The Effects of Assortment on Population Structuring Traits on the Evolution of Cooperation

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Abstract

Population structure plays an important role in the evolution of social behaviours, particularly by generating positive assortment on social interactions. This enables cooperative behaviours that have a net cost to the individual to spread by directing their benefits towards other cooperators. Previous work on the coevolution of population structures and social behaviours has suggested that the evolution of population structuring traits is strongly influenced by the dominant social strategies. Here we investigate the idea that the coevolution of population structure and behaviour can be enhanced in favour of cooperation when there is also assortment on the population structuring traits themselves. This paper presents a simulation model that investigates the effects of evolving this second-order assortment and introduces a mathematical framework to model it in terms of the replicator equation. We find that with second order assortment the dominant social behaviour trait does not necessarily have to control the evolution of population structure, increasing the range of social scenarios in which population structures that support increased co-operation can evolve.

Introduction

Population structures that promote positive assortment on social behaviours are a key pathway to the evolution of cooperation (Nowak and May, 1992). When cooperators interact disproportionately with other cooperators then the benefits of the cooperative acts will fall predominantly on cooperators, raising their fitness while reducing the risk of defectors taking the benefits without assuming the costs. There are many mechanisms that can support the evolution of cooperation, including genetic relatedness, signalling (greenbeard effects) and reciprocity through repeated interactions. The common principle at work is that these mechanisms generate correlated interactions by co-operators (Godfrey-Smith, 2009). Only when the benefits of cooperation are directed at other cooperators in this way can cooperative behaviours that benefit the recipient at a cost to the individual spread (Hamilton, 1964; Lehmann and Keller, 2006).

This is important both to explain the otherwise surprising ubiquity of cooperative behaviours and because of the underlying importance of altruism to the major transitions in evolution, the processes through which new levels of biological organisation emerge as previously independently replicating entities become higher-order individuals that must reproduce as a unit (Maynard Smith and Szathmáry, 1997). The altruistic sacrifice of individual reproductive capability at the lower level is such a characteristic of this process that the major transitions can be viewed as extreme examples of social integration (Michod, 2000; Queller and Strassmann, 2009; Bourke, 2011).

Traditionally social evolution models have investigated the evolution of cooperation against a fixed population structure. But many organisms possess individual-level genetic traits that affect population structure, such as a group size preferences or dispersal radius (Pepper and Smuts, 2002). Recent work has begun to look at how population structuring traits and social behaviours can coevolve in a process of *social niche construction* (Powers et al., 2011). Artificial Life models of the coevolution of group size preferences and social behaviours have shown that linkage disequilibrium develops connecting a preference for small groups with cooperative social traits (Powers and Watson, 2011). In such circumstances between group effects can outweigh within group competition due to the high variance between groups, caused by sampling small groups from a large population (Wilson and Colwell, 1981), leading to a positive feedback loop in favour of increasing levels of cooperation and decreasing group size even when the social game is unfavourable to co-operators.

It is generally well accepted then that positive assortment can enable cooperation to prevail when it would not in a well-mixed population. In previous work we have been investigating the factors that lead population-structuring traits to support the evolution of cooperation using evolutionary game theory. Many changes in population structure can be represented as transformations to the social game being played, including reciprocity, kin selection (Taylor and Nowak, 2007) and group structure (Van Veelen, 2011). We have looked at the coevolution of population structures and social behaviours through abstract models of *metagames* in which populations evolve not just their social behaviours but

also the payoff matrix of the game they are playing. These metagame models have demonstrated that the strongest influence on the selective pressure on the population structure is the dominant social strategy; when co-operators are the dominant social type population structures more favourable to cooperation evolve, and likewise when defectors dominate. This is in apparent contradiction with the logical arguments that support social niche construction (Powers et al., 2011), and would imply a limited causal significance for population-structuring traits if they only increase the spread of cooperative behaviours in situations where co-operators are already favoured.

