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THE IMPORTANCE OF SPACE IN MODELS OF SOCIAL LEARNING, CULTURAL EVOLUTION AND NICHE CONSTRUCTION

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This article focusses on the importance of space in mathematical models of cultural evolution, cooperation, niche construction and social learning. We discuss the benefits of including spacial effects in these evolutionary models and illustrate how the inclusion of space has changed accepted and long-standing results. We also briefly discuss the spatial dynamics of these systems and suggest future directions for research investigating spatial evolution.

Keywords: Spatial structure; culture; cooperation; niche construction; social learning.

1. Introduction

> *"All models are wrong, but some are useful."*[a]

Mathematical modeling in the social and biological sciences is in many ways an exercise in being wrong; the trick is to be wrong in the most useful possible way. Social systems of biological agents are sufficiently complex that even tasks as apparently simple as choosing parameters for a model and making assumptions about their relations becomes extremely difficult. It is for this reason that the early models of social learning might have appeared simplistic, yet these were pioneering attempts to elucidate a system — human culture — that is challenging to understand. Human culture has, in fact, been described as the most complex phenomenon known to science [45].

[a]Box, George E. P.; Norman R. Draper (1987). Empirical Model-Building and Response Surfaces, p. 424, Wiley.

The sheer complexity of culture has led to a variety of different modeling techniques being applied to a range of different questions. Social learning and cultural transmission systems have been modeled using mean-field approaches (e.g. population genetic models) [4, 5], non-spatial evolutionary game theory [38], reaction-diffusion systems that assume infinite populations [5, 19], and interacting particle systems e.g. [12, 40, 47, 49]. It is the interacting particle systems, dealing with space and time explicitly, and implemented as cellular automata, that we discuss here. This review of the literature is by no means exhaustive and there are a number of alternative approaches to modeling cultural evolution that we will be unable to examine in detail including direct demographic models [46], and network analyses [44]. We briefly discuss the effects of space in some evolutionary games but another, more detailed discussion can be found in [41]. We concentrate instead on simple analytical models and their spatial extensions.

Although different models may be useful in different circumstances, depending on the scale and level of detail required to answer specific questions, they may also give different results when applied to the same problem [7]. Thus, the choice of method goes deeper than pure mathematical or computational convenience. Here we will concentrate largely on individual agent-based simulation models of social learning and niche construction, and the analytical models that preceded them. As the theme of this issue is centered on spatially structured populations, we review here the leap in understanding that the inclusion of spatial effects in such models brings. Of course, cellular automata with no, or highly local, dispersal constitute an extreme of population viscosity, and most natural populations will fall between these and the perfect mixing non-spatial cases. Hence results from cellular automata models should be interpreted as reflecting possible, rather than inevitable outcomes.

Social learning, defined as "learning from interactions with, or observations of, other individuals or their products" [17], is widespread in the animal kingdom, in both vertebrates and invertebrates, e.g. [34]. A strong reliance on social learning [4, 5, 50], as well as a huge capacity for cooperation [2, 4, 55], are both thought to underlie the unique human ability to generate vast, diverse and cumulative cultures. Social learning can thus help to explain our species' demographic and ecological success. The ubiquity of social learning in the animal kingdom suggests that a reliance on it has some fitness advantage, a hypothesis that has received theoretical support [4, 8, 47, 48]. This advantage is usually thought to derive from the gain of useful or high pay-off information at little cost to the copier. However, this is premised on the assumption that the copied individual possesses useful knowledge relevant to the copier, and it is easy to envisage situations where this would not hold. The unbiased, random copying that featured in many early models came with considerable costs as well as the obvious benefits, since the information obtained through social learning could easily be passed from individual to individual and across generations, spreading, but also becoming outdated and inappropriate in a changing environment [51]. Nonetheless, the widespread interest in social learning stems from the idea that our human ability to learn from each other and generate

varied and plastic cultures corresponds to an increase in absolute fitness. For example, the ability to learn to manufacture suitable clothing, to build or find shelter, control fire, and so forth, was plausibly instrumental in hominins being able to move from Africa across the globe, to colonize a huge range of habitats. This flexibility in what we can do and learn has undoubtedly enhanced our ability to colonise new habitats and create niches [27, 29, 30, 43]. Here we review a collection of spatial models of social learning, niche construction and cooperation, ostensibly three of the most important social processes that shaped our evolutionary history.

