

Evolution of Symbiosis in the Game of Life:

Three Characteristics of Successful Symbiotes

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Abstract

In past work, we developed a computational model of the evolution of symbiotic entities (Model-S), based on Conway's Game of Life. In this article, we examine three trends that biologists have observed in the evolution of symbiotes. (1) *Management*: If one partner is able to control the symbiotic relation, this control can reduce conflict; thus evolutionary selection favours symbiotes that have a manager. (2) *Mutualism*: Although partners in symbiosis often have conflicting needs, evolutionary selection favours increasing cooperation among partners. (3) *Interaction*: Repeated interaction among partners in symbiosis tends to promote increasing fitness due to evolutionary selection. We have added new components to Model-S that allow us to observe these three trends in runs of Model-S. The new components are analogous to the practice of staining cells in biology research, to reveal patterns that are not usually visible. When we measure the fitness of a symbiote by the number of children it has, we find that fitter symbiotes have significantly more management, mutualism, and interaction than less fit symbiotes. These results confirm the trends observed in nature by biologists. Model-S allows biologists to study these evolutionary trends and other characteristics of symbiosis in ways that are not tractable with living organisms.

Keywords: Symbiosis, evolution, cellular automata, mutualism, interaction, management.

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1 Introduction

The word *symbiosis* comes from the Greek *syμβίωσις*, meaning *living together*. Often symbiosis is understood as a mutually beneficial relationship, but biologists define symbiosis more generally as any long-term interaction between two or more different species. Martin and Schwab (2013) propose a set of terms based on whether two species in a symbiotic relationship experience a beneficial effect (+), a harmful effect (-), or a neutral effect (0). This yields six types of symbiosis: neutralism (0/0), antagonism (-/-), amensalism (0/-), agonism (+/-), commensalism (+/0), and mutualism (+/+).

It is often assumed that symbiotes are composed of two species, but many symbiotes are composed of more than two species. For example, the human body is estimated to contain 500 to 1000 species of symbiotic bacteria (Gilbert et al., 2018). In this article, we study symbiotes composed of two to five species. Following Douglas (2010), we call the members of a symbiote *partners*.

In previous publications (Turney, 2020; 2021a), we presented Model-S, a computational simulation of the evolution of symbiosis, based on a variation of John Conway’s Game of Life (Gardner, 1970). A run of Model-S begins with a randomly generated population of single organisms (no symbiotes). An evolutionary algorithm allows the population to change over time, with mutation, asexual reproduction, sexual reproduction, selection, and symbiosis. We allow the simulation to run for 100 generations. As it runs, the number of symbiotes in an organism increases. There is no fixed limit on the number of symbiotes in an organism. Given 100 generations, the final generation typically consists of symbiotes containing four to five species.

Model-S was developed to provide insight into the major cooperative transitions in biological and cultural evolution (Maynard Smith and Szathmáry, 1995; Nolan and Lenski, 2010). In the current article, we show that Model-S provides a simple computational model of three observations that biologists have made, concerning the evolution of successful symbiotes.

Douglas (2010) provides an authoritative analysis and summary of research in symbiosis. Based on this work, we identified three prominent hypotheses about the characteristics of symbiotes that tend to be selected by evolution:

1. *Management*: Douglas (2010, p. 90) wrote, “... many symbioses are not associations of equals, but involve one organism that can control many of the traits of its partners.” Also (Douglas, 2010, p. 72), “The incidence of cheating depends on opportunity, and opportunity can be minimized by the controlling partner.” In this article, we call the controlling partner the *manager* and the other

partners *workers*. In our experiments with Model-S (Section 4.1), we observe that evolution tends to select symbiotes with one manager and one or more workers.

2. *Mutualism*: Douglas (2010, p. 56) wrote, “Conflict is inherent to the reciprocal exchange of benefits that underpin symbiosis.” Furthermore (Douglas, 2010, p. 67), “Just as conflict arises from a difference in selective interest between the partners of a symbiosis, conflict can be resolved by increasing the overlap in selective interest of the partners.” We call a partner that benefits from belonging to the symbiote an *insider*. A partner that does not benefit from belonging to the symbiote is an *outsider*. In Model-S, we can easily distinguish these two cases by measuring the growth of a partner both inside the symbiote and outside the symbiote. If the partner grows more inside, it is an insider; otherwise, it is an outsider. This kind of measurement is much easier in a computational model than in a biological organism, because it is usually difficult to remove a partner from a symbiote without harming it. In our experiments (Section 4.2), evolution tends to select insiders and winnow outsiders.
3. *Interaction*: Douglas (2010, p. 58) wrote, “If repeated interactions with one partner reveal it to be a cooperator, then a player may have a vested interest in the continued well-being of that partner.” We call a partner that interacts with the other partners an *ensemblist*. A partner that avoids interacting with the other partners is a *soloist*. In our experiments (Section 4.3), evolution tends to select ensemblists and eliminate soloists.

Model-S has two parts, a cellular automaton in which seed patterns grow and interact with each other and an external evolutionary algorithm in which seed patterns undergo mutation, crossover, asexual and sexual reproduction, and symbiosis (Turney, 2020; 2021a). The Golly software is used for the cellular automaton (Trevorrow et al., 2022) and Python code is used to implement the evolutionary algorithm (Turney, 2022). Both parts are freely available for downloading (see the two preceding references).

In Section 2, we introduce three variations on John Conway’s Game of Life (Gardner, 1970). The first game, the original Game of Life, is usually displayed as a grid of two colours (black and white cells). The second game, the Immigration Game, created by Don Woods (Wainwright, 1971), is usually displayed as a grid of three colours (red, blue, and white cells). In this article, we introduce a new game, the Management Game, which is displayed as a grid of six colours (red, blue, orange, green, purple, and white cells). All three of these games follow the rules of the original Game of Life, except there are new rules governing the colours in the Immigration Game and the Management Game. The same patterns unfold in all three games, but the patterns are coloured differently. In particular, the new colours in the Management Game enable us to see interactions among groups of cells that cannot readily be seen in the Game of Life. The new colours

are analogous to the practice of staining cells in biology experiments. The additional colours allow us to distinguish managers and workers, insiders and outsiders, and ensemblists and soloists.

Section 3 describes how Model-S works. Each run of Model-S yields 20,000 evolved organisms (symbiotes and non-symbiotes). Over a period of a month, we ran 40 instances of Model-S on three computers, resulting in a total of 800,000 organisms ($40 \times 20,000$). The fitness of the organisms varies greatly from the earlier generations of a run (relatively small and unfit organisms) to the later generations of a run (relatively large and fit organisms). To reduce the noise produced by this high variability in fitness, we analyzed the data somewhat like a twin study, by creating matched pairs of symbiotes (ignoring non-symbiotes). Combining the 40 runs, we identified 210 distinct *groups* of symbiotes. We say that two symbiotes belong to the same group of symbiotes if and only if they share a common ancestral symbiote that contains the same partners. That is, each partner in the ancestor is also a partner in both descendants and no partner in the descendants is absent in the ancestor. From each symbiotic group, we extracted the most fit and the least fit symbiote, resulting in 210 matched pairs of symbiotes. These pairs form the dataset that we use to test the three hypotheses about the evolution of successful symbiotes. Note that these matched pairs are not joined together as symbiotes. They are paired together only for comparison purposes (as in a twin study). The characteristic that each member of a pair shares is that they belong to the same group. The pairing removes the noise that would be produced by comparing symbiotes across different groups, with varying numbers of partners sampled from varying generations.