Here we suggest that one of the keys to the strength of social niche construction is that not only do population-structuring traits (*PSTs*) induce assortment on the social behavioural traits but that there is also a degree of assortment on the PSTs — a *second order assortment*. In the example of a group size preference trait, if the group size preference leads to a greater chance of living in a group of the desired size it also implicitly creates groups composed of individuals with similar group size preferences (Powers et al., 2011). Not all population-structuring traits do result in second-order assortment. It is argued that the key distinction between kin-selection and greenbeard traits is that relatedness leads to the same average measure of correlation for all the genes of an organism while greenbeard traits only lead to correlation on a few genes (Ridley and Grafen, 1981; Bourke, 2011). As a consequence greenbeard traits may be susceptible to parasitism (Okasha, 2002) and intragenomic conflict — suppressor mutations arising at other *loci* (though others have argued that this is not inevitable as selection for greenbeard and greenbeard-imitation traits may be aligned (Gardner and West, 2010; Biernaskie et al., 2011)). So we might expect that when assortment is generated by relatedness there would be the same degree of assortment on population-structuring and behavioural traits, while if it was generated by a greenbeard signal this is not necessarily the case.

In this paper then we investigate the effects of second-order assortment on the evolution of population-structuring traits that support cooperation, in particular the nature of the second-order assortment. We do this through an artificial life model in which different levels of assortment are expressed literally — assorters are physically more likely to interact with each other. We also develop a novel way to model these results mathematically by modifying the replicator equation. We show that when second-order assortment is random or absent then the spread of population-structuring traits that support increased cooperation is strongly linked to the success of co-operators. When population-structuring traits affect both assortment on social behaviours and on themselves, then the conditions under which populations can evolve population structures beneficial to cooperation are enlarged.

Social Dilemmas in Evolutionary Game Theory

The standard mathematical tool for analysing the evolution of social behaviours is evolutionary game theory (Maynard Smith, 1982). Evolutionary game theoretic models are appropriate when the fitness of a strategy depends on the frequency with which it and other strategies are found in the population as well as the inherent qualities of the strategy — as is the case for social behaviours. There are a number of ways to interpret game theoretic models; here we think of a population divided into a n genetically determined types corresponding to pure strategies of the game. The fitness payoffs for the interactions between types determines the payoff matrix of the game. The changing frequencies of the different strategies are modelled using the *replicator equation* (Taylor and Jonker, 1978).

$$\dot{x}_i = x_i(f_i(\mathbf{x}) - \bar{f}(\mathbf{x})) \tag{1}$$

Where x_i is the frequency of the i-th strategy, f_i is the fitness of that strategy given a population state vector $\mathbf{x} = (x_1, \ldots, x_n)$ and $\bar{f} = \sum_{i=1}^{n} x_i f_i(x)$ is the mean fitness of the population given that state. The stable equilibria of the population state under the replicator equation determine *evolutionarily stable states* (ESS) to which the population will return if the frequencies are subject to small perturbations.

Here we focus on social interactions with two social strategy types — co-operators and defectors. Although they are the simplest types of game, these two strategy games include the canonical social dilemmas such as the Prisoner's Dilemma. An arbitrary such game can by defined by the 2×2 payoff matrix $G = \left(\begin{smallmatrix} R & S \\ T & P \end{smallmatrix} \right)$. R is the reward for mutual cooperation, P the punishment for mutual defection, T the temptation to defect and S the suckers payoff. The two strategies are labelled C for co-operate and D for defect. We impose the condition that $R > P$ as the benefits of mutual cooperation are assumed to outweigh those from mutual defection. The complete four-dimensional space of games is determined R, S, T and P; varying their relative magnitudes leads to a diverse range of social scenarios. By normalising R to 1 and P to 0 it is possible to project this space onto to a two dimensional plane parameterised by S and T (Santos et al., 2006) that we call the ST-plane. This projection is done via the transformation:

$$\begin{pmatrix} R & S \\ T & P \end{pmatrix} \rightarrow \begin{pmatrix} \frac{R-P}{R-P} & \frac{S-P}{R-P} \\ \frac{T-P}{R-P} & \frac{P-P}{R-P} \end{pmatrix} = \begin{pmatrix} 1 & S' \\ T' & 0 \end{pmatrix} \tag{2}$$

