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The Effect of Between-Group Cooperation on the Evolution of Within-Group Cooperation

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Category	Min	Max	Chosen
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System Development and Implementation	0	15	5
Results, Findings and Conclusion	10	20	20
Aim Formulation and Background Work	10	15	15
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The Effect of Between-Group Competition on the Evolution of Within-Group Cooperation

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ABSTRACT

The Nested Tug-of-War model for the evolution of cooperation places a strong emphasis on the importance of between-group competition for the evolution of within-group cooperation (cooperation between agents within groups). The level of between-group competition is determined by the patchiness of resources in an environment. To test this model empirically, an Agent-Based System was created that simulates a simple foraging task. Agents in the simulation are driven by artificial neural network controllers that determine their behaviour. These controllers are adapted using Neuro-Evolution in order for agent behaviour to change over time. Multiple experiments were conducted in environments of varying resource patchiness. It was found that resource patchiness has a statistically significant effect on the level of within-group cooperation that evolves. As predicted by the Nested Tug-of-War model, increasing the level of between-group competition in an environment by manipulating resource patchiness led to an increase in the level of within-group cooperation that evolved. However, past a threshold of resource patchiness, the opposite effect was observed. This suggests that, in terms of facilitating the evolution of within-group cooperation, there is an optimum level of between-group competition.

CCS Concepts

•Computing methodologies → Agent / discrete models; *Artificial life;* Neural networks; •Applied computing → Computational biology; •Mathematics of computing → *Evolutionary algorithms;*

Keywords

Agent-Based Systems; Cooperation; Competition; Tug-of-War; Evolution

1. INTRODUCTION

A mathematical model is claimed to be a good explanation of how cooperative behaviour may have evolved in the biological world [27]. The model is based on a game-theoretical nested tug-of-war, where competition between individuals takes place within the larger context of competition between groups. An interesting aspect of this theory is its emphasis on the importance of competition between groups as a necessity for the evolution of cooperation between individuals in those groups. The aim of this research is to assess the impact of between-group competition on the evolution of within-group cooperation using an Agent-Based System [10]. The Nested Tug-of-War model has not yet been empirically tested [27], and the importance of competition as a motivator for cooperation is relatively unexplored. To the contrary, competition has almost exclusively been viewed as an obstacle to the evolution of cooperation [8, 32, 24, 33, 34]. This research aims to examine the relationship between competition and cooperation, and give evidence for the validity of the Nested Tug-of-War model.

1.1 Models of Cooperation

Many researchers in the field of evolutionary biology feel that the classical model of Natural Selection [6], which operates on a purely individual and competitive basis, cannot possibly account for altruistic behaviour as it is observed in so many species [15]. Several different theories and models that attempt to explain how cooperation may have evolved exist, each of which makes its own additions to the rules of Natural Selection in an attempt to explain how the trait of cooperative behaviour is selected for.

Kin Selection [15] posits that the evolution of cooperative behaviour is explained when genetic relatedness between individuals is taken into account - agents are more likely to cooperate with those that they are closely related to. The more genes two individuals have in common, the more sense it makes for them to cooperate with each other, as they are effectively helping some of their own genes to propagate forward.

The Units of Selection Model [19] suggests that Natural Selection operates at the level of the group as well as that of the individual. This allows a group to be seen as fitter than another by virtue of the interactions between the individuals that comprise it. This 'group selection' provides the evolutionary imperative for cooperative behaviour between agents in groups.

Observations of highly cooperative societies in nature have revealed three key trends [17]:

1. Cooperation is more likely to occur between agents with similar genetics.

2. Large colony sizes lead to higher levels of cooperation.

3. Resource patchiness and between-group competition are strongly associated with cooperation.

The Nested Tug-of-War model [27] predicts all three of these trends. The model is an amalgam of straightforward Darwinism, Kin Selection, and the Units of Selection model. In this model, individual agents have their own limited supply of energy. Moving expends this energy, and collecting resources in the environment replenishes it. Agents have to decide whether to remain stationary, conserving energy, or to forage for resources. This energy level serves as the measure of an agent's fitness, with fitter agents being the ones with larger amounts of energy. All agents belong to a group, and all energy gathered is shared amongst the agents in that group. An agent that moves and collects resources is therefore cooperating with its group (since it shares the resources it collects). An agent that chooses to conserve energy, by remaining motionless, is uncooperative. The model predicts that as group sizes and genetic relatedness between agents in groups increase, so will the proportion of agents that choose to behave cooperatively. In the Nested Tug-of-War Model, between-group competition is facilitated by resources patchiness. As resource patchiness increases (resources are divided into smaller, more dense patches), the likelihood that competing agents will be foraging in the same patch grows, leading to increased levels of between-group competition. The Nested Tug-of-War model emphasises the importance of competition between groups. As between-group competition increases, so should within-group cooperation.

1.2 Research Objectives

The main objective of this research is to examine the relationship between within-group cooperation and between-group competition. Mathematical analysis of the Nested Tug-of-War model reveals that as between-group competition increases, so does within-group cooperation [27]. We wish to find empirical evidence that either supports or refutes this result. Our hypotheses are therefore:

H_0: *The level of between-group competition has no effect on the evolution of within-group cooperation.*

H_1: *As between-group competition increases, so does the level of within-group cooperation that evolves.*

1.3 Agent-Based Systems

There are three main methods of assessing biological theories: mathematically, by observations in nature, and by simulation. The Nested Tug-of-War model has, up to this point, only been tested mathematically [27]. Mathematical analysis of a model is an important first step in ascertaining its validity. The fact that this method of assessment does not account for behaviour at the level of the individual is its key weakness, particularly where cooperation, which is defined by the behaviour of individuals, is the area of focus.