In the core of the paper, Section 4, we test the three hypotheses, *management*, *mutualism*, and *interaction*. All three hypotheses are supported by the results. Section 5 discusses limitations of our work and ideas for future work. We conclude in Section 6.

2 Cellular Automata: Three Games of Life

Figure 1 shows examples of the three cellular automata, the Game of Life, the Immigration Game, and the Management Game. The left column contains the initial seed patterns, the states of the games at time $t = 0$. The right column contains the final seed patterns, at time $t = 1000$. After 1000 time-steps, the games have usually settled into stable configurations, which are called *ashes* in the Game of Life community. Ashes are patterns that are static, oscillating, or moving through space (LifeWiki, 2022).

Insert Figure 1 here.

The Game of Life, the Immigration Game, and the Management Game are identical if we ignore colour, but colour gives us important information. In the Immigration Game, we can see that the blue pattern in

Image C is responsible for creating the two blue patterns in Image D, and the red pattern in Image C is responsible for the three red patterns in Image D, but this information is not available in the Game of Life when we look at Images A and B. Likewise, the Management Game gives us information in Image F that is not visible in Image D.

2.1 The Game of Life

John Conway's Game of Life (Gardner, 1970) is played on an infinite, two-dimensional grid of square cells, where each cell is either *dead* (state 0) or *alive* (state 1). Often the dead state (the background) is coloured white and the live state (the foreground) is coloured black. The state of a cell changes with time, based on the state of its eight nearest neighbours (the *Moore neighbourhood*). Time passes in discrete intervals, and the states of the cells at time t uniquely determine the states of the cells at time $t + 1$. There is only one player in the game and the player's only actions are to choose the initial states of the cells at time $t = 0$ and the time limit for the game, given by a maximum value for t . The states for $t > 0$ are calculated by a computer. The initial states form a seed pattern that determines the course of the game. The rules are summarized in Table 1.

Insert Table 1 here.

The rules for updating states in the Game of Life are compactly expressed as B3/S23: A cell is *born* (it switches from state 0 to state 1) if it has exactly three living neighbours (B3). A cell *survives* (it remains in state 1) if it has two or three living neighbours (S23). Otherwise, the cell *dies* (it switches from 1 to 0) or remains *unborn* (it remains in state 0).

2.2 The Immigration Game

Don Woods' Immigration Game (Wainwright, 1971) is almost the same as the Game of Life, except there are two different live states (states 1 and 2, usually represented by red and blue colours). The rules for updating remain B3/S23, but there are two new rules for determining colour: (1) Live cells do not change colour unless they die (they become white). (2) When a new cell is born, it takes the colour of the majority of its living neighbours. Since birth requires three live neighbours, there is always a clear majority. The initial states at time $t = 0$ are chosen by the two players of the game; one player makes a red seed pattern and the other player makes a blue seed pattern. The players agree on a time limit, given by a maximum value for t . The rules are summarized in Table 2.

Insert Table 2 here.

In the Immigration Game, if states 1 and 2 were coloured black, instead of red and blue, the game would appear to be exactly the same as the Game of Life. The purpose of the two colours is to score the two players, to convert the Game of Life from a solitaire game into a two-player competitive game. In Model-S, we score each player by the *growth* of their initial seed, defined as the final number of cells of their colour minus the initial number of cells of their colour. Growth will be negative if the final number is less than the initial number. The motivation for this method of scoring is to avoid biasing the game in favour of the seed that has the most living cells at the beginning of the game. The winner is the player whose colour has grown the most over the course of the game.

2.3 The Management Game

The Management Game (a new game, introduced here) extends the Immigration Game by adding two more *live* states, orange and green. The Management Game also adds one more *dead* state, purple, to serve as a border for separating the partners of a symbiote. This brings the total number of states to six. Table 3 lists the six states and introduces some terminology.

Insert Table 3 here.

Table 4 presents the rules of the Management Game. Like the Game of Life and the Immigration Game, the basic rule is still B3/S23. The only change is how colours are handled. We colour one partner of the symbiote red and the other partners blue and then play the Management Game. If red and blue do not interact, then we will only see changing red and blue patterns. If red and blue do interact, then we will start to see orange and green colours appearing.

Insert Table 4 here.

We noted above that, if states 1 and 2 in the Immigration Game were displayed as black, then the Immigration Game would look exactly like the Game of Life. The only difference between the Game of Life and the Immigration Game is colouration. Likewise, in the Management Game, if state 3 (orange) were displayed as red, state 4 (green) were displayed as blue, and state 5 (purple) were displayed as white, then the Management Game would look exactly like the Immigration Game. In the Management Game, orange is used to mark a subset of the cells that would be red in the Immigration Game, green is used to mark a subset of the cells that would be blue, and purple is used to mark a subset of the cells that would be white.

3 Model-S: A Model of the Evolution of Symbiosis

Model-S is a genetic algorithm for evolving seed patterns that are good at playing the Immigration Game (Turney, 2020; 2021a; 2022). It is based on a GENITOR-style genetic algorithm (Whitley, 1989), with one-at-a-time reproduction, a constant population size, and rank-based tournament selection. Model-S uses Golly (Trevorrow et al., 2022), an open source, cross-platform application for exploring cellular automata. Golly can be controlled with Python code. Model-S consists of Python routines that manage a population of seed patterns, passing the patterns on to Golly in order to measure their fitness.

Model-S is a computational model of symbiosis with shifting levels of selection (Turney, 2020). In Model-S, when two entities enter a symbiotic relation, they are fused together, hence they live or die as a unit. This kind of fusion, in which evolutionary selection shifts from the two components to the fused whole, is called *endosymbiosis*. The paradigmatic example of endosymbiosis is the major cooperative transition in which two prokaryotic cells merged to form a eukaryote (Margulis, 1970; 1981; Maynard Smith and Szathmáry, 1995).

Model-S uses the Immigration Game as a contest for measuring the fitness of seed patterns. Two black and white seed patterns are sampled from the population. One of the seeds is altered by switching black cells to red and the other seed is altered by switching black cells to blue. These two seeds are the initial states of the two players of the Immigration Game. Model-S selects a time limit for playing the game, based on the sum of the live cells in the two seeds. Larger seeds are given more time, since it takes longer for them to settle into stable configurations (*ashes*). The growth of the red seed is the total number of live red cells when the time limit is reached minus the number of live red cells in the initial seed pattern. The growth of the blue seed is measured likewise. The winner of the Immigration Game is the seed that grows the most. A given seed's fitness is measured by the average number of Immigration Games it wins when competing against every seed in the current population.

3.1 Time Scales

There are three different scales of time involved in Model-S. First, each competition between two seeds takes a certain amount of time, depending on the size of the two competing seed patterns. This time is spent running the Immigration Game in the Golly cellular automaton software (*game time*). Second, each seed has a *lifetime*, which begins when it enters the population and ends when it leaves the population. This time passes in the Python code that implements the model of evolution. Third, there is the length of time that a particular instance of Model-S runs, from the first generation to the last generation. This time also passes in the Python code (*evolutionary time*).

A typical Immigration Game runs for about a thousand steps (*game time*). Model-S has a constant population size of 200. The initial population consists of 200 randomly generated entities. The initial seed patterns are small (5×5 cell grids) and none of them are symbiotes. Each subsequent newly born entity replaces an existing entity in the population (the least fit member of the population is replaced). When 200 new entities have been born, we say that one generation of time has passed. Model-S runs for 100 generations, which results in 20,000 evolved seeds (200×100). The initial 200 random seeds are considered as generation zero; they are not counted as evolved seeds. We store all of the seeds for later analysis. We also record family trees for all of the seeds.