2. The Effects of Space on the Evolutionary Dynamics of Social Learning

Early models of the evolution of social learning commonly assumed a perfectly mixed population, meaning that each individual was equally likely to interact with any other. While this was a sensible place to start, and led to important insights, the spatial structure of most real populations should give pause to this assumption [5]. Early models of social learning and cultural evolution built on population genetic models to track gene and cultural trait frequencies in well-mixed populations, to investigate the evolution of social learning, cooperation and culture, creating a body of work today known as cultural evolution, gene-culture coevolution, or dual-inheritance theory [4, 5, 9, 50]. The methods of genetic analysis were useful here because evolutionary social learning systems, like ecological systems, are complex, involving a number of individual agents whose collective, average behavior and fitness can allow a trait to evolve or hinder its spread. Cavalli-Sforza and Feldman [5] briefly considered the effects of space on the systems they studied. Although these researchers examined the spread of information across a spatially stratified population, rather than the effects of space on the evolution of traits, they gave a valid insight into the possible dynamics of the invasion of social learning and innovation (or cooperation and defection), characterizing the invasions as waves spreading in fronts, following reaction-diffusion dynamics. These models use reaction-diffusion methods originally designed to describe chemical reactions to take account of social learning, innovation and the spread of information over time.

In 1988, anthropologist Alan Rogers set out to examine the relative effectiveness of social and asocial learning [51]. Rogers' model was a simple thought experiment resting on a series of basic assumptions. The model assumed that there were just two behavior patterns available to learn, matching two possible environmental states. For each of the individuals in his population, choosing the correct behavior for the current environment yielded a fitness pay-off. Having just two environmental states, however, meant that all environmental changes (bar the first one) reversed the previous change.

The model led to one of the most influential ideas in the study of the evolution of social learning to date, known as Rogers' Paradox. Rogers found that when social learners (who copy the behavior of a randomly selected member of the

population) are in a minority, their fitness is higher than that of asocial learners directly sampling the environment and who have a constant fitness. However, the fitness of social learners is frequency-dependent and declines as the proportion of social learners increases. This happens because as asocial learners decline in number there are fewer individuals producing accurate information about the appropriate behavior to perform in the current environmental state. Eventually, the population evolves to a mixed equilibrium where the fitness of social learners equals the fitness of asocial learners [11, 16]. Essentially, this implies that the evolution of social learning does nothing to improve the mean fitness of the population, since absolute fitness is unchanged. Contrary to the notion that copying underlies increases absolute fitness, the average fitness at equilibrium is the same as that in a population of solely asocial learners. It is a testament to the surprise with which this result was met, that the effect Rogers detected was called a paradox, when strictly it is a non-paradoxical consequence of the insight that the effectiveness of social learning could be dependent on its frequency in a population. Boyd and Richerson [4] examined the paradox and concluded that it would arise in any evolutionary game where social and asocial learners played against each other and the value of the learned information remained frequency independent. This confirmed that the problem was general.

There have now been many proposed solutions to Rogers' paradox, one of the most important and general of which is the *selective* use of social and asocial learning embodied in the concept of "social learning strategies" [1, 4, 16, 20, 26]. The key idea here is that natural selection is expected to fashion evolved psychological rules that specify when an individual should copy others and from whom they should learn. The presence of social learning strategies meant that the blind, random social learning that was assumed in Rogers' original model was replaced with more strategic copying combined with interaction with, and learning directly from, the environment.

The extensions proposed, that succeeded in solving the paradox, relaxed some of the assumptions of Rogers' model, making them more general than the original. For example, in [8] Enquist *et al.* extended the Rogers model to allow a social learning strategy "critical social learning" to play the evolutionary game outlined by Rogers with social learners and asocial learners. Critical social learners would use social learning first and would use asocial learning only if social learning failed to give the right answer. Enquist *et al.* also adjusted the regime of environmental change ensuring that changes in the environment could not reverse previous changes. Rogers' model assumed that those partaking in individual learning always found the correct solution for the environment at that time. Enquist *et al.* [8] relaxed this assumption too, by introducing a parameter describing the efficacy of asocial learning, which varied between 0 and 1.