Natural observations can and have been useful in supporting or refuting biological models [14, 33, 1]. However, natural observation has several disadvantages. In all but the most short lived of creatures, observation over multiple generations, which is necessary for gleaning insight into the evolutionary process, is impractical at best, and impossible at worst. Crucially, natural observation does not allow for the manipulation of important variables and measurement of consequences.

Simulations do not suffer from these shortfalls. Individual behaviour can be directly observed. The evolutionary process can be greatly accelerated, allowing for the observation of long term trends and changes in behaviour. And finally, experiments on all aspects of a theory can be conducted by changing parameters responsible for anything from the agents to the environment. Agent-Based Systems are a form of such simulations.

Agent-Based Systems (ABS) [10] are a method of computation that facilitate simulation of agent interactions in an environment. ABS are used in a variety of fields, including computer science [29], economics [4], distributed robotics [18], and biology, where they are used to investigate questions pertaining to epidemiology, population dynamics, and many others [25]. ABS are also used to test theories of evolution and interaction among 'biological' agents, giving explanatory insight into collective behaviour between agents that follow simple rules [9, 8, 32]. ABS are therefore the most applicable method for the purposes of this research, which aims to measure the emergence of complex behaviour (cooperation) from interactions between simple agents. There are two major components to an ABS: the agent, and the environment.

The environment is the virtual world in which agents act [10]. This environment can be changed in any number of ways, and made as neutral or interactive as is desired. Biological applications of ABS tend to try to emulate an ecosystem in which agents can 'live'.

Agents are a distinct part of the simulation that interact with, and within, an environment [10]. They are used to represent real entities. Their behaviour, how exactly they react to the environment and each other, is dictated by a controller. The design of this controller depends on the environment and the simulated task that agents are expected to perform.

ABS have been used extensively to assess biological models such as Kin Selection [9, 8], and the Units of Selection Model [32]. ABS have been classified by some as a social simulation meta-model, and lauded for their importance as a tool for replicating organic social systems [12]. In the cases of Kin Selection and the Units of Selection model, cooperative behaviour between simulated agents was achieved, emphasising the importance of genetic relatedness and population size in predicting the evolution of cooperative behaviour. However, these experiments also revealed that certain environmental conditions nullified the effects of population size and genetic relatedness [8, 32], as did competition [24, 33], lending credence to the Nested Tug-of-War model, which specifically highlights the importance of environmental factors and competition for the evolution of cooperation.

1.4 Controller Design and Neuro-Evolution

In order for the agents in an ABS to exhibit behaviour, they require controllers. A controller is a computational artefact that allows a simulated or robotic agent to exhibit behaviour. A controller takes some input, and based upon that input, produces an output. This output dictates the agent's actions. There are many different types of agent

controllers such as rule-based systems [16], finite-state machines [11], decision trees [28], and artificial neural networks (ANNs) [21]. ANNs are inspired by the biological brain. Artificial neurons (nodes) are interconnected to form a network. Each node has a number of inputs and one output (note, however, that this single output can be passed as input to many other nodes). Each input to a node has a connection weight associated with it. The total (net) input to a neuron is described below:

$$net = \sum_{i \in I} w_i x_i \qquad (1)$$

where w_i is the weight for the ith input, and x_i is the ith input. This net output is then converted to an output via a sigmoid function:

$$S(t) = \frac{1}{1 + e^{-t}} \qquad (2)$$

where $S(t)$ is the final output, and t is the net input passed to the sigmoid function. A typical node is shown in Figure 1a.

Such nodes are connected to each other to form a network which is organised into layers. Nodes in the input layer receive stimuli directly from the outside world. Nodes in the hidden layer receive output from the input layer as their input. Finally, nodes in the output layer receive output from the hidden layer. The output from the output nodes is the final output of the network, and can be used to drive behaviour. Figure 1b shows a typical multi-layer ANN.

It has been demonstrated that an ANN with one layer of input nodes, one hidden layer, and one output layer is a universal function approximator [5]. This is useful for control tasks where a set of sensory inputs need to be mapped in some way to a set of outputs that can control an agent. The biological nature of ANNs, coupled with their applicability to the kind of control problem presented by ABS, makes them well suited to biological ABS control tasks.

In order for simulated agents to change their behaviour over time, to exhibit evolution, it is necessary to be able to adapt agent controllers in some way. Evolutionary Computation (EC) [7] is a sub-field of artificial intelligence that is concerned with Evolutionary Algorithms (EAs), and is a promising approach to the design of cooperative teams of agents [32]. EAs are based on Darwinian principles, using selection to find the 'fittest' of a group of initially random candidate solutions to a given problem. EC is renowned for its applicability to investigating cooperation between multiple agents [7], and an effective way of generating controls systems for agents that must demonstrate collective behaviour [2]. EAs use mechanisms inspired by biological evolution to adapt solutions: recombination, mutation, and selection. How exactly these mechanisms function depends on how the candidate solutions are represented. This combination of mechanisms iteratively refines a pool of candidate solutions, until the solution criteria are satisfied. A fitness function is used to determine the quality of a candidate solution, and provides the basis for selection. The general structure for all EAs is shown in Algorithm 1. The application of EAs to the adaptation of ANNs is known as Neuro-Evolution.