3.2 Four Layers

Model-S is constructed with four layers, each subsequent layer building on the previous layers, as shown in Figure 2. The purpose of having four layers is to measure each layer's contribution to the fitness of the evolving population, by selectively enabling or disabling layers. In the current article, we use all four layers.

Insert Figure 2 here.

Layer 1 implements a simple form of asexual reproduction, with a fixed genome size (that is, a fixed matrix size). A member of the population is selected for reproduction using tournament selection (Whitley, 1989). The chosen seed pattern is mutated by randomly flipping some of the bits in the seed matrix and it then competes in a series of one-on-one Immigration Games with the other members of the population. Its fitness is the average fraction of games it wins.

Layer 2 implements a slightly more sophisticated form of asexual reproduction. A member of the population is selected for reproduction using tournament selection. Layer 2 allows the seed matrix to grow or shrink by appending or removing a row or column to or from the seed matrix. Layer 2 then passes the seed on to Layer 1 for mutation by flipping bits.

Layer 3 selects two seeds from the population using tournament selection and then combines them with genetic crossover (sexual reproduction). Layer 3 requires the two seeds to be somewhat similar for crossover to proceed. If a suitable match is found, then Layer 3 combines the two seeds with crossover and passes the new seed on to Layer 2 for row or column adjustments. Otherwise, if no suitable match is found, Layer 3 passes only one of the two seeds on to Layer 2, without making any changes to the chosen seed.

Layer 4 adds symbiosis to Model-S. Two seeds are selected from the population and they are fused together, side-by-side, creating a new symbiotic genome. This new fused seed is treated as a whole; that is, selection shifts from the level of the two partners to the level of the whole. The parameters in Model-S are

set so that fusion is rare. Most of the time, Layer 4 makes no changes and simply passes control to Layer 3. The main result of our past work (Turney, 2020) is evidence that symbiosis (Layer 4) promotes fitness improvements in the Immigration Game.

Each symbiote created by Layer 4 is composed of partners (seed patterns) that have been fused together to make a new whole (a new, fused seed pattern). In Layer 4, seed patterns are fused two at a time. In the earliest generations of a run of Model-S, when two seeds are selected for fusion, they will not have experienced fusion before; therefore the selected seeds will not be composed of partners. The result of fusion with these seeds will be a new seed with two partners. Over the course of a long run of Model-S, eventually one or both of the two seeds that are selected for fusion will have experienced fusion in the past, so the new, fused seed will have three or more partners. In our 40 runs of Model-S, there are seeds with two, three, four, and five partners.

The state of a seed pattern at time $t = 0$ is analogous to the genome of an organism. When a seed pattern enters a game, it develops over time, following the rules of the game, as t increases. The developing pattern is analogous to the developing phenome of an organism. The genome is static and the phenome is dynamic. Model-S records the genome of each organism (the pattern at time $t = 0$), but it keeps no record of the phenome (any patterns at $t > 0$). All the information that Model-S requires for evolving new genomes is provided by the fitness score of the phenome. The phenome itself is ephemeral.

When Model-S is running, symbiotes and non-symbiotes compete against other symbiotes and non-symbiotes, in order to measure the fitness of the entities in the population. The competitions use the Immigration Game to compare two entities sampled from the population. These competitions determine which entities can reproduce; that is, the competitions determine life and death in the population. All entities, symbiotic or not, are treated the same way. Model-S does not analyze the partners inside a symbiote in any way: a symbiote is treated as a whole.

After Model-S has finished running, we can analyze the stored record of all seed patterns (genomes), across all generations of the run. We inspect the record of seed patterns and extract all symbiotic seed patterns from the record, skipping over non-symbiotes, since our focus in this article is symbiotes.

3.3 Summary of the Data

Since fitness is measured relative to the current population, Model-S has no absolute measure of fitness. For example, a seed that wins 90% of its Immigration Games in the early generations will be much less fit relative to a seed that wins 90% of its games in the later generations, when the competition is much stronger. However, the two seeds have the same fitness (90%) relative to their respective current populations.

As we mentioned in the introduction, our analysis is based on data from 40 runs of Model-S. The data includes information from all generations, and thus there is much variation in fitness, as measured by competition in Immigration Games. We use two methods to handle the variation in fitness. First, we use the number of children that a seed has as a surrogate for the seed's fitness. As an indicator of fitness, the number of children born is more robust and stable over many generations, compared to the percentage of games won, although the two measures are closely related. Second, we identified 210 groups of symbiotes, based on their recorded family trees, and extracted the most fit and the least fit symbiote from each group, where fitness is measured by their number of children. These 210 pairs constitute the data that we use to test the three hypotheses, management, mutualism, and interaction. The objective is that matched pairs will reduce the variability in the data analysis.

In the context of Model-S, we define a *symbiotic group* as a family tree that begins with a new symbiotic fusion as the root of the tree, each new child forms a new node in the tree, and the leaves of the tree end with seeds that have no children. The nodes in a given family tree will necessarily be symbiotes that all have the same number of partners. If one of the nodes undergoes fusion, it is considered to be a new group, and it does not belong to the family tree. The nodes in a family tree will vary from one another due to mutations and sexual recombination, but they will not vary in their number of partners.

In our 40 runs of Model-S, we found 210 symbiotic groups. Many of these groups have hundreds or thousands of children. We also found 1,565 new symbiotes that had zero children. These singleton symbiotes could be considered as groups with one member, but we simply discarded these cases. Since the most fit and the least fit member of a singleton group is the same seed, these seeds are not useful for our analysis.

Table 5 shows the growth of the 210 pairs of seeds. The growth of a seed is measured by running a game for 1000 steps and then counting the increase in the number of living squares in the game. The growth of a given seed is the same for all three games, the Game of Life, the Immigration Game, and the Management Game (see Figure 1). The table shows that the more prolific seeds have more children than the less prolific seeds and the more prolific seeds also grow considerably more than the less prolific seeds.

Insert Table 5 here.

The ratio of the growth of the more prolific seeds over the growth of the less prolific seeds varies from 14.4 for seeds with three partners to 6.1 for seeds with four partners. The growth of a seed (in isolation) is correlated with the number of Immigration Games it wins in Model-S (in one-on-one competitions) and with the number of children the seed has (in its family tree). In the next section, we will see that the more

prolific seeds have three characteristics that distinguish them from the less prolific seeds. These are characteristics that have been selected by evolution.

4 Three Hypotheses about the Evolution of Symbiotes

The Immigration Game is sufficient for evolution in Model-S. It is a two-person game with a clear goal: the winner is the player that grows the most. The Management Game is not necessary in Model-S. However, after we have run 40 instances of Model-S and collected the data from these runs, the Management Game becomes a useful tool for data analysis, outside of Model-S. The extra colours in the Management Game allow us to see interactions that are not visible in the Immigration Game.

Figure 3 shows how we analyze the partners in a three-partner symbiote. Given the initial seed pattern of the symbiote, we focus on one of the partners in the symbiote and colour that partner red. The other partners are coloured blue. We then run the Management Game for 1000 steps and observe the results. This process is repeated for each of the three partners in the symbiote.

Insert Figure 3 here.