This transformation has the important property that every game with $R > P$ is equivalent to a game on the ST-plane — there is a corresponding game that has the same dynamics (though the speed of selection may change). This is because the transformation multiplies the replicator equation

by a constant, leaving the evolutionary stable states determined by the equation's fixed points unchanged. The projection is valid whenever $R \neq P$ (which is always true for the games we are interested in as $R > P$). This makes the ST-plane an extremely useful tool to aid conceptual understanding as a representative subset of the two-strategy social dilemmas. The convention is to assume that mutual cooperation is preferable to unilateral cooperation ($R = 1 > S$) and to an equal probability of unilateral cooperation or defection ($2R = 2 > T + S$)(Macy and Flache, 2002), hence the ST-plane is plotted for the region $-1 \leq S \leq 1, 0 \leq T \leq 2$. Note that we assign a neutral payoff $P = 0$ to mutual defection; recent work has suggested that ecological constraints leading to negative payoffs for one or both of R and P may lead to alternate pathways to altruism in the absence of population structure (Doncaster et al., 2013).

Social dilemmas essentially occur when there is a conflict between the rational outcome and the Pareto-efficient outcome, the individually rational choices for each player leading to a deficient outcome for both. This can arise due to *greed*, the difference between unilateral defection and mutual cooperation ($T - R$), or *fear*, the difference between unilateral cooperation and mutual defection ($S - P$), or both (Santos et al., 2006). These two factors correspond to the two axes of the ST-plane. The lines $S - P = 0$ and $T - R = 0$ split the ST-plane into four quadrants corresponding to four fundamental two player games that cover the most common types of conflict (Figure 1):

The *Harmony game* ($R > T > S > P$), the least seen of the four as there is no social dilemma — group and individual interests are aligned with cooperation always the most successful strategy. A population of all cooperators is the ESS.

The *Prisoner's Dilemma* ($T > R > P > S$) where the ESS is a population of no cooperators. The Prisoner's Dilemma is a particularly important example of a game and it models scenarios in which individual selection results in defection, to the detriment of the population as a whole.

The *Snowdrift game* ($T > R > S > P$), an anti-coordination game in which interactions with other strategies carry higher payoffs than same-strategy interactions. The Snowdrift game is thus significant as the only game that sustains a stable polymorphic population — the evolutionarily stable state has $\frac{S-P}{S+T-R-P}$ cooperators.

The *Stag-Hunt game* ($R > T > P > S$), a coordination game in which populations of all cooperators and no cooperators are both ESS. There is an unstable equilibrium with $\frac{S-P}{S+T-R-P}$ of the population cooperators which divides the two basins of attraction; this is the only game in which the initial frequency of cooperators is significant in determining the ESS.
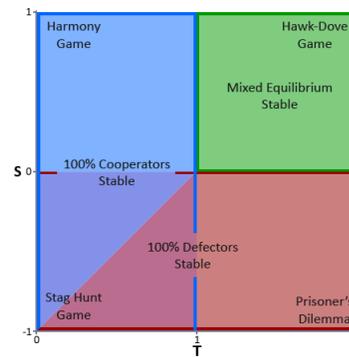

Figure 1: The ST-plane showing the four fundamental games and how they are determined by the regions in which the different ESS exist.

Model Details

To investigate the effects of population-structuring trait assortment on the evolution of population structures favourable to cooperation we created an evolutionary algorithm based on a fixed size population of asexual agents living in non-overlapping generations. A range of potential assorting behaviours are abstractly represented by having agents physically cluster to varying extents determined by their population-structuring traits. This physical assortment influences fitness by affecting who each agent plays with, specifically as each agent's fitness is determined by playing a specified evolutionary game G against its nearest neighbour.

The model consists of a population of $P = 100$ agents living in a continuous space that is topologically toroidal. Each agent is represented as a circle $r = 4$ units in radius. The dimensions of the world is $100r \times 100r$ units. Each agent's genotype is haploid with two *loci* — a social trait gene that determines its social behaviour (with either 'co-operator' C or 'defector' D alleles) and a population-structuring trait with alleles A for assorting behaviours and M for freely mixing behaviour. This gives four genotypes: CA, DA, CM and DM. The model is initially populated with these four genotypes present at equal frequency with agents placed randomly in the world.