Neuro-Evolution (NE) [22] carries the biological metaphor a step further, with each candidate solution being described by rudimentary 'DNA' which is crossed over, mutated, and selected from to refine the candidate population. NE is one of the most popular approaches in agent-based systems and evolutionary robotics, and has proven to be an excellent

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Algorithm 1: Structure of an Evolutionary Algorithm [36]

INITIALIZE population with random candidate solutions EVALUATE each candidate
REPEAT UNTIL (TERMINATION CONDITION is satisfied)

1. SELECT parents

2. RECOMBINE pairs of parents

3. MUTATE the resulting offspring

4. EVALUATE new candidates

5. SELECT individuals for the next generation

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choice for implementations that seek to evolve complex behaviour in simple agents [22].

NE works by refining a pool of candidate solutions that are represented as ANNs using an EA. This is done by modifying the connection weights in the ANN, by modifying the connections between the nodes in the ANN, or by the addition or removal of nodes into or from the ANN. Modifications to the ANNs result in changes to agent behaviour, and therefore fitness. This fitness is then used to select the genotypes which led to the fittest phenotype, so that they may be recombined, mutated, and selected for the next generation. In this way, the behaviour of agents evolves over time. There are two approaches to encoding the genotype for each ANN - indirect encoding, and direct encoding.

Indirect encoding is only concerned with the most important parameters of the genotype architecture, the number of hidden layers and the number of nodes in each layer [36]. Other parameters, such as connectedness and connection weights, are left up to the adaptation process to determine. Direct encoding allows the specification of every node, connection, and connection weight at the level of the 'DNA' from which ANNs are assembled. Direct encoding can be divided into several different techniques: Conventional Neuro-Evolution (CNE) [36], Symbiotic Adaptive Neuro-Evolution (SANE) [23], Enforced Sub-Populations (ESP) [13], and Neuro-Evolution of Augmenting Topologies (NEAT)[30].

While SANE, ESP, and NEAT all offer various improvements over CNE, their high implementation complexity, as well as the relative simplicity of the sort of task required of agents in a biological ABS (such as a foraging task), makes CNE a preferred method. CNE encodes a genotype architecture by concatenating all of the connection weights in an ANN [36]. Evolution in the CNE approach works by optimizing only these connection weights, while the topology of the network remains fixed.

The remainder of this paper focusses on the design of the the ABS (Section 2), presenting the results obtained from experimentation (Section 3), and finally, concluding remarks (Section 4).
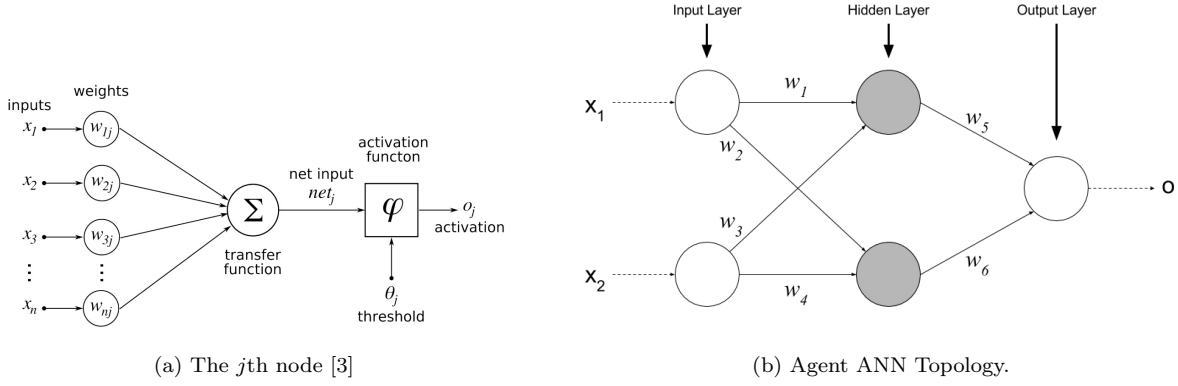
(a) The jth node [3]

(b) Agent ANN Topology.

Figure 1: Artificial Neuron (a), and Example ANN (b)

2. METHODS

In order to assess the Nested Tug-of-War model an ABS was constructed[1]. The environment is a continuous two-dimensional world with resources that agents can collect. The agents are driven by fixed topology neural networks which are evolved over time using CNE. The simulation was run multiple times with varying environmental conditions and the level of cooperation that evolved in each case was recorded.

2.1 Environment

Between-group competition is facilitated by resource patchiness in the environment. Patchiness refers to both the number of patches of resources in the environment, and the richness of these patches (which is determined by their size relative to the environment). Large, low density resource patches represent low competition environments, where all groups and agents will at all times be close to resources and will not have to move far to gather them. Conversely, environments with small, dense resource patches represent a high competition environment. In this case, agents may have to move far to reach a resource patch, but getting to a resource patch will result in a large pay-off due to the high density of the patch. In this situation, it is more important that agents get to the patch quickly to secure the resources for their own group, and more likely that agents from competing groups will both be foraging in the same patch, increasing competition intensity[27]. To explore the effect of these environmental effects on the evolution of cooperation, five different environments were created. In each case, it is only the patchiness of the environment that changes, the total number of resources available is kept constant throughout environments.