Given the seed pattern in image A, we can tell that the red partner played a majority role in creating the orange pattern in image B, and it played a minority role in creating the green patterns in image B. This follows from the rules of the Management Game (see Table 4). In image C, the central red partner played a minority role in all of the green patterns in image D. In image E, the rightmost red partner played a majority role in creating the orange patterns in image F. The rightmost red partner had no role in creating the blue pattern in image F. The blue pattern in image F was created solely by the two blue patterns in image E.

The four rows of Table 4 tell us four things: (1) A newly born red cell is always the work of three other red cells. (2) A newly born blue cell is always the work of three other blue cells. (3) When we see an orange cell, we know that, at some time in the past, a blue or green cell played a *supporting* role (one of three cells for B3) in forming the orange cell (since the initial seed pattern contains no orange). The *leading* role (two of three cells) was played by orange or red. (4) When we see a green cell, we know that, at some time in the past or in the current birth, a red or orange cell played a *supporting* role (one of three cells for B3) in forming the green cell (since the initial seed contains no green). The *leading* role (two of three cells) was played by green or blue.

In the following subsections, we will show how the Management Game allows us to define (1) *managers* and *workers* to test the management hypothesis, (2) *insiders* and *outsiders* to test the mutualism hypothesis, and (3) *ensemblists* and *soloists* to test the interaction hypothesis.

4.1 Management

Suppose we have a symbiote at time $t = 0$ with N partners. Let us focus on one of those partners and colour that partner red. All other partners are coloured blue. Then we run the Management Game for $t = 1000$ steps and observe the results. If the number of orange cells is greater than the number of green cells at $t = 1000$, then we define the red partner of the seed at $t = 0$ as a *manager*. If the number of orange cells is less than or equal to the number of green cells, then we define the red partner as a *worker*.

The motivation for these definitions of *manager* and *worker* is the observation that, when orange dominates green, we know that the red partner played a leading role in creating the orange cells (see Table 4). Furthermore, the red partner did not work alone. If it had worked alone, the final pattern it created would be red, not orange. Thus the orange cells represent both a leading role and interaction with others partners of the symbiote. On the other hand, green cells represent both a supporting role and interaction with other partners of the symbiote.

Looking at Figure 3, images A and B, we can see that the leftmost partner of the symbiote is a worker (because green dominates orange). Images C and D tell us that the central partner of the symbiote is also a worker (because green dominates orange). Images E and F indicate that the rightmost partner of the symbiote is a manager (because orange dominates green). Thus the three-partner seed in Figure 3 consists of one manager and two workers.

Table 6 gives the statistics for the 210 *most* prolific seeds. For each possible combination of M managers and N workers, such that $M + N$ ranges between two and five, the table shows the number of seeds that have M managers and N workers.

Insert Table 6 here.

Table 7 gives the statistics for the 210 *least* prolific seeds. For each possible combination of M managers and N workers, such that $M + N$ ranges between two and five, the table shows the number of seeds that have M managers and N workers.

Insert Table 7 here.

What we would like to know is, what is the difference between the 210 most prolific seeds and the 210 least prolific seeds? Table 8 answers this question. Each value in Table 8 for M managers and N workers corresponds to the value in Table 6 for M managers and N workers (the most prolific seeds) minus the value in Table 7 for M managers and N workers (the least prolific seeds).

Insert Table 8 here.

Table 8 shows that there is a shift away from having zero managers (see the bottom row of the table, where $M = 0$), and a corresponding shift towards having one manager ($M = 1$). In the row totals, we see -43 for zero managers and $+40$ for one manager. This shift in the number of managers is statistically significant with greater than 95% probability, based on Fisher's exact test. The results confirm the hypothesis (in Section 1) that evolution selects for one manager, rather than zero managers.

Although our focus here is on biology, we expect that this analysis also applies to human organizations, since they can be viewed as symbiotic structures (Stewart, 1995; 1997; 2014; 2020). Of course, large human organizations usually need more than one manager, but our experiments involve symbiotes with at most five partners. It appears that one manager is sufficient for symbiotes with five partners or less.

4.2 Mutualism

We define an *insider* as a partner inside a symbiote that benefits from being inside the symbiote, whereas an *outsider* is a partner inside a symbiote that would benefit from leaving the symbiote. When there is mutualism in a symbiote, all of the partners are insiders; all of the partners benefit from being in the symbiote. We use growth as a measure of benefit. If a partner grows more when it is inside the symbiote than when it is outside the symbiote, then the partner benefits from being in the symbiote: it is an *insider*. Otherwise, the partner is an *outsider*.

In biology, it is often not possible to remove a partner from a symbiote without damaging the partner. In Model-S, it is easy to remove a partner without damaging it. A computational model of mutualism allows us to perform experiments that would be very difficult with living creatures.

Figure 4 shows what happens when we extract the three red partners from the symbiote in Figure 3 and then allow them to grow individually, outside of the symbiote. Their growth as individuals (Figure 4, right column) is quite different from their growth in the symbiote (Figure 3, right column).

Insert Figure 4 here.

We can easily measure the growth of the individuals (the partners removed from the symbiote), as shown in Figure 4: The first partner grows by 3 cells (B in Figure 4), the second partner grows by 50 cells (D), and the third partner grows by 79 cells (F).

Measuring the growth of the partners inside the symbiote (Figure 3) is more complicated, because we need to take the various colours into account. We weight the colours as follows: red = 1, blue = 0, orange = $2/3$, green = $1/3$. The reasoning here is that the initial red seed should get full credit for any new red cells that it creates (that is, each new red cell has a value of 1). The initial red seed should not get any credit for blue cells, since it cannot create any blue cells (see Table 4: only blue cells can make new blue cells). The initial red seed should get a credit of $2/3$ for each new orange cell that it creates, since an orange cell is the work of two red or orange cells (and one other cell that is neither red nor orange). The initial red seed should get a credit of $1/3$ for each new green cell that it creates, since one red or orange cell (and two other cells that were neither red nor orange) was responsible (at some time in the past or present) for creating the new green cell.

Table 9 gives an example of how to measure the growth of partners inside a symbiote (as in Figure 3) and outside a symbiote (as in Figure 4). We can see from the table that seed A grows more when it is inside the symbiote (4.33 inside versus 3 outside), whereas seed C grows more when it is outside the symbiote (7 inside versus 50 outside) and D also grows more when it is outside than inside (9.33 inside versus 79 outside). Thus the three-partner symbiote in Figure 3 consists of one insider and two outsiders.

Insert Table 9 here.

Table 10 is analogous to Table 8 in Section 4.1: it shows the difference between the 210 most prolific seeds and the 210 least prolific seeds for insiders and outsiders, just as Table 8 shows the difference for managers and workers. In Table 10, we can see a shift towards zero outsiders. The second row has the largest drop in outsiders, -69 for two outsiders. The bottom row has the largest increase in insiders, $+74$ for zero outsiders. The drop in seeds with two outsiders (-69) and the rise in seeds with zero outsiders ($+74$) is statistically significant with greater than 95% probability, based on Fisher's exact test.

Insert Table 10 here.

Table 10 confirms our hypothesis that evolution tends to select insiders and winnow outsiders. Comparing the least prolific seeds with the most prolific seeds, we can see that the most prolific seeds have

made a shift towards strongly reducing the number of outsiders. The ideal number of outsiders is zero, which is what we have with mutualism: mutual benefit for all of the partners in a symbiote.

If we compare the shift in management (Table 8, Section 4.1), away from zero managers (−43) and towards one manager (+40), with the shift in mutualism (Table 10, Section 4.2), away from two outsiders (−69) and towards zero outsiders (+74), it seems that the evolutionary push towards mutualism is stronger than the push towards management, although both are strong.