There are two stages to the evolutionary algorithm. First the agents selectively aggregate for $T = 10000$ timesteps. Then each member of the population plays a game with its nearest neighbour to determine its fitness. 'Nearest neighbour' is not a symmetric relationship, so while all agents play at least one game (against their own nearest neighbour), some may be played against multiple other times by other agents that have it as their nearest neighbour. As all the games here are symmetric this is equivalent to the agent playing multiple times with different opponents. For this model, an agent's fitness was defined to be its average payoff received per interaction rather than cumulative payoff;

we chose not to reward or penalise an agent for being involved in multiple games. Recording the payoff of the focal player would have also achieved this result but would mean a co-operator closest to another co-operator but surrounded by defectors recieved the same payoff as a co-operator with no defectors near it; however, there are arguments in favour of other mechanisms and the choice of average payoff represented a trade-off. After the fitnesses were calculated the population was reproduced using tournament selection up to the fixed size P again: for P repetitions two agents were drawn from the population and the agent with the highest fitness (or a random agent if they had equal fitness) is reproduced clonally with a small chance of mutation. To represent the intuition that population structure evolves more slowly than social behaviours, the mutation rate for the social behaviour allele was set to a probability $m_{SB} = 0.01$, while the probability of a mutation of the population-structuring trait was $m_{PST} = m_{SB}/2$.

The agents' movement is modelled by a variation on gravitational attraction. To simplify calculations, each agent is defined to have a mass of 1. The 'gravitational' force between agents i and j is then calculated as $\frac{G_{i,j}}{d^2}$. Here d is the distance between the two agents' centers taking into account the fact that the world is toroidal. $G_{i,j}$ is the attractive constant between the two agents, which is determined by their genotypes and three parameters - α, β and γ. These parameters influence the levels of first and second-order assortment in the model:

- α is the attractive force that agents with the assorting allele A feel towards agents with the same social trait as themselves. So agents with the genotype CA feel an attractive force of strength α towards other CA and CM-typed agents.

- β is the attractive force between agents with the assorting PST allele A.

- γ is the attractive force between agents with the mixing PST allele M.

Figure 2 shows diagrammatically the different forces that exist between each genotype. The combined forces can be tabulated to give the strength of attraction between genotypes (Table 1). Note that the attractive forces are not symmetrical, unlike real models of gravitation — agent i may be attracted to agent j more than j is to i. $G_{i,j}$ is then computed as rg where g is the attractive force from agent i to agent j as given in the table.

There is also a repulsive force with magnitude -1 that effects the agents when they are closer than $2r$ apart that prevents the agents from overlapping. At each timestep the forces between all agents are calculated and the net force F_i for each agent calculated. Friction is then accounted for using the equation $F_i = F_i - 0.2v_i$ where v_i is the agent's
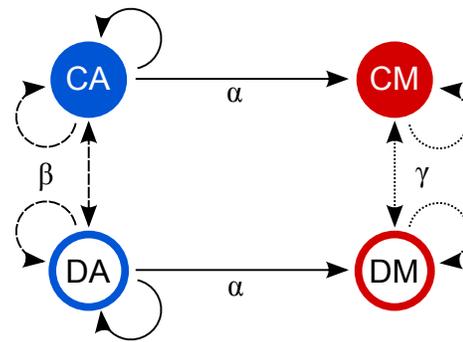

Figure 2: The attraction between the different genotypes is determined by the three parameters α, β and γ

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	CA	DA	CM	DM
CA	$\alpha + \beta$	β	α	0
DA	β	α	0	α
CM	0	0	γ	γ
DM	0	0	γ	γ

Table 1: The attractive force from an agent of one genotype (rows) to an agent of another genotype (columns).

previous velocity. Each agent's acceleration, velocity and position are then calculated and updated using numerical integration and the standard equations of motion in a plane using an integration timestep of 0.1.

Model Scenarios

The model was run using four different sets of parameters, the relative strengths of α, β and γ defining four different scenarios with respect to the levels of first and second-order assortment and the nature of the second-order assortment:

No Assortment ($\alpha = 0$, $\beta = 0$, $\gamma = 0$). In this control scenario there is no attraction between agents. Consequently each agent's nearest neighbour is randomly determined by the initial placement of agents in the world and frequencies of the social strategies are expected to reach the equilibrium of the game being played.

