier J.C.-Gutierrez C. Cornish-Bowden A. Soto-Andrade J. Cardenas, M.L.

- Closure to efficient causation, computability and artificial life.  
*Journal of Theoretical Biology*, 263:79–92, 2010.
- [104] J. Piaget.  
*Knowledge and Development*, chapter The role of action in the development of thinking, pages 17–42.  
Springer US, 1977.
- [105] Wikipedia contributors.  
Evolution — wikipedia, the free encyclopedia, May 2018.
- [106] C. Darwin.  
*The Origin of Species*.  
Wordsworth Classic of the World, 1998.
- [107] B. McMullin.  
30 years of computational autopoiesis: A review.  
*Artificial Life*, 10(3), 2004.
- [108] S.T. Piantadosi and J.P. Crutchfield.  
How the dimension of space affects the products of pre-biotic evolution: The spatial dynamics of structural complexity and the emergence of membranes.  
SFI Working Paper, 2013.
- [109] T.M. Cover and J.A. Thomas.  
*Elements of Information Theory*.  
2nd edition. Wiley Series in Telecommunications, New York, 2006.
- [110] B.D. Johnson, J.P. Crutchfield, C.J. Ellison, and C.S. McTague.  
Enumerating finitary processes, 2010.
- [111] B. Schonfisch and A. de Roos.  
Synchronous and asynchronous updating in cellular automata.  
*BioSystems*, 51(3):123–43, 1999.
- [112] S.A. Kauffman.  
Metabolic stability and epigenesis in randomly constructed genetic nets.  
*Journal of Theoretical Biology*, 22:437–467, 1969.
- [113] N. Barnett and J.P. Crutchfield.

- Computational mechanics of input-output processes: Structured transformation and the  $c$ -transducer.  
Sante Fe Institute Working Paper 14-12-046, January 2016.
- [114] G Nicolas and I Prigogine.  
*Exploring Complexity*.  
W.H. Freeman and Co, 1989.
- [115] S Klamt and A von Kamp.  
Computing paths and cycles in biological interaction graphs.  
*BMC Bioinformatics*, 10(181), 2009.
- [116] A Filisetti, M Villani, C Damiani, A Graudenzi, A Roli, W Hordijk, and R Serra.  
On raf sets and autocatalytic cycles in random reaction networks.  
In C Pizzuti and G Spezzano, editors, *Communications in Computer and Information Science*, volume 445. Springer, Cham., 2014.
- [117] N Fernandez, C Maldonado, and Gershenson C.  
*Information Measures of Complexity, Emergence, Self-Organization, Homeostasis and Autopoiesis*.  
Springer, 2013.
- [118] T. Schreiber.  
Measuring information transfer.  
*Physical Review Letters*, 85:461–464, 2000.
- [119] J.T. Lizier, M. Prokopenko, and A.Y. Zomaya.  
Local measures of information storage in complex distributed computation.  
*Information Sciences*, 208:39–54, 2012.
- [120] S.J.Goerner-N.McLaren B. Lietaer, R.E.Ulanowicz.  
Is our monetary structure a systemic cause for financial instability? evidence and remedies from nature.  
*Journal of Future Studies*, 14(3):89–108, 2010.
- [121] B. Lietaer R. Gomez R.E. Ulanowicz, S.J. Goerner.  
Quantifying sustainability: Resilience, efficiency and the return of information theory.  
*Ecological Complexity*, 6(1):27–36, 2009.

## BIBLIOGRAPHY

---

- [122] O. Gornerup and J.P. Crutchfield.  
Hierarchical self-organization in the finitary process soup.  
*Artificial Life*, 14(3):245–254, 2008.
- [123] J. Maynard Smith.  
*The Problems of Biology*.  
Oxford University Press, 1986.
- [124] E.P. Favvas and A.C. Mitropoulos.  
What is spinodal decomposition?  
*Journal of Engineering Science and Technology Review*, 1:25–27, 2008.
- [125] A. Turing.  
On computable numbers with an application to the entscheidungsproblem.  
*Proc. of the London Math Soc.*, 42:230–265, 1937.
- [126] J.D. Murray.  
Parameter space for turing instability in reaction diffusion mechanisms: A comparison of models.  
*Journal of Theoretical Biology*, 98:143–163, 1982.
- [127] L.N. Guin.  
Spatial patterns through turing instability in a reaction-diffusion predator-prey model.  
*Mathematics and Computers in Simulation*, 109:174–185, 2015.
- [128] F.A. dos S. Silva, R.L. Viana, and S.R. Lopes.  
Pattern formation and turing instability in an activator-inhibitor system with power-law coupling.  
*Physica A: Statistical Mechanics and its Applications*, 419:487–497, 2015.
- [129] B. Corominas-Murtra, J. Goni, R.V. Sole, and C. Rodriguez-Caso.  
On the origins of hierarchy in complex networks.  
*PNAS*, 110(33):13316–13321, 2013.
- [130] E. Mones, L. Vicsek, and T. Vicsek.  
Hierarchy measure for complex networks.  
*PLoS ONE*, 7(3), 2012.
- [131] C. Alcocer-Cuaron, A.L. Rivera, and V.M. Castano.