Again, although our focus here is on biology, we expect that this analysis also applies to human organizations. It may be more important for employees in a company to feel that they are better off inside the company than outside (Table 10) than to feel that they have a good manager (Table 8).

4.3 Interaction

We define a *soloist* as a partner in a symbiote that prefers to work on its own, whereas an *ensemblist* prefers to work as partner in a team. A soloist avoids interaction with others, but an ensemblist seeks interaction. Given a red partner in a symbiote, if the red partner produces more red cells, then it is growing, but it is not interacting with the other partners of the symbiote. If the red partner produces orange or green cells, then it is interacting with the other partners of the symbiote. If the sum of orange growth and green growth is greater than the red growth, then we say that the partner is an *ensemblist*. Otherwise, if red growth dominates orange and green growth, then we say that the partner is a *soloist*. Blue growth is irrelevant, since the red partner cannot cause a new blue cell to appear (see Table 4).

Looking at Figure 3, we see that all three partners (the red partners in A, C, and E) produce some orange or green growth (in B, D, and F), but none of them produce red growth. Therefore the symbiote in Figure 3 has three ensemblists and zero soloists.

Table 11 is analogous to Table 8 in Section 4.1 and Table 10 in Section 4.2: it shows the difference between the 210 most prolific seeds and the 210 least prolific seeds for ensemblists and soloists, just as Table 8 and Table 10 show the difference for managers and workers (management) and for insiders and outsiders (mutualism).

Insert Table 11 here.

Table 11 shows that there is a shift away from having one soloist (−24) and a shift towards having zero soloists (+26). This shift in the number of soloists is statistically significant with greater than 95% probability, based on Fisher's exact test. The results confirm the hypothesis (in Section 1) that evolution

selects for zero soloists; that is, evolution selects for symbiotes with partners that all tend to interact with other partners.

If we compare the shift in management (-43 for zero managers and $+40$ for one manager) and the shift in mutualism (-69 for two outsiders and $+74$ for zero outsiders), the shift in interaction is not as strong (-24 for one soloist and $+26$ for zero soloists), but it is statistically significant. Evolution selects for increased interaction among the partners in a symbiote. The ideal number of soloists is zero.

This lesson is not surprising in the context of human organizations. In general, an employee who does not interact with other employees is not a valuable employee.

5 Future Work and Limitations

In this article, we have used Model-S to test three hypotheses that were suggested by the research of biologists who study symbiosis (Douglas, 2010). A closer study of this body of biological research is likely to turn up other hypotheses that could be tested using Model-S. Biologists may also discover ways in which Model-S fails to account for the observations of biologists. These observations could lead to better computational models of symbiosis, and better models could also lead biologists to new discoveries.

We have used three different cellular automata in our work (see Section 2). Although the Management Game was specifically designed for studying symbiosis, it seems unlikely that it is the best cellular automaton for studying symbiosis, given the huge space of possible cellular automata (Turney, 2021b). Even if we restrict our attention to Conway's Game of Life and the various ways colours can be added to the game, we are faced with an infinite number of possible variations.

This project was inspired by research on the major cooperative transitions in evolution. The major cooperative transitions in biological and cultural evolution may be seen as cases of particularly successful symbioses. Attempts to explain the processes that drive the major cooperative transitions include the work of Buss (1987), Maynard Smith (1988), Maynard Smith and Szathmáry (1995), Stewart (1995; 2014; 2020), Michod (1999), Wilson and Wilson (2007), Wilson (2015), West et al. (2015), Szathmáry (2015), and Wilson (2019). In future work, we plan to focus on a specific major cooperative transition and attempt to create a computational model of that transition.

In Section 4, we briefly mentioned how Model-S and the Management Game might be applied to modeling human culture, such as employees working together in a company. We hope to explore this in future work.

6 Conclusion

Model-S evolves a population of seed patterns using a fitness measure based on competitive growth. Seed patterns compete in the Immigration Game, where the winner is the pattern that grows the most. The fitness of a seed pattern in Model-S is measured by the average number of games that it wins, competing against all of the other seeds in the population. The experiments in Section 4 show that evolutionary selection in Model-S favours symbiotes with one manager, zero outsiders, and zero soloists. These results are consistent with what we would expect, based on the research of biologists who study symbiosis.

More generally, Model-S shows that cellular automata combined with an evolutionary algorithm can yield computational models of symbiosis that are consistent with the discoveries of biologists. We expect that computational models of this kind will be useful for many aspects of biological research, and perhaps for many aspects of research in models of human cultural development.

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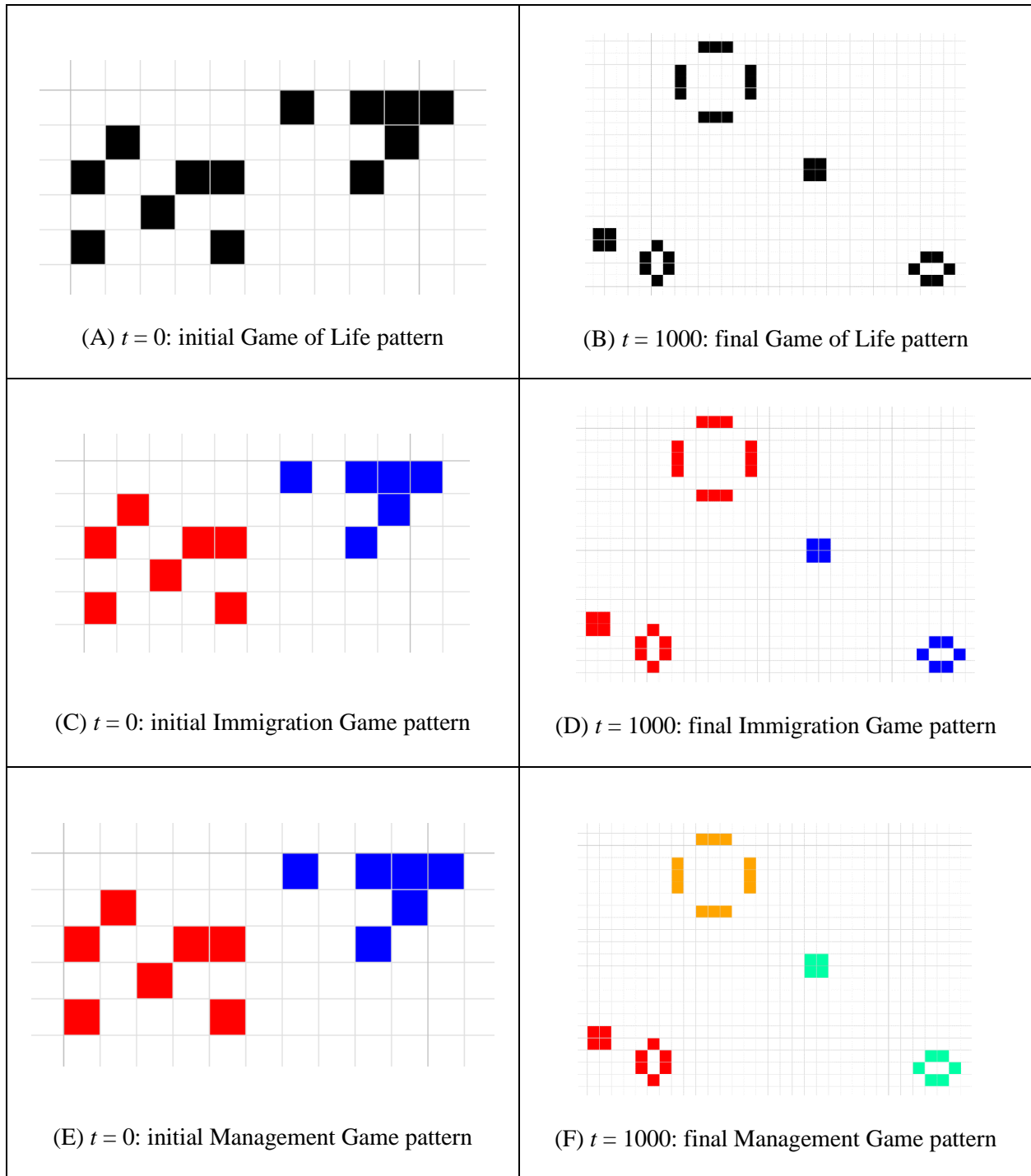


Figure 1. The Game of Life, the Immigration Game, and the Management Game at time $t = 0$ and $t = 1000$. Adding colours to the games reveals how parts of the initial patterns determine parts of the final patterns.