The resource density d of an environment is calculated as follows:

$$d = \frac{r/p}{a} \qquad (3)$$

where r is the total number of resource nodes in the environment, p is the number of resource patches into which resources are divided, r/p is the number of resource nodes per patch, and a is the area of a resource patch.

The simulation was run on five different environments with patch density ranging from $d = 0.003$ to $d = 0.02$. When $d = 0.003$, there is no patchiness in the environment. Rather, resource nodes are placed in the environment in a uniform random configuration as depicted in Figure 2a. At $d = 0.02$, resources are grouped into several very rich patches as depicted in Figure 2b. These density bounds were determined experimentally. With values lower than $d = 0.003$, the carrying capacity of the environment would have necessitated a very small population of agents. Higher values than $d = 0.02$ resulted in distances between resource patches too great for agents to reliably find them, causing premature extinction of populations. The other environments[2] fall between these two extremes with $d = 0.007$, $d = 0.01$, and $d = 0.016$. Resources nodes are placed randomly within patches, and patches are placed randomly within the environment.

2.2 Agents

Agents in the environment are able to move and gather resources if they collide with them. Moving costs energy, of which each agent has a limited supply, and gathering resources replenishes this energy. Remaining stationary expends no energy. Agents are able to 'see' in a small radius around them. If there is a resource node within this radius, and the agent is cooperative, an agent will move straight towards it (if there are several, it will move towards the closest one). If there are no nearby resources, a cooperative agent will move in a random direction. Uncooperative agents will remain stationary. The agents' controllers determine whether they will choose to be cooperative or uncooperative at any given point in time.

Each agent is driven by a fixed topology ANN as depicted in Figure 1b. X_1 and X_2 are the inputs to the network. X_1 is the distance to the nearest resource within the agents vision radius (set to a maximum if there are no resources in this radius). X_2 is the amount of energy that the agent started out with at the beginning of a generation. Both of these values are scaled to a value between -1 and 1 using linear scaling. w_1 to w_6 are the weight values for the connections between the nodes in each layer. They are constrained to a value between -1 and 1. o is the final output of the network

(a) Low Competition Environment ($d = 0.003$).   (b) High Competition Environment ($d = 0.02$).
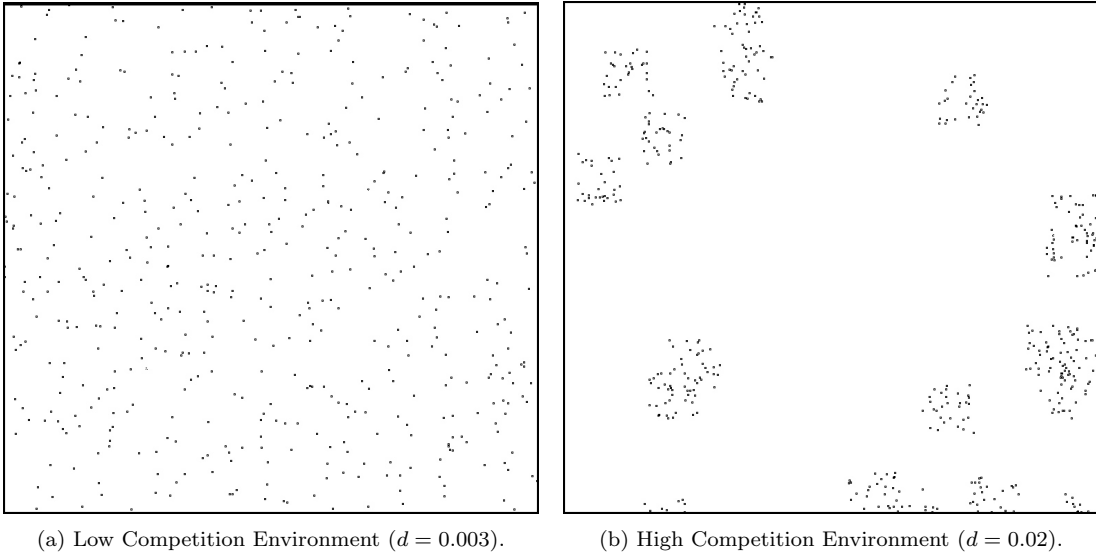
Figure 2: Illustration of the two extremes of the resource density spectrum.

and is also a value between -1 and 1. This value determines the behaviour of the agent. If $o > 0$, the agent will choose to move, else it will choose to remain stationary. The output from each node in each layer is the net input to that node (as described by Equation 1) which is then passed through a sigmoid activation function as input to the next node. This is a fully connected network, with all nodes in a layer being connected to all nodes in the next. The network is feed-forward, with summed weights passing through transfer functions at hidden layer nodes.

The weight values in the ANN are what determines the overall behaviour of the agent (and are altered by the EA). These weight values are stored in a vector, or chromosome, which can be used to describe a given ANN.

Each agent belongs to a group. At the beginning of a run, each group is assigned energy. This energy is then equally split among its constituent agents. During the course of a generation, agents will either spend this energy to move and gather resources (cooperate), or conserve it by remaining motionless (be uncooperative). At the end of this generation, all collected energy is given back to the group, to be redistributed at the beginning of the next.

2.3 Evolutionary Algorithm

At the end of each generation, before agents' energy is returned to their group, the parents of the next generation are selected. Parents, through crossover and mutation, produce enough children to replace the entire population.