First-Order Assortment Only ($\alpha = 1$, $\beta = 0$, $\gamma = 0$). In this scenario, the only assortment is between social behaviours, where agents with the assorting population-structuring trait are attracted to agents with the same social strategy traits, regardless of whether or not the other agent possesses the assorting trait.

Emergent Second-Order Assortment ($\alpha = 1$, $\beta = 1$, $\gamma = 0$). In this model agents with the assorting trait are attracted to others with the same strategy, but there is also attraction between agents with the assorting trait and other agents with the assorting trait. This produces a scenario in

which second-order assortment is tied to the mechanism that generates first-order assortment, as may be the case where strategy-assorters possess greenbeard traits.

Enforced Second-Order Assortment $(\alpha = 1, \beta = 1, \gamma = 1)$. In this model as well as first order assortment there is also uniform assortment on population-structuring traits. This is intended to produce a situation in which levels of assortment are uniform across different traits such as may be the case with relatedness.

Results

Custering occurs in the model as the agents aggregate. In the control scenario, no clustering takes place. In the scenario with only first-order assortment, cooperators cluster with cooperators and defectors with defectors. Predominantly though it is agents with the CA genotype grouping with other CAs and DAs grouping with DAs as these are the agents attracted to others with the same strategy allele. In the second variation cooperators and defectors cluster together, with CAs and DAs at the heart of the clusters and CMs and DMs at the edges attracted to other cooperators and defectors respectively. In the third scenario where second order assortment is enforced the clusters are more mixed.

To investigate the effects of second-order assortment over a wide range of social dilemmas we took a 21×21 lattice of points on the ST-plane spaced 0.1 units apart and ran each scenario for every game on the lattice. Each scenario was repeated 5 times for every game and the results averaged. One of the dynamics in the model is that there is no selective difference between individuals with the same social strategy allele in the absence of individuals with the other social strategy allele. The difference in fitness between, for instance, the CA and CM genotypes comes from their different interactions with the DA and DM genotypes. So when the model reaches a state in which only one of the social strategy alleles is present then there is no selective pressure between them and their frequencies begin to take a random walk. Experimental testing indicated 20 generations proved a balance between letting the model reach equilibrium and mitigating the effects of the random walk, so this was the length of each run of the model.

Our hypothesis was that increasing second-order assortment would increase the spread of the assorting population-structuring trait. We found some support for this view but with complications, some of which were obvious in retrospect. Figure 3 plots the mean absolute frequency of the C allele over the ST-plane in all four models. In all scenarios in which there is assortment, cooperators perform better than in the control. However, counter to our initial expectations, cooperation is more successful when there is just assortment on social strategies.

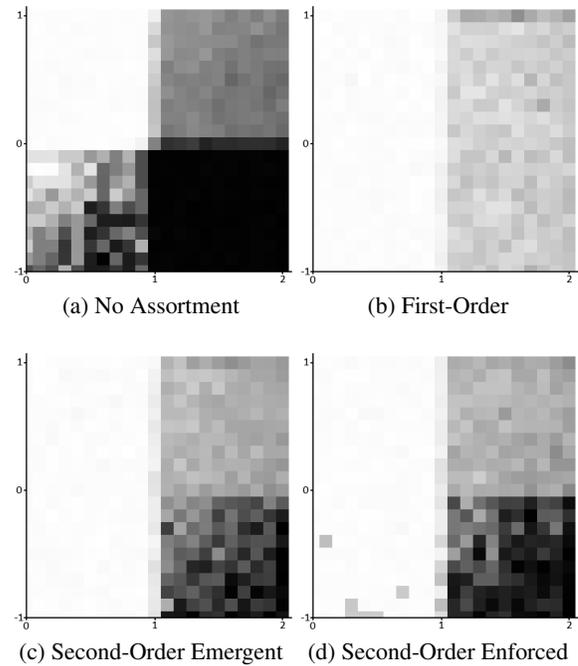Figure 4 plots the mean frequencies of the A allele over

(a) No Assortment (b) First-Order

(c) Second-Order Emergent (d) Second-Order Enforced

Figure 3: The mean absolute frequency of the C allele over the ST-plane in all four models on a scale where white indicates 100% cooperators, black 100% defectors.

the ST-plane. In the control model there frequency of the A is essentially random. In the other models, as expected, increasing levels of assortment increases the spread of the A allele. These results are summarised in Table 2 which records the mean frequencies of the C and A alleles over all games and all runs. As the table shows, there is essentially no net change in frequencies over the whole of the ST-plane in the control model. In the three scenarios with assortment, the frequencies of the C and A alleles increase, but with a trade-off between increased levels of cooperation and assortment on the population-structuring trait.