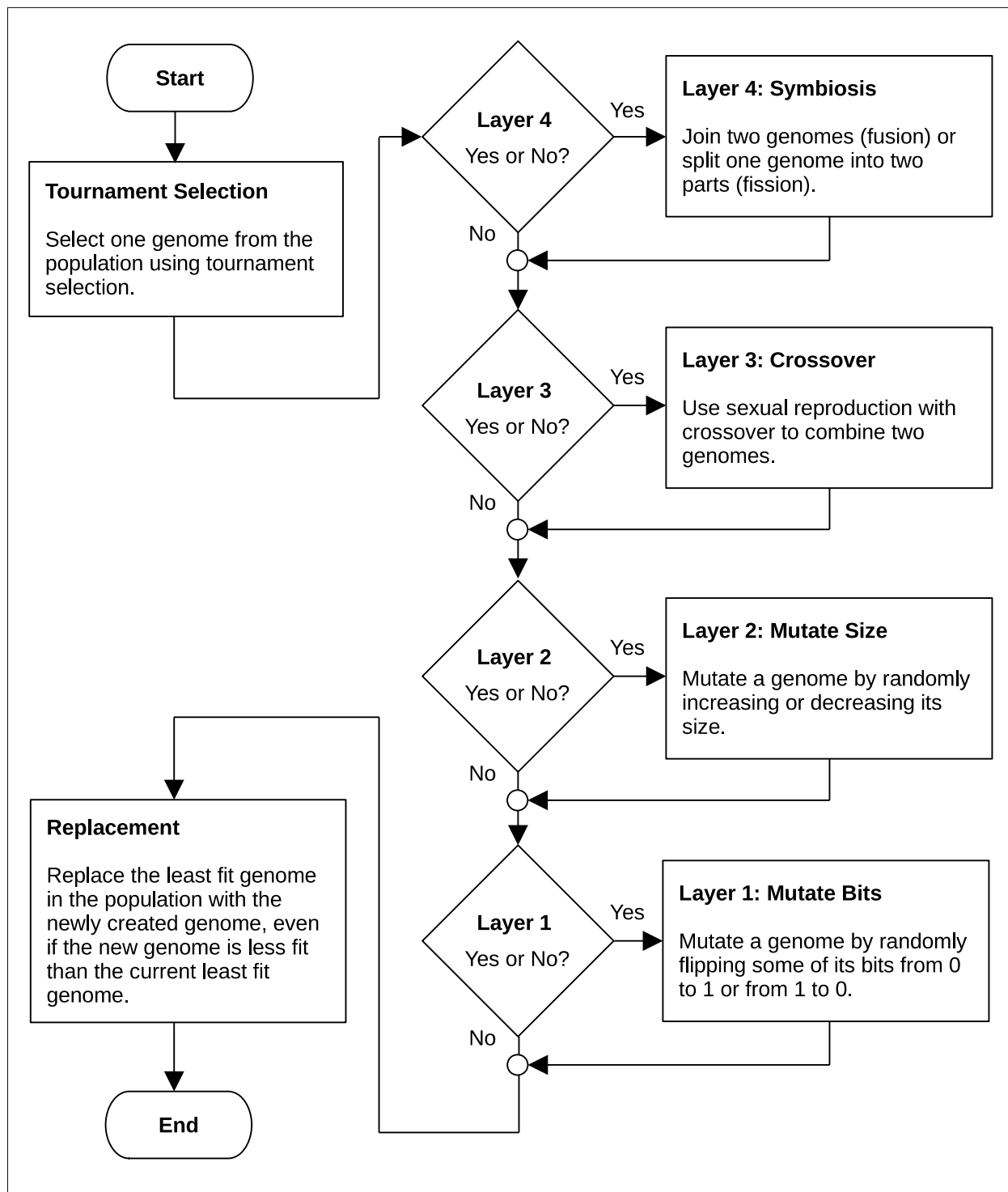


Figure 2. This flowchart outlines the process for selecting an individual's genome from the population and creating a new genome. This process is a subroutine in a loop that produces a series of new individuals. The decision to use a given layer is determined by the parameters of Model-S. This flowchart first appeared in a previous article (Turney, 2021a). A more detailed four-figure flowchart is available (Turney, 2020).