Parents are selected from the old population using linear rank-based selection. The old population is ranked based on individual agents' fitness. These ranks determine the likelihood that they will be selected based on the following equation:

$$P_i = \frac{1}{N}\left(n^- + (n^+ - n^-)\frac{i-1}{N-1}\right) \qquad (4)$$

where P_i is the probability that the agent of rank i will be selected, N is the population size, n^+ is the selection pressure ($n^+ \in [1, 2]$), and n^- is defined as $2 - n^+$.

A selection pressure of 1.5 was used. This is a moderate value for selection pressure that tends to favour fitter agents for selection, but still gives weaker agents a chance to be selected so that population diversity is maintained.

After parents are selected, they are paired to produce children via single-point crossover. A random point in the chromosome is chosen. The child is given genes from the first parent up to this point, and genes from the second parent thereafter. After the children are created, they undergo mutation. During this process, each gene in the child chromosome is perturbed by a value between -0.1 and 0.1 with probability 0.1.

2.4 Experimental Method

The parameters varied between experiments are the total number of resources in the environment (R), the total number of agents (N), the total number of groups into which agents are equally divided (G), and the patchiness of resources in an environment (d).

Small scale initial experiments were conducted to determine a set of baseline values for these parameters. Subsequently, five large scale experiments were conducted. Each experiment varied the values for R, N, and G. For each experiment, the simulation was run 50 times on each of 5 different resource environments (different values for d). Each of these 50 runs lasted up until 200 generations. The level of within-group cooperation for each group at the end of each generation was recorded. Details of these five experiments can be found in Table 1. In each experiment, all other parameters were held constant. Table 2 shows a summary of these general parameters[3].

In the Nested Tug-of-War model, within-group cooperation is implicitly defined through the investment agents make for the benefit of the group that they are in. To facilitate empirical measurement, a more concrete measure of cooperation was used. If an agent gathers at least one resource during the course of a generation, that agent is considered cooperative. The agent is uncooperative otherwise.

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[3]For a list of all parameters, please consult http:// poseidonhonours.github.io/competition.html.

Experiment	Experiment Description	R	N	G	d
A	Baseline experiment. Default values for R, N, and G	600	60	2	0.003
					0.007
					0.01
					0.016
					00.2
B	Larger overall population and corresponding increase to number of resources.	900	90	2	0.003
					0.007
					0.01
					0.016
					0.02
C	Smaller overall population and corresponding decrease to number of resources.	300	30	2	0.003
					0.007
					0.01
					0.016
					0.02
D	Baseline population size divided into larger number of groups.	600	60	4	0.003
					0.007
					0.01
					0.016
					0.02
E	Baseline population size divided into larger number of groups.	600	60	6	0.003
					0.007
					0.01
					0.016
					0.02

Table 1: Experimental Parameters (where R is the total number of resources in the environment, N is the total population of agents, G is the number of competing groups of agents, and d is the resource patch density of the environment).

General Parameters	
Number of Runs Per Environment	50
Number of Generations Per Run	200
Agent Lifetime (Length of Single Generation)	2000 Simulation Ticks
Environment Size	800x800 Pixels
Agent Move Speed	$\sqrt{2}$ Pixels Per Simulation Tick
Group/Resource Starting Positions	Random: $x, y \in [100, 700]$
Neuro-Evolution Parameters	
Recombination Operator	Single-Point Crossover
Recombination Probability	1 (All Children Created Through Crossover)
Mutation Operator	Perturbation of Single Connection Weight $\in [-0.1, 0.1]$
Mutation Probability Per Weight	0.1
Selection Operator	Linear Rank-Based
Probability of Selection	$p \in [0.05, 0.15]$ Dependent On Agent Fitness

Table 2: General and NE Parameters Used In all Experiments

3. RESULTS AND DISCUSSION

It was found that differing levels of competition, facilitated by resource patchiness, had a significant effect on the level of cooperation that evolved among agents within groups. As predicted by Reeve and Hölldobler [27], increasing the level of competition in an environment led to higher levels of within-group cooperation, confirming the results of their own testing. However, this was only true up to a point. Beyond this point, subsequent increases in resource patchiness led to decreased within-group cooperation.

Figure 3 shows the level of within-group cooperation that evolved in each of five resource environments over 200 generations. The resource environments are described by their resource patchiness (where p is the number of resource patches and d is the density of the patches). The value for cooperation that is shown is the proportion of agents in a group that were cooperative during a generation, averaged over all five different experimental set-ups. Random initialization of agents meant that the starting level of within-group cooperation was about 50% in all environments. Groups evolved fairly stable behaviour after 150 generations. After 150 generations, the low competition environment ($d = 0.003$) led to the evolution of groups where approximately 58% of agents were cooperative. An increase to $d = 0.007$ led to approximately 61% within-group cooperation. A further increase to $d = 0.01$ yielded still higher values for within-group cooperation, at 72%. However, higher values for d led to dramatically diminished within-group cooperation, with 56% of agents being cooperative at $d = 0.016$, and only 34% of agents cooperating at $d = 0.02$.

Figure 4 shows the average amount of within-group cooperation that evolved in each environment, and more clearly demonstrates the rise and fall in within-group cooperation as resource patchiness increases.