Scenario	Mn C	Var C	Mn A	Var A
No Assortment	0.505	0.140	0.501	0.005
First-Order	0.814	0.019	0.669	0.017
2nd-order Emergent	0.748	0.088	0.684	0.025
2nd-order Enforced	0.729	0.103	0.731	0.028

Table 2: The mean final frequencies of the C and A alleles over the ST-plane in each scenario.

Mathematical Model of Altered Interaction Frequencies using the Replicator Equation

Agent-based simulation models like the one presented here are subject to noise and it can be difficult to tune the desired
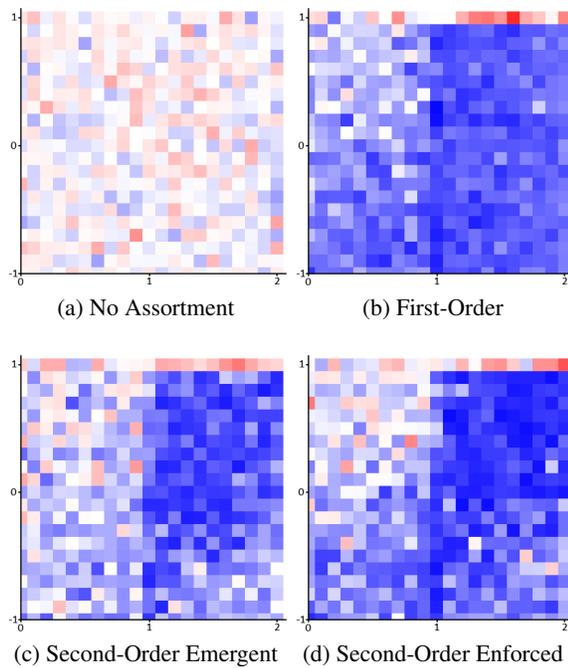
(a) No Assortment   (b) First-Order

(c) Second-Order Emergent   (d) Second-Order Enforced

Figure 4: The mean frequencies of the A allele over the ST-plane on a red-white-blue scale. Red indicates the A allele decreases in frequency (< 0.5), blue that the A allele increases in frequency (> 0.5)

behaviours precisely, so there are benefits to reproducing the results in a mathematical model. Here we present a formalism to do so by modifying the replicator equation. The replicator equation models the evolutionary success of a group of genotypes based on the difference between the fitness of the genotype and the mean fitness of the population. The fitness of a genotype is given by its expected payoff based on social dilemma it is engaged in — the payoff for its interaction with each other genotype multiplied by the probability of interacting with that genotype. When the population is freely mixed, these interaction probabilities match the frequencies at which the genotypes occur in the population, but they can be changed by population-structuring mechanisms.

A population state vector $x \in S_n$ is a vector of the frequencies of different genotypes in a population; alternatively it can be viewed as the probabilities of interacting with a given genotype. The entries of the vector must sum to 1 so it is defined on the simplex $S_n = \{(x_1, \ldots, x_n : \sum_i^n x_i = 1\}$. We can define a family of n *interaction functions* $e_i : S_n \to S_n$ that map the population vector to the actual frequencies at which the i-th genotype encounters other genotypes. The fitness of the type is the composition of the fitness and interaction functions $f_i \circ e_i(x)$, and the mean fitness is $\sum_j^n x_j f_j \circ e_j(x)$. This gives the new replicator equation:

$$x_i = \dot{x}_i \Big(f_i \circ e_i(x) - \sum_j^n x_j f_j \circ e_j(x) \Big) \quad (3)$$

The key idea here is that essentially whenever the replicator equation is used there an implicit interaction function, but in a well-mixed population the interaction functions are just the identity. This generalises the replicator equation by explicitly recognising other interaction functions. The set of fitness functions $g_i : g_i = f_i \circ e_i$ then defines a new game that when played in a well-mixed population is equivalent to the original game played with the given population structure. If the interaction functions can be represented by matrices then they can be used to find the payoff matrix for the transformed game, but that does not apply in this instance where the interaction functions are non-linear.