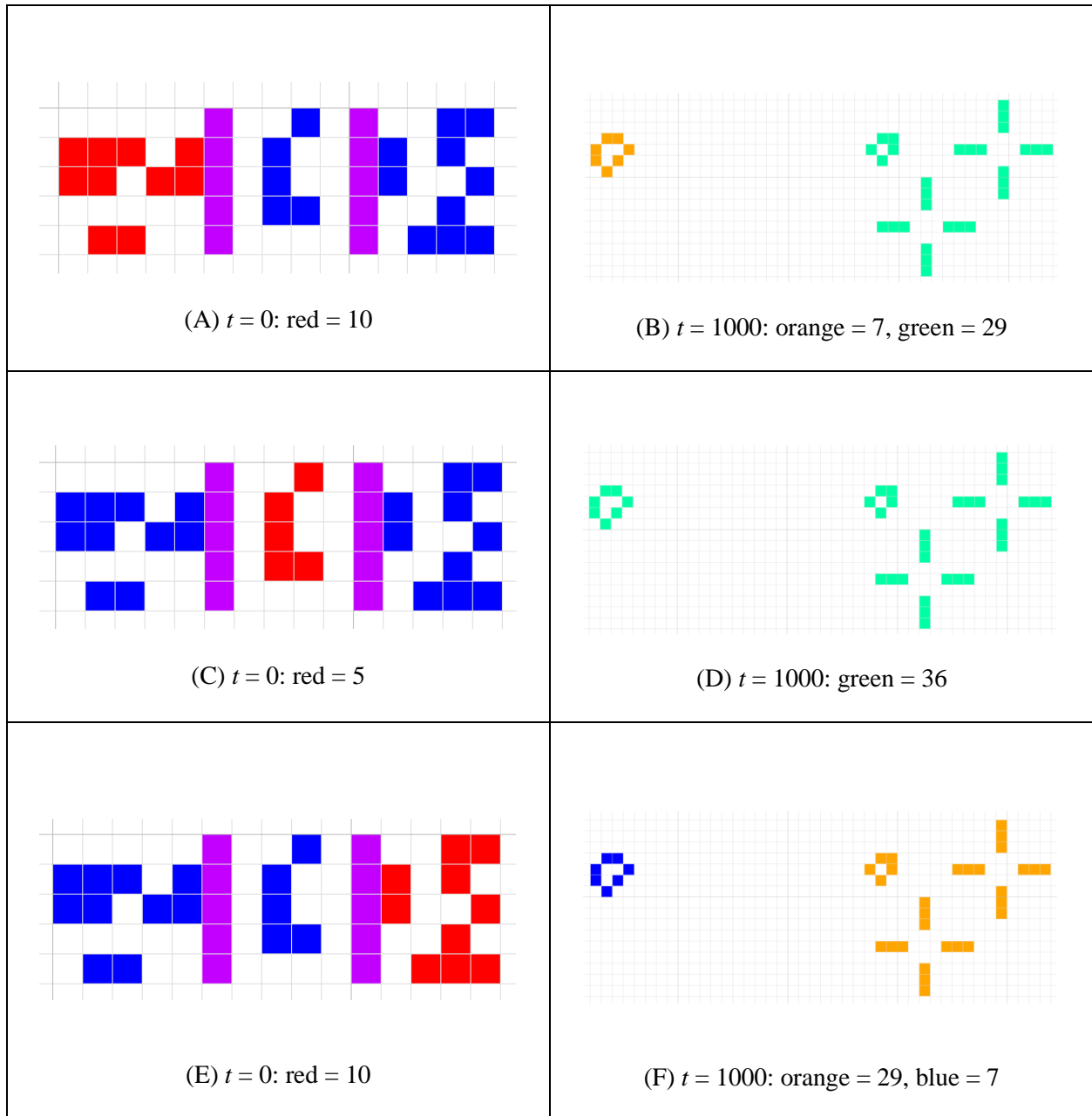


Figure 3. Image A shows an initial seed pattern ($t = 0$) with three partners, one red partner and two blue partners. The three partners are separated by purple borders, which disappear when $t > 0$. We focus on the red partner and watch how it interacts with the two blue partners. Image B shows the final pattern after one thousand steps ($t = 1000$) in the Management Game. By shifting the red partner from A to C to D, we can see how the red partner affects each of the final patterns, from B to D to F.

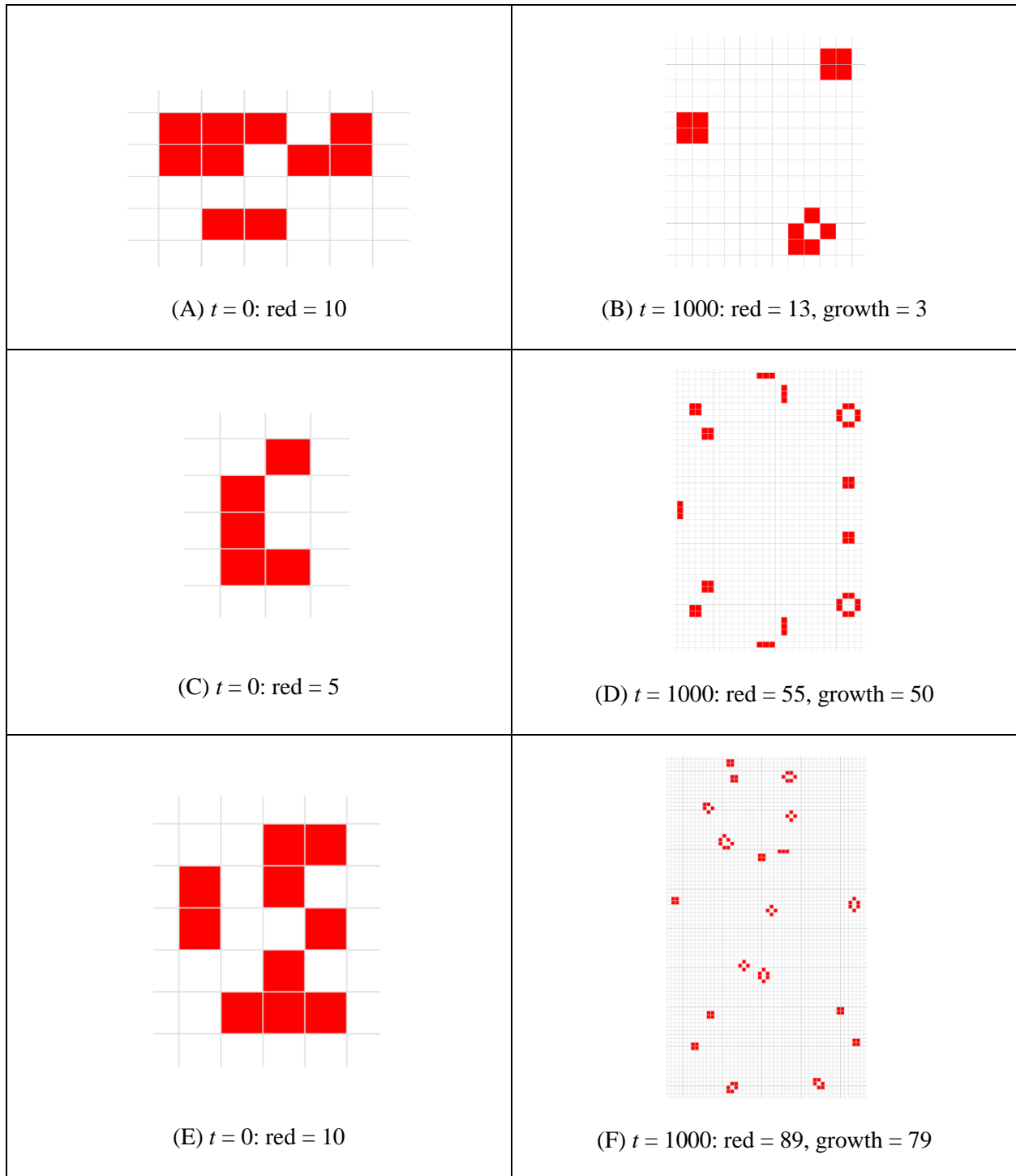


Figure 4. The three red patterns in the left column here (A, C, E) correspond to the three red patterns in the left column of Figure 3, but here they have been separated from their blue partners. Comparing Figure 3 and Figure 4, we can see how the growth of a partner in a symbiote differs from the growth of the same partner when alone.

Table 1. This table presents the rules of the Game of Life. Black cells are *alive* (state 1 in the cellular automata grid) and white cells are *dead* (state 0 in the grid). Let B represent *born*, S represent *survive*, D represent *die*, and U represent *unborn*. We use the convention that B3 implies its complement U01245678 and S23 implies its complement D0145678. This convention allows us to summarize the rules of the Game of Life as B3/S23.

Description of change	State of 8 neighbouring cells at time t	State of central cell at time t	State of central cell at time $t + 1$	Abbreviation
born	3 black neighbours	white	black	B3
survive	2 or 3 black neighbours	black	black	S23
die from overpopulation	4 or more black neighbours	black	white	D45678
die from underpopulation	0 or 1 black neighbours	black	white	D01
unborn	anything other than 3 black neighbours	white	white	U01245678

Table 2. This table summarizes the rules of the Immigration Game. The Immigration Game follows the rules of the Game of Life, except when a new cell is born (B3); therefore the table only shows the rules for birth. White cells are *dead* (state 0) and red and blue cells are *alive* (states 1 and 2). At time t , we have an empty central cell (state 0) with eight neighbouring cells around it. The empty central cell comes alive (it is born) at time $t + 1$ if exactly three of the neighbouring cells are alive at time t . This is the same as the Game of Life. The Immigration Game diverges from the Game of Life in the way that the colour of the central cell at time $t + 1$ is determined.