Before hypothesis testing, a Kolmogorov-Smirnov test for normality was conducted on the data yielded by each of the five environments. The test revealed that the data set collected for each environment was non-normal with confidence $p < 0.01$ in all cases. As such, the assumptions made by one-way ANOVA were not met, making this test unsuitable for comparing the environments. The Kruskal-Wallis test was therefore used to determine whether the difference in within-group cooperation in the different environments was significant. The Kruskal-Wallis test revealed a significant effect of environment on within-group cooperation, with an H-statistic ($H = 822.303$) far greater than the region of rejection ($R = 9.488$), and a confidence level of $p < 0.01$. In order to establish the origin of this significant effect, post-hoc pairwise Mann-Whitney tests with Bonferroni correction were conducted between the environments. The Mann-Whitney tests revealed that the differences between environments with $d = 0.003$ and $d = 0.007$, were insignificant ($p = 0.08$). The differences between all other pairs of environments were statistically significant, with confidence $p < 0.01$. Thus, the null hypothesis, H_0, is rejected. Between-group competition has a significant effect on the evolution of within-group cooperation.

These results partially support prior findings obtained by mathematical analysis [27] and by observations in nature [35, 17]. Higher levels of within-group competition do lead to higher levels of cooperation. Particularly in the case where resource patchiness was increased from $d = 0.003$ to $d = 0.01$, there was a significant increase in the level
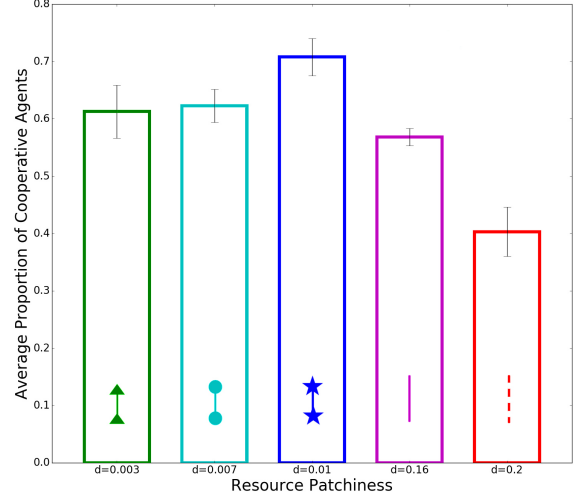

Figure 4: Average within-group cooperation per resource environment. Environments range from non-patchy random uniform distribution of resources ($d = 0.003$) to dense pathces of resources ($d = 0.02$). Difference between $d = 0.003$ and $d = 0.007$ is not significant, with p=0.08. Difference between all other environments is significant, with p<0.01. Averages for each environment calculated over 250 runs (50 in each of 5 experimental setups).

of within-group cooperation that evolved ($p < 0.01$). This result is evidence in favour of H_1, and supports results obtained by Reeve and Hölldobler [27]. However, the relationship between competition and cooperation is not straightforward.

Between-group competition has been found to decrease within-group cooperation in some cases, nullifying the positive effects of factors that are meant to increase it [34, 33, 24]. Certain environmental conditions can also confound the evolution of cooperative behaviour [8, 32]. These results are echoed by our findings, as within-group cooperation was seen to decrease if between-group competition was too high. An increase in resource patchiness from $d = 0.01$ to $d = 0.016$ led to a sharp decline in the amount of within-group cooperation that evolved. The same was true for a subsequent increase to $d = 0.02$. In both cases the decrease in within-group cooperation was statistically significant, with confidence $p < 0.01$.

Greater cooperation is expected to increase group competitiveness [27]. Figure 5 illustrates that the results confirm this. For every generation, the level of within-group cooperation for each group is plotted against the proportion of global resources that that group collected (the group's competitiveness). The more cooperation between agents in a group, the more competitive the group. The line of best fit shown in Figure 5 is described by the equation $y = 0.8x - 0.007$, indicating an almost perfectly linear relationship between within-group cooperation and between-group competitiveness.

The significance of these findings is twofold. Between-group competition is clearly a factor in the evolution of cooperation, echoing findings obtained by observations in
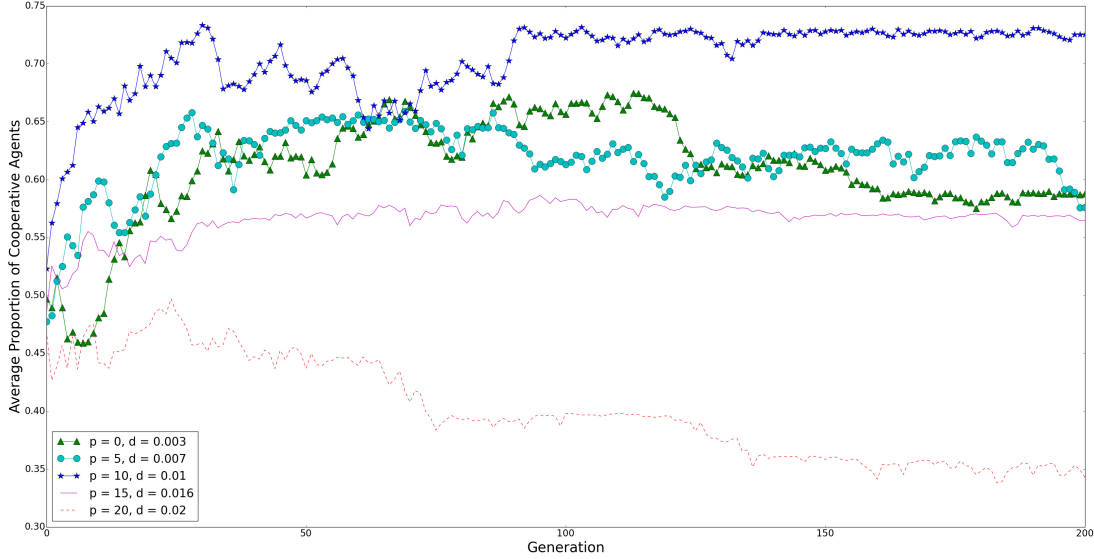
Figure 3: Evolution of within-group cooperation over time in different environments (Where p is the number of resource patches in the environment, and d is the density of these resource patches. Values averaged over 50 runs in each environment across all experimental conditions).
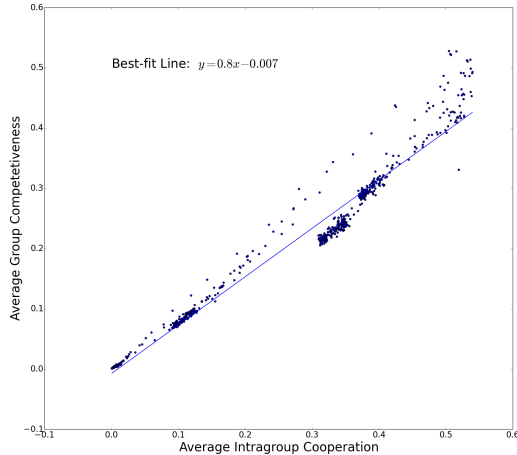