The non-linearity of the interaction functions in practise is often forced by the requirement that they map valid population states to valid population states (where the entries sum to 1). In general any map of S_n can be normalised to one of S_n to itself by dividing the resulting vector by the sum of its entries, but this results in non-linearity. As long as the interaction functions are continuous though the replicator equation can still be used.

Modelling the Results with Interaction Functions

We used the formalism of interaction functions to mathematically model the results of the simulated scenarios. This was done by constructing interaction functions based on data from the simulations. First we define the four strategy game in the absence of interaction functions. If we consider the strategies to be $x_1 = CA$, $x_2 = DA$, $x_3 = CM$, $x_4 = DM$ then for an arbitrary social game $G = \big(\begin{smallmatrix} R & S \\ T & P \end{smallmatrix} \big)$ the matrix of the full four strategy game is:

$$\begin{pmatrix} R & S & R & S \\ T & P & T & P \\ R & S & R & S \\ T & P & T & P \end{pmatrix} \quad (4)$$

This is then modified using interaction functions. To represent the changed number of interactions due to the population structure we use a simple non-linear interaction function — multiplying each entry in the population state vector by a scalar representing an increased chance of encountering that genotype and then normalising the resulting vector so the entries sum to 1. The scalars were calculated by running the model until the first reproduction event (at $T = 10000$) 100 times starting from evenly distributed population frequencies and recording the total number of games played between each pair of genotypes. Dividing this by the total number of interactions gave the mean frequencies at which a given genotype would encounter each other genotype when the actual frequency of each genotype was 0.25, so dividing

again by 0.25 gives the the actual encounter rate between different genotypes as a multiple of what would have been expected in a well-mixed population. We used these scalars to define the interaction functions for the four types in the model. This was a basic way of determining the interaction functions — a more complex way would have been to generate scalars for different actual population frequencies and interpolate between them to create more complex interaction functions. However, this simple method was sufficient to capture the behaviour of the three non-control models; the match between the results is illustrated in Figure 5.

	CA	DA	CM	DM
CA	2.32	0.14	1.19	0.36
DA	0.13	2.35	0.33	1.18
CM	1.54	0.44	0.93	1.09
DM	0.46	1.53	1.09	0.92
CA	2.14	0.93	0.72	0.20
DA	0.93	2.15	0.21	0.70
CM	0.96	0.28	1.22	1.54
DM	0.26	0.94	1.55	1.25
CA	2.22	1.07	0.49	0.22
DA	1.06	2.21	0.22	0.50
CM	0.51	0.23	1.50	1.76
DM	0.24	0.54	1.77	1.45

Table 3: The rows define the interaction functions giving the coefficients that modifying how likely it is for the row genotype to encounter the column genotype for the three scenarios with assortment, listed in order.

Table 3 gives the interaction coefficients that were used to define the interaction functions for the three scenarios in which there was assortment in the model. For example the first row defines the interaction function e_1, describing the transformation in the interaction frequencies for the genotype CA in the social strategy assortment-only model:

$$e_1 \begin{pmatrix} x_{CA} \\ x_{DA} \\ x_{CM} \\ x_{DM} \end{pmatrix} = \frac{1}{2.32x_{CA} + 0.14x_{DA} + 1.19x_{CM} + 0.36x_{DM}} \begin{pmatrix} 2.32x_{CA} \\ 0.14x_{DA} \\ 1.19x_{CM} \\ 0.36x_{DM} \end{pmatrix}$$

Discussion

Our expectations for this model were that increasing levels of assortment on population-structuring traits (PSTs) would lead to the increased prevalence of the PST that supported cooperative behaviours — in this model represented by a PST that directly increased correlated interactions between individuals with the same social strategy. This was true, but we did not anticipate that there would be a degree of trade-off between increased levels of the cooperative (C) and assorting (A) alleles. The comparison of the different scenarios reveals that cooperative strategies are more successful

when there is just first order assortment, though the frequency of cooperators still increases when there is second-order assortment relative to when there is no assortment at all.