State of 8 neighbouring cells at time t	State of central cell at time t (dead)	State of central cell at time $t + 1$ (alive)
3 red neighbours	white	red
3 blue neighbours	white	blue
2 red neighbours + 1 blue neighbour	white	red
2 blue neighbours + 1 red neighbour	white	blue

Table 3. This table introduces some terminology that we will use to define the rules of the Management Game. In our experiments, the initial seeds at time $t = 0$ are always red or blue. Orange and green only appear later at $t > 0$ as red and blue interact with each other. The purple borders function as if they were dead, like the white background. The borders only appear at time $t = 0$. They turn white at time $t = 1$.

States	Colours	Descriptions	
0	white	the background colour	dead
1	red	initial seed colour or a child born from 3 red parents	alive
2	blue	initial seed colour or a child born from 3 blue parents	alive
3	orange	red origins but with some past non-red contact	alive
4	green	blue origins but with some past non-blue contact	alive
5	purple	the colour of the borders that separate partners in a seed	dead
2, 3, 4	non-red	blue, orange, or green	alive
1, 3, 4	non-blue	red, orange, or green	alive
2, 4	blue/green	blue or green	alive
1, 3	red/orange	red or orange	alive

Table 4. This is a summary of the rules of the Management Game. We focus here on the rules for the birth of a new cell (B3), since this is the only case where the Management Game differs from the Game of Life and the Immigration Game. At time t , we have an empty (white or purple) cell with eight neighbouring cells around it. For birth to happen in the empty central cell, exactly three of the eight neighbours must be alive. The table specifies the colour the central cell will have at time $t + 1$, based on the colours of the neighbouring cells at time t . Table 3 explains the terminology used here.

State of 8 neighbouring cells at time t	State of central cell at time t (dead)	State of central cell at time $t + 1$ (alive)
3 red neighbours	white or purple	red
3 blue neighbours	white or purple	blue
2 red/orange + 1 non-red neighbour	white or purple	orange
2 blue/green + 1 non-blue neighbour	white or purple	green

Table 5. Evolved seed patterns were sampled from 40 runs of Model-S. From 210 different groups of symbiotes, we extracted the most prolific seed (the seed with the most children) and the least prolific seed, yielding 210 pairs of matched seeds. The two members of a pair are similar, in that they come from the same groups and have the same number of partners, but they are different, in that one is highly fit (it had many children) and the other is not fit.

Number of partners in symbiotes	Number of groups of symbiotes	Average growth of least prolific symbiotes	Average growth of most prolific symbiotes	Ratio of most prolific to least prolific
5	1	33.0	358.0	10.8
4	32	54.8	335.4	6.1
3	27	18.3	264.0	14.4
2	150	25.3	158.9	6.3
all	210	28.9	200.3	6.9

Table 6. This table looks at the partners in the 210 most prolific seeds, considering the partners as managers and workers. Each seed is composed of two to five partners. To classify a given partner as a manager or worker, we first colour the selected partner red, then all other partners in the seed are coloured blue. We then run the Management Game for 1000 steps and count the final colours. See Figure 3 for example, where we classify each of the partners in a three-partner seed. A given partner is a manager if there are more orange squares than green squares; otherwise, the given partner is a worker. If there is a tie, the partner is a worker. The 210 seeds are grouped in this table according to how many partners in a seed are managers and how many are workers. For example, we see here that 131 seeds have one manager and one worker.

210 most prolific seeds		Column totals						Total
		0	134	43	31	2	0	210
Number of seeds with M managers	5	0						0
	4	0	0					0
	3	0	0	0				0
	2	0	3	2	0			5
	1		131	22	29	1		183
	0			19	2	1	0	22
		0	1	2	3	4	5	
		Number of seeds with N workers						

Table 7. This table looks at the partners in the 210 *least* prolific seeds (whereas Table 6 looks at the *most* prolific seeds), considering the partners as managers and workers. For example, we see here that 98 seeds have one manager and one worker.

210 least prolific seeds		Column totals						Total
		0	98	77	25	10	0	210
Number of seeds with M managers	5	0						0
	4	0	0					0
	3	0	0	0				0
	2	0	0	2	0			2
	1		98	23	21	1		143
	0			52	4	9	0	65
		0	1	2	3	4	5	
		Number of seeds with N workers						

Table 8. What we would like to understand is the difference between the 210 most prolific seeds and the 210 least prolific seeds. To do this, we take Table 6 (the most prolific seeds) and we subtract Table 7 (the least prolific seeds). The positive numbers are highlighted in green and the negative numbers are highlighted in pink. The negative numbers (pink) are mostly associated with zero managers (the bottom row in the table) and the positive numbers (green) are mostly associated with one manager (the row above the bottom row). In the row totals, we see -43 for zero managers and $+40$ for one manager.

Most prolific minus least prolific		Column totals						Total
		0	36	-34	6	-8	0	0
Number of seeds with M managers	5	0						0
	4	0	0					0
	3	0	0	0				0
	2	0	3	0	0			3
	1		33	-1	8	0		40
	0			-33	-2	-8	0	-43
		0	1	2	3	4	5	
		Number of seeds with N workers						

Table 9. This table shows how the growth of the partners in a symbiont is calculated, using the symbiont in Figure 3 and its partners in Figure 4 as an example. The growth of A into B (4.33) is greater in Figure 3, when the partners are together in the symbiote, than in Figure 4 (3.00), when the partners are alone. Therefore A, the first red partner in Figures 3 and 4, is classified as an *insider*. The other two partners (C and E) are classified as *outsiders*, since they grow more outside of the symbiont.

	Colours:	Red	Blue	Orange	Green	Weighted
	Weights:	1.000	0.000	0.666	0.333	total
Growth together in Figure 3	A → B	-10	-15	7	29	4.33
	C → D	-5	-20	0	36	7.00
	E → F	-10	-8	29	0	9.33
Growth apart in Figure 4	A → B	3	0	0	0	3.00
	C → D	50	0	0	0	50.00
	E → F	79	0	0	0	79.00

Table 10. This table presents the differences between the 210 most prolific seeds and the 210 least prolific seeds with respect to mutualism, considering the partners of a seed as insiders and outsiders. Insiders are partners that benefit from belonging to the whole, whereas outsiders are partners that do not benefit. Outsiders would be better off (more fit) if they could leave the symbiote. In the row totals, we see -69 for two outsiders and $+74$ for zero outsiders.

Most prolific minus least prolific		Column totals						Total
		-81	-6	64	11	12	0	0
Number seeds with M outsiders	5	-1						-1
	4	-10	0					-10
	3	-7	-6	0				-13
	2	-63	-6	-1	1			-69
	1		6	8	5	0		19
	0			57	5	12	0	74
		0	1	2	3	4	5	
		Number of seeds with N insiders						

Table 11. This table presents the differences between the 210 most prolific seeds and the 210 least prolific seeds with respect to interaction, considering the partners of a seed as soloists and ensemblists. In the row totals, we see -24 for one soloist and $+26$ for zero soloists.

Most prolific minus least prolific		Column totals						Total
		0	-12	7	-5	9	1	0
Number of seeds with M soloists	5	0						0
	4	0	0					0
	3	0	0	0				0
	2	0	0	-2	0			-2
	1		-12	-3	-8	-1		-24
	0			12	3	10	1	26
		0	1	2	3	4	5	
		Number of seeds with N ensemblists						