Figure 5: Relationship between within-group cooperation and between-group competitiveness (where between-group competetiveness is defined by the total proportion of global resources gathered by a group).

nature [35, 17]. And, at least to some extent, increasing between-group competition leads to higher levels of within-group cooperation. This is strong evidence in support of the Nested Tug-of-War model, which places an emphasis on competition as motivator for cooperation.

It is of particular interest that the relationship between within-group cooperation and between-group competition was found to be non-linear. The results suggest that there

is an optimum level of between-group competition in terms of facilitating the evolution of cooperation. That is, there is a level of between-group competition after which it is better for agents to stop cooperating within their own group, indirectly investing in the success of the other group. This is a concept that is relatively unexplored by the current literature, with the effect of competition on the emergence of cooperation ususally being viewed either as having a positive [27, 35, 17] or negative impact [34, 33, 24] only.

A prevailing biological theory regarding how uncooperative agents may start cooperating, and vice versa, is Mutualism [31]. Strictly speaking, Mutualism is cooperation between different species. More generally, Mutualism can be considered as cooperation between inferior competitors [37]. Within the context of the Nested Tug-of-War, there are two tiers of competition: competition between groups, and competition between agents within a group. If between-group competition is stronger than within-group competition, agents within groups can be thought of as 'inferior competitors', and agents in opposing groups can be thought of as 'superior competitors'. As long as between-group competition is of a higher intensity than within-group competition, group members remain inferior competitors, and Mutualism dictates that they should be inclined to cooperate with one another [37]. Facilitating between-group competition by altering resource patchiness likely increased the level of within-group competition as well as between-group competition. As resource patchiness increased, within-group competition may have surpassed the level of between-group cooperation, leading to the decline of within-group cooperation in favour of mutualistic behaviour. In this case, agents within the same group would be 'superior competitors', and therefore less inclined to cooperate [37]. Mutualism affords one possible explanation for the observed non-linearity of the

relationship between within-group cooperation and between-group competition.

4. CONCLUSIONS

Empirical evidence in support of the Nested Tug-of-War theory [27] was found. It was shown that between-group competition, facilitated by resource patchiness, has a significant effect on the evolution of within-group cooperation. Furthermore, it was found that increasing between-group competition leads to increased levels of within-group cooperation.

Previous results obtained during empirical analysis of the Kin-Selection [24] and Units of Selection [32] models were also corroborated. It is possible for between-group competition, if the level of which is too high, to serve as a hindrance to the evolution of within-group cooperation.

The reason that the results of this research are able to unite these opposing views is because the relationship between cooperation and competition seems to be non-linear. Increased levels of competition led to increased levels of cooperation up to a critical point, after which further increases in competition produced the opposite effect. Additionally, it was found that increased within-group cooperation led to higher levels of between-group competitiveness (better group performance). This research has therefore demonstrated that for a group to achieve the level of cooperation necessary for it to thrive, optimal levels of competition are required. Too much or too little competition is to the detriment of the group. This echoes the work of Makowsky and Smaldino [20], who found that cooperative strategies similar to those that evolve in human societies require intergroup interactions such as warfare and raiding to emerge. Between-group competition creates a scenario where individual self-ishness jeopardises the evolutionary success of a group, and therefore favours the suppression of this trait [26]. Too much competition between groups, however, means that it is in an agent's best interest to cooperate with other groups rather than their own [20].

Future work will investigate the non-linear relationship between competition and cooperation, paying particular attention to the effects of factors such as group and population sizes, and genetic relatedness. This would be a first step in attempting to define the optimal level of competition in a given scenario as a function of various environmental factors, as well as providing further empirical evidence for other predictions made by the Nested Tug-of-War model. Integrating and testing elements of additional biological theories, particularly the theory of Mutualism, is a further avenue for future research.

5. ACKNOWLEDGEMENTS

6. REFERENCES

[1] R. Axelrod and W. D. Hamilton. The evolution of cooperation. *Science*, 211(4489):1390–1396, 1981.

[2] G. Baldassarre, S. Nolfi, and D. Parisi. Evolving mobile robots able to display collective behaviors. *Artificial life*, 9(3):255–267, 2003.