(a) SM C (b) MM C (c) SM A (d) MM A

(e) SM C (f) MM C (g) SM A (h) MM A
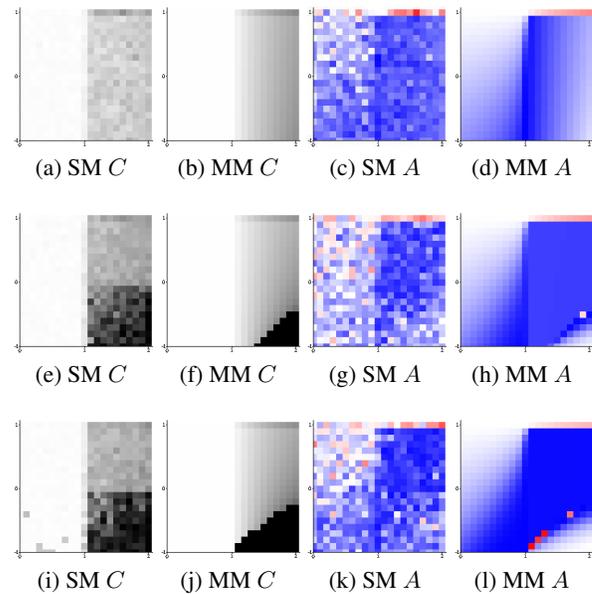
(i) SM C (j) MM C (k) SM A (l) MM A

Figure 5: Visual comparison of simulation model (SM) results and the mathematical model (MM) using interaction functions for the three scenarios with assortment. The simulation model results are as in Figures 3 and 4, the mathematical model graphs reproduce these scenarios.

The reason for this trade off is that assortment on social strategy and population structuring traits are not orthogonal processes. When there is just social strategy assortment, co-operators interact preferentially with cooperators and defectors with defectors, greatly reducing the number of cross-strategy interactions. The inclusion of assortment on the population structure alleles reduces this effect by bringing together cooperators and defectors with the same PST allele. While increasing second order assortment decreases the frequencies of co-operators (relative to strategy assortment only), it increases the spread of the PSTs that ultimately promote cooperation. Hence essentially second order assortment decreases the dependency between cooperation and cooperation-promoting PSTs; when there is second-order assortment the A allele is able to spread even when the local social game is a prisoner's dilemma dominated by defectors.

An alternate way of looking at this is that it demonstrates that the dominant social behavioural trait does not necessarily have to control the evolution of population structure. This is an important result for social niche construction – population structures that support enhanced cooperation must be able to evolve even in conditions unfavourable to coop-

erative behaviours or social niche construction would be a mechanism that just accelerates the evolution of cooperation rather than enabling it where otherwise defection would be favoured. If we imagine that there is a separation of timescales where population structures evolve more slowly than social behaviours then when there is second-order assortment on PSTs, population structures can evolve to become more supportive to cooperation even when the current social dilemmas are dominated by defectors. This would then establish a basis in population structure for cooperative traits to then spread more easily when conditions change to become more favourable.

The model could be extended in a number of ways, such by allowing for repeated interactions and hence iterated strategies, or examining a wider range of model parameters. The successful realisation of the simulation results in a mathematical model using interaction functions to change the replicator equation also opens up avenues for future work. In particular it is possible to more precisely model different levels of first and second-order assortment using interaction functions; because the assortment in the simulation model is generated by the gravitational attraction it is difficult to tune and potentially presents an issue in comparing the results across different scenarios. Interaction functions have many potential applications that can be pursued beyond this model; they can provide a general mechanism to determine the effective game played when types interact within a population at non-random frequencies and hence allow comparisons between the actual and effective games that are being played by the population in a principled manner. This work also demonstrates that they can be applied to empirical or simulation-derived data to model the results mathematically.

In conclusion, here we have shown that although second-order assortment on population structuring traits can partially disrupt assortment on social behaviours, it increases the range of behaviours in which population structures that support increased cooperation can evolve.

Acknowledgements

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