This more general model found that the combination of adaptation and inventiveness offered by critical social learning led to a solution of Rogers' paradox in which critical social learners always out-competed pure social learners and under

most circumstances, asocial learners as well. This, Enquist *et al.* claimed, was due to the adaptive evaluation and filtering of information. The individuals deploying the critical social learning strategy necessarily evaluated the adaptiveness of the solution they had obtained and, using this information, they then decided whether to learn again (this time through asocial learning). Whether or not their results hold when individual learners, for example, were given a similar capacity for evaluation and a second chance to learn individually was not examined even though the importance of the filtering effect itself was repeatedly stressed. The real advantage to conditional strategies like critical social learning and its converse "conditional social learning" where individuals first try asocial learning and use social learning only if this fails, is that they do not lead to the fitness depression associated with pure social learning. Conditional social learning was also found to be a similar solution to Rogers' paradox [8, 48].

A further assumption of Enquist *et al.* is that the fitness functions are discrete, meaning that a solution matching the environment gets the maximum fitness pay-off and any other solution gets no fitness pay-off at all. A more recent simulation model replaced binary fitness pay-offs with a pay-off distribution in which the best solution is rewarded with a maximum pay-off while others getting progressively further away from the ideal are rewarded a lower pay-off tending towards zero [48]. This pay-off distribution allowed Rendell *et al.* to capture the harshness of an environment, with a harsher environment giving a steeper decline in pay-offs when moving away from the best solution. This analysis also introduced spatial or demographic structure to the models [48].

The technical problems involved in implementing spatial, cellular automata-based simulation models have been greatly reduced as more powerful computers have become available. The availability of simulation software like NetLogo makes spatially explicit cellular automata models easy to construct and analyze, while more flexible programming environments like MATLAB and python facilitate the construction of bespoke models. The presence of space in the Rogers' paradox model meant that interactions were restricted to an agent's immediate neighbors. This refinement led to some surprising results.

The model runs in an $x \times x$ lattice (where $x^2 = n$) with each cell communicating only with its closest four neighbors (Von Neumann neighborhood) or with its eight surrounding neighbors (Moore neighborhood). Each lattice square is assigned a value between 1 and N_s, representing the current environmental state of that lattice square, which can change with a certain probability every model iteration. Each square is occupied by one individual who has one of several possible social learning strategies encoded in its genome. The strategy allows the individual to learn a behavior, b, which takes a numerical value in the same range as those taken by the environmental state (between 1 and N_s in this case).

Since an individual's task is to choose a behavior to closely match its environment, an individual's fitness, W, is then defined by the difference between the environmental state in the cell it occupies and the behavior it currently shows,

minus the cost of the learning strategy encoded in its genome. W is given by the equation

$$W = h^{-S} - c_{\text{strat}}, \tag{1}$$

where h^{-S} is the pay-off associated with having a behavior S steps away from an environment-matching behavior and c_{strat} is the cost of the strategy employed. The parameter h can be interpreted as the harshness of the environment. As the behavior gets further away from the optimum, the pay-off decreases at a rate dependent on h.

Each individual is assumed to reproduce with a probability proportional to their fitness, with each giving rise to an offspring that shares the parent's social learning strategy and behavior prior to their own learning experiences. There is also a small probability that some mutation event causes the offspring to gain a different strategy to their parent's (this is how new strategies are introduced to the population). Each new individual replaces another at random, either in their parent's neighborhood or throughout the population as a whole. In each model iteration, each individual (1) learns, (2) has their fitness evaluated and (3) may reproduce. The model ran for 10,000 of these iterations per set of conditions with overlapping generations.

Rendell *et al.*'s model was applied to a grid of individuals who could interact with their eight closest neighbors (Moore neighborhood) only, with periodic boundary conditions. They found, somewhat surprisingly, that this extension offered a further solution to the original Rogers' paradox, while drawing attention to another counter-intuitive finding: that the proportion of pure social learners could actually continue to increase in the population even while driving fitness below that of the original purely asocial learner population. The spatial aspect of this model also meant that the authors were able to find some circumstances in which pure social learning out-competed not only individual learning but both critical and conditional social learning strategies too.

The root of this surprising finding was that the social learning genotype was buffered from the invasion of more fit asocial learners in social learning spatial clusters (Fig. 1(a)(i)), with a cluster here defined as a contiguous group of individuals who have at least one immediate neighbor sharing their particular strategy [33].