[3] C. Burgmer. The jth neuron, 2005.

[4] A. Chaves and P. Mase. An agent marketplace for buying and selling goods. In *Proc. 1st International Conference on the Practical Application of Intelligent Agents and Multi-Agent Technology. London, UK*, 1996.

[5] G. Cybenko. Approximation by superpositions of a sigmoidal function. *Mathematics of control, signals and systems*, 2(4):303–314, 1989.

[6] C. Darwin and W. F. Bynum. *The origin of species by means of natural selection: or, the preservation of favored races in the struggle for life.* AL Burt, 2009.

[7] A. E. Eiben and J. E. Smith. *Introduction to evolutionary computing.* Springer Science & Business Media, 2003.

[8] D. Floreano and L. Keller. Evolution of adaptive behaviour in robots by means of darwinian selection. *PLoS Biol*, 8(1):e1000292, 2010.

[9] D. Floreano, S. Mitri, S. Magnenat, and L. Keller. Evolutionary conditions for the emergence of communication in robots. *Current biology*, 17(6):514–519, 2007.

[10] G. N. Gilbert. *Agent-based models.* Number 153. Sage, 2008.

[11] A. Gill et al. Introduction to the theory of finite-state machines. 1962.

[12] C. Goldspink. Modelling social systems as complex: Towards a social simulation meta-model. *Journal of Artificial Societies and Social Simulation*, 3(2):1–23, 2000.

[13] F. J. Gomez and R. Miikkulainen. Solving non-markovian control tasks with neuroevolution. In *IJCAI*, volume 99, pages 1356–1361, 1999.

[14] J. C. Gorrell, A. G. McAdam, D. W. Coltman, M. M. Humphries, and S. Boutin. Adopting kin enhances inclusive fitness in asocial red squirrels. *Nature communications*, 1:22, 2010.

[15] W. D. Hamilton. The evolution of altruistic behavior. *American naturalist*, pages 354–356, 1963.

[16] F. Hayes-Roth. Rule-based systems. *Communications of the ACM*, 28(9):921–932, 1985.

[17] B. Hölldobler and E. O. Wilson. *The ants.* Harvard University Press, 1990.

[18] H. Kitano, M. Asada, Y. Kuniyoshi, I. Noda, E. Osawai, and H. Matsubara. Robocup: A challenge problem for ai and robotics. In *RoboCup-97: Robot Soccer World Cup I*, pages 1–19. Springer, 1998.

[19] R. C. Lewontin. The units of selection. *Annual review of ecology and systematics*, pages 1–18, 1970.

[20] M. D. Makowsky and P. E. Smaldino. The evolution of power and the divergence of cooperative norms. *Available at SSRN 2407245*, 2014.

[21] W. S. McCulloch and W. Pitts. A logical calculus of the ideas immanent in nervous activity. *The bulletin of mathematical biophysics*, 5(4):115–133, 1943.

[22] R. Miikkulainen. Neuroevolution. In *Encyclopedia of Machine Learning*, pages 716–720. Springer, 2010.

[23] D. E. Moriarty and R. Mikkulainen. Efficient reinforcement learning through symbiotic evolution. *Machine learning*, 22(1-3):11–32, 1996.

[24] M. G. Murray and R. Gerrard. Conflict in the neighbourhood: models where close relatives are in direct competition. *Journal of theoretical biology*, 111(2):237–246, 1984.

[25] M. Niazi and A. Hussain. Agent-based computing from multi-agent systems to agent-based models: a visual survey. *Scientometrics*, 89(2):479–499, 2011.

[26] H. K. Reeve. The evolution of altruism: Two ways in which selfishness generates superorganisms.

[27] H. K. Reeve and B. Hölldobler. The emergence of a superorganism through intergroup competition. *Proceedings of the National Academy of Sciences*, 104(23):9736–9740, 2007.

[28] S. R. Safavian and D. Landgrebe. A survey of decision tree classifier methodology. *IEEE transactions on systems, man, and cybernetics*, 21(3):660–674, 1991.

[29] R. Schoonderwoerd, O. Holland, and J. Bruten. Ant-like agents for load balancing in telecommunications networks. In *Proceedings of the first international conference on Autonomous agents*, pages 209–216. ACM, 1997.

[30] K. O. Stanley and R. Miikkulainen. Evolving neural networks through augmenting topologies. *Evolutionary computation*, 10(2):99–127, 2002.

[31] P. Van Beneden. Animal parasites and messmates. 1889. *Contains much that is interesting.*

[32] M. Waibel, L. Keller, and D. Floreano. Genetic team composition and level of selection in the evolution of cooperation. *Evolutionary Computation, IEEE Transactions on*, 13(3):648–660, 2009.

[33] S. A. West, M. G. Murray, C. A. Machado, A. S. Griffin, and E. A. Herre. Testing hamilton's rule with competition between relatives. *Nature*, 409(6819):510–513, 2001.

[34] S. A. West, I. Pen, and A. S. Griffin. Cooperation and competition between relatives. *Science*, 296(5565):72–75, 2002.

[35] E. O. Wilson and B. Hölldobler. Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences of the United States of America*, 102(38):13367–13371, 2005.

[36] X. Yao. Evolving artificial neural networks. *Proceedings of the IEEE*, 87(9):1423–1447, 1999.

[37] Z. Zhang. Mutualism or cooperation among competitors promotes coexistence and competitive ability. *Ecological Modelling*, 164(2):271–282, 2003.