- Hierarchical structure of biological systems: A bioengineering approach.  
*Bioengineered*, 5(2):73–79, 2014.
- [132] E. Quill.  
When networks network : Once studied solo, systems display surprising behavior when they interact.  
*ScienceNews*, 182(18), 2012.
- [133] J. Gao, L. Daqing, and S. Havlin.  
From a single network to a network of networks.  
*National Science Review*, 1(3):346–356, 2014.
- [134] J. Aguirre, D. Papo, and J.M. Buldu.  
Successful strategies for competing networks.  
*Nature Physics*, 9:230–234, 2013.
- [135] R.M. D’Souza.  
Complex networks : A winning strategy.  
*Nature Physics*, 9:212–213, 2013.
- [136] S. Kauffman and E. Weinberger.  
The nk model of rugged fitness landscapes and its application to the maturation of the immune response.  
*Journal of Theoretical Biology*, 141(2):211–245, 1989.
- [137] Whitman W, Coleman D, and Wiebe W.  
Prokaryotes : the unseen majority.  
*Proc Natl Acad Sci USA*, 95(12):6578–83, 1998.
- [138] A.V. Markov, V.A. Anisimov, and A.V. Korotayev.  
Relationship between genome size and organismal complexity in the lineage leading from prokaryotes to mammals.  
*Paleontological Journal*, 44(4):363–373, 2010.
- [139] G. Hardin.  
The competitive exclusion principle.  
*Science*, 131(3409):1292–1297, 1960.
- [140] A. Gamal and K. Young-Han.  
*Network Information Theory*.  
Cambridge University Press, 2011.

## BIBLIOGRAPHY

---

- [141] T.M.A Neildez-Nguyen, A. Parisot, C. Vignal, P. Rameau, D. Stockholm, J. Picot, V. Allo, C. Le Bec, C. Laplace, and A. Paldi.  
Epigenetic gene expression noise and phenotypic diversification of clonal cell populations.  
*Differentiation*, 76:33–40, 2008.
- [142] A. Singh and M. Soltani.  
Quantifying intrinsic and extrinsic variability in stochastic gene expression models.  
*PLoS ONE*, 8(12), 2013.
- [143] P.B. Adler and J.M. Drake.  
Environmental variation, stochastic extinction, and competitive coexistence.  
*The American Naturalist*, 172(5):186–195, 2008.
- [144] P.L. Chesson.  
The stabilizing effect of a random environment.  
*Journal of Mathematical Biology*, 15(1):1–36, 1982.
- [145] P.B. Adler, J. HilleRisLambers, P.C. Kyriakidis, Q. Guan, and J.M. Levine.  
Climate variability has a stabilizing effect on the coexistence of prairie grasses.  
*PNAS*, 103(34):12793–12798, 2006.
- [146] F. Valladares, C.C. Bastias, O. Godoy, E. Granda, and A. Escudero.  
Species coexistence in a changing world.  
*Frontiers in Plant Science*, 6(866), 2015.
- [147] P.L. Chesson.  
Multispecies competition in variable environments.  
*Theoretical Population Biology*, 45(3):227–276, 1994.
- [148] W.R. Ashby.  
*An Introduction to Cybernetics*.  
Chapman and Hall, London, 1956.
- [149] G. Longo and M. Montevil.  
*Computation, Physics and Beyond. Lecture Notes in Computer Science.*, pages 289–308.  
Springer Berlin Heidelberg, 2012.
- [150] C. O’Donovan, A. Meade, and C. Venditti.

- Dinosaurs reveal the geographical signature of an evolutionary radiation.  
*Nature Ecology and Evolution*, 2018.
- [151] S.J. Gould.  
*The Structure of Evolutionary Theory*.  
Belknap Press of Harvard University Press, 2002.
- [152] M. Wibral, J.T. Lizier, S. Vogler, V. Priesemann, and R. Galuske.  
Local active information storage as a tool to understand distributed neural information processing.  
*Frontiers in Neuroinformatics*, 8(1):1–11, 2014.
- [153] GFR Ellis.  
Top-down causation and emergence: some comments on mechanisms.  
*Interface Focus*, 2:126–140, 2012.
- [154] Anya D. Alexandra F. Vincent R. Abdoulaye, S.  
A viability approach for robustness measurement, organizational autopoiesis, and cell turnover in a multicellular system.  
*Journal of Computational Biology*, 23(4), 2016.
- [155] R. Landauer.  
Irreversibility and heat generation in the computing process.  
*IBM Journal*, pages 183–191, 1961.
- [156] M. Prokopenko and I. Einav.  
Information thermodynamics of near-equilibrium computation.  
*Physical Review E*, 91(062143):1–8, 2015.
- [157] J.M.R. Parrondo, J.M. Horowitz, and T. Sagawa.  
Thermodynamics of information.  
*Nature Physics*, 11:131–139, 2015.
- [158] J.L. England.  
Statistical physics of self-replication.  
*The Journal of Chemical Physics*, 139(121923), 2013.
- [159] T. Froese and T. Ziemke.  
Enactive artificial intelligence: Investigating the systemic organization of life and mind.  
*Journal of Artificial Intelligence*, 173:466–500, 2009.