The clustering effect in social learning models is a subtle one. Social learners are essentially parasites, gleaning useful information from asocial learners and suffering little or no cost for doing so, if the information is correct. This free information, however, is recycled again and again, becoming outdated as the environment changes. This means that as social learners cluster together, the individuals at the center of the cluster, surrounded by other information parasites, will quickly decline in fitness in a changing environment. However, as soon as one individual learner appears, by mutation, inside the cluster, the fitness of its social learning neighbors jumps above the population average for asocial learners. This means that asocial learners are unable to re-invade once social learning is established, even though the global fitness of social learners is very low. Added to this are edge effects around the clusters themselves. The social learners at the edge of the clusters interact

(i) Behavioural strategy

(ii) Fitness

(a)

(i) A locus genotypes

(ii) E cultural trait

(*AA* = white, *Aa* = grey, *aa* = black)　　(*E* = white, *e* = black)

(b)
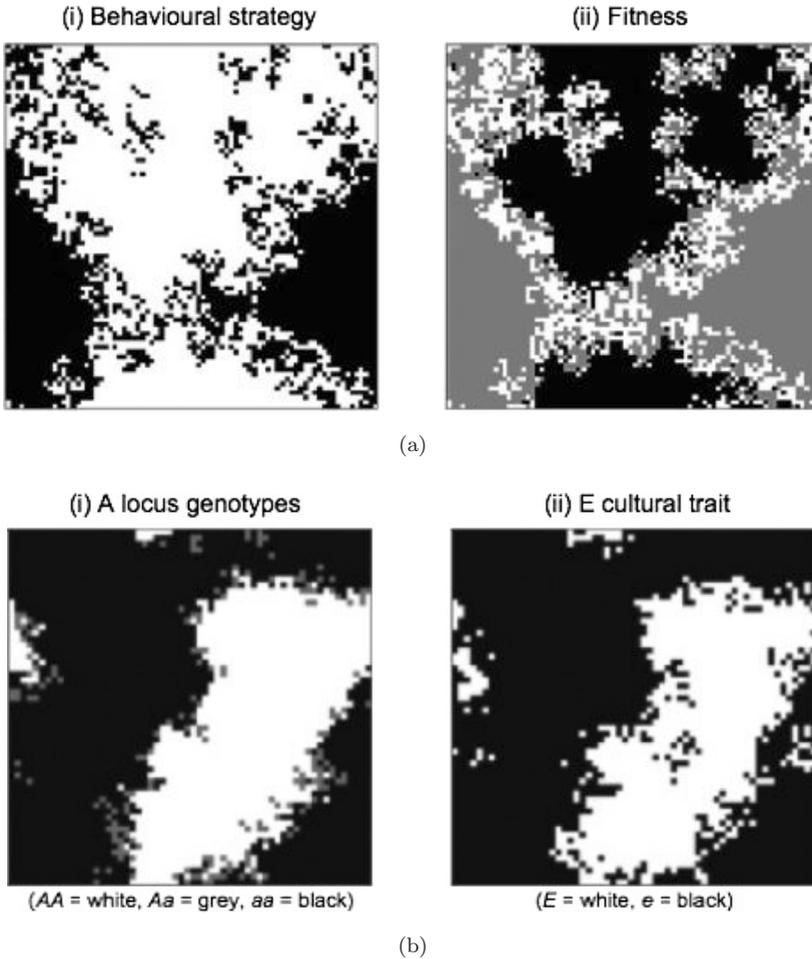
Fig. 1.　Snapshots from (a) Rogers' paradox simulations (after [48]) showing social learning clusters forming as white patches in a population of asocial learners shown in black, and (ii) the corresponding fitness of the population with higher fitness increasingly light in colour. The low fitness of social learning clusters is clearly visible. (b) shows a snapshot from cultural niche construction simulations (after [49]), (i) shows the frequencies of the different A genotypes with (ii) showing the linkage of these genotypes with the *E* cultural trait.

with social learners inside the cluster and asocial learners outside. This means that they can, in effect, ferry new information into the social learning cluster. The leading edge of a social learning cluster therefore has extremely high fitness and so they allow the spread of social learning despite its low fitness at the center of the cluster (Fig. 1(a)(ii)). This low fitness persists, lowering the average fitness of the population as social learning extends its reach. Clustering in evolutionary models in general seems to allow costly behavior, usually open to exploitation by defectors, to persist in the population for a number of generations. This can be seen not only in

social learning models but also in closely linked cooperation and niche-construction models. Rendell *et al.*'s analysis highlights the possibility that social learning can propagate maladaptive information in a structured population.

3. The Effects of Space on the Evolutionary Dynamics of Niche-Construction and Cultural-Niche-Construction

Niche construction is the process by which an organism alters the environment in which it exists and thereby modifies the selection pressures to which it is subjected [30, 37, 43]. This encompasses both ecosystem engineering in which the organism alters its environment — a beaver building a dam for instance, or a bird building a nest — and the evolutionary feedback from the changed environment to the constructor, its descendants, and other organisms that cohabit its niche. Humans are particularly potent niche constructors, not least because the transformations that they bring about in environmental states are reliant on cultural knowledge (henceforth "cultural niche construction") [28, 31, 32, 43, 54].

Analytical genetic models of niche construction [29, 30] were successful in showing that organisms could, through their own actions, alter the course of their own evolution. Such models showed that niche construction could fix genes that would otherwise be deleterious in a population and generate unusual evolutionary dynamics, such as momentum and inertia effects. Early models adopted a two-locus population genetic approach, with each individual genotype having two loci, a niche-constructing locus, **E**, and a resource-dependent "recipient" locus, **A**. Each of these, in turn, had two possible alleles: at the **E** locus E, a niche constructing allele and e a non-niche constructing allele, and at the **A** locus A, an allele that increased in fitness with a change in resource frequency (thus affected by local niche constructing activity) or a, an allele that decreased in fitness. These models, however, rested on strict assumptions of infinite population size and lack of stochastic processes.

Silver and DiPaolo [53] assumed finite populations in a simulation framework, allowing a certain amount of stochasticity to affect the population dynamics. They also situated the populations in a spatially stratified, cellular automaton framework. These alterations actually increased the parameter space across which niche construction and recipient alleles could survive and become fixed in a population. Silver and DiPaolo [53] suggested two reasons why the effects of space made such a profound difference to the outcome of the model in terms of both likelihood of alleles fixing in the population and the range of parameter values over which fixation was possible. Firstly, clustering buffered costly alleles for a time, allowing them to become established in the population and to spread when conditions improved through their own niche construction (Fig. 1(b)). Secondly, a localized resource distribution allowed strong linkage disequilibrium (a non-random association of independent alleles) between niche-constructing traits and recipient alleles to form.

In the niche-constructing case the spatial clusters were formed of a core of homozygote niche constructors ($AAEE$) with this homozygote core surrounded by a ring of individuals forced to interact and interbreed with the non-niche-constructing majority ($AAEE$ homozygotes). This process of mixing formed a layer of heterozygote individuals in the boundary regions of the clusters. The heterozygotes were capable of supporting the immigration of A alleles into the boundary layer. As this process allows the accumulation of A alleles, these alleles became sufficient in frequency to form a link with E alleles and the cluster of niche constructors could grow. In this way the costly trait existed for a short time in poor conditions while the heterozygote layer improved the environment enough to subsequently favor its expansion. In other words, the niche-constructing traits hitchhiked to fixation through association with the recipient alleles that their activities favored through selection. This model showed that the effects of space allowed niche-constructing alleles to evolve and spread in circumstances that the more traditional non-spatial models were unable to detect.

Rendell *et al.* [49] continued this work with a spatial model of cultural niche construction, where a cultural bias for or against the niche-constructing trait was assessed with regard to the impact on the evolution of both niche construction and hitchhiking resource-dependent traits. This model focused on the same di-allelic system with resource-dependent locus **A**, but the second niche-constructing locus **E** was conceptualized as a cultural rather than genetic trait, subject to cultural transmission biases. Rendell *et al.* also added a further locus **B**, which represented a costly genetic trait that could increase the underlying capacity for niche constructing. This can usefully be conceptualized as a capacity, such as a larger brain, that allows the individual to increase the rate or effectiveness of niche construction at some cost.

This cultural model yielded similar results to the previous genetic model, with the niche constructors forming clusters by chance, allowing the statistical associations to form between the recipient A allele and the niche-constructing cultural trait E. This happened because the assortative mating between neighbors meant that the increased resource frequency created by the E individuals favored A alleles and thus favored E through the aforementioned positive feedback effect. The consequences of including space are also apparent here as the random global mating in the non-spatial model did not allow the build-up of the statistical associations between A and E required for them to become sufficiently linked to drive the co-evolutionary cycle. The authors found that the cultural-niche-constructing practice could overcome some counter selection especially when a cultural bias in favor of the trait was in effect. In almost all cases considered, the effects of space were to increase the possibility of a niche-constructing trait spreading, and to allow the hitchhiking of recipient traits at other loci, over an extremely broad range of conditions, including costly alleles at the **B** locus that enhanced the niche-constructing capability. Thus niche constructing traits could not only drive themselves to fixation but increase their potency in the process.

The spatial model in this case reflects well the kind of agriculture- or technology-driven gene-culture coevolution to which humans are thought to have been frequently subject [32, 49, 54]. The heterozygote boundaries of niche-constructing clusters can easily be envisaged as an advancing wave of agriculture or technological adoption such as that discussed by Kandler and Steele [19] in their analytical reaction–diffusion models of similar processes. The important point here is that spatial models have revealed potentially important processes that non-spatial models failed to detect.

4. The Effects of Space on the Evolutionary Dynamics of Cooperation

Models of the evolution of cooperation show similar changes in evolutionary dynamics in spatial extensions of initially non-spatial models. Cooperation is an interesting evolutionary puzzle because in fitness terms it seems to pay on a group level to cooperate but on a personal level it may pay to take advantage of cooperators and defect in most cases. To understand the evolutionary models of cooperation, it is important to understand the concept of an evolutionarily stable strategy (*ESS*), a term taken from evolutionary game theory. A strategy used to play an evolutionary game is an *ESS* when it is essentially unbeatable. If the dominant strategy in a population is an *ESS*, an individual with any alternative strategy cannot do better than those already present and invade the population. Hence, in game-theoretic terminology, cooperation does not, at first glance, appear to be an *ESS*. This formulation of game theory was designed specifically to address evolutionary problems [38]. Many models of cooperation are based on traditional games like the prisoners' dilemma, snowdrift game or public-goods game. Here we review a small section of this vast literature focusing on spatial extensions of the prisoners' dilemma and the snowdrift game to illustrate the effects of space on two very different models of the same biological system.

The prisoners' dilemma is traditionally a symmetric two-person game where the players have two possible moves: cooperate or defect. The story goes like this: you and an accomplice have been apprehended in commission of a crime. You are faced with two options, you can either tell the police everything you know — or keep quiet. In the cell beside yours, your accomplice faces the same choice. If you both choose to stay quiet, cooperating with each other, you both get a lenient sentence, say five years. However, if one talks, defecting on their partner, while the other stays quiet, the talker gets off scott free while the accomplice gets a maximum penalty, the suckers' pay-off, of ten years in prison. Finally, you could both choose to talk, defecting on each other. In this case, you both receive a sentence that is higher than you would have gotten had you cooperated (five years) but crucially is also lower than the sentence you would get if you stayed quiet and your partner squealed (ten years). Ultimately this pay-off structure means that it pays to defect regardless of what your partner does. If you defect and they cooperate, you go free, if you defect

Table 1. The pay-off matrices for two evolutionary cooperation games where b is the benefit of the resource obtained through cooperating and c is the cost associated with cooperation. The matrix shows the pay-off awarded to an individual playing the strategy shown in the first column when playing against that shown in the first row. (a) shows the pay-off matrix for the prisoners dilemma where it pays to play the same strategy as your opponent, and (b) shows the pay-off matrix for the snowdrift game where it pays more to play the opposite of your opponent's strategy in any given round.

(a) Prisoners' dilemma	Cooperator	Defector
Cooperator	$b - c$ (Reward)	$-c$ (Sucker)
Defector	b (Temptation)	0 (Punishment)
(b) Snowdrift game		
Cooperator	$b - c/2$ (Reward)	$b - c$ (Sucker)
Defector	b (Temptation)	0 (Punishment)

and they defect, you have avoided the worst outcome and the longest prison sentence which you would have suffered had you cooperated in that case. The pay-offs in the game follow this pattern: Temptation > Reward > Punishment > Sucker.

The pay-off matrix (shown in Table 1(a)) shows that in a one-shot interaction, the only ESS is defection, not cooperation. However, when the game is altered to allow repeated interactions, and to allow agents in the game a perfect memory of their previous interactions, then strategies that can support the evolution of cooperation in certain circumstances emerge. In Axlerod's famous tournaments [3], agents participated in just such an iterated prisoner's dilemma game. The tournament revealed that *TIT-FOR-TAT*, where agents retaliated when their opponent failed to cooperate but not before, was a good strategy — it won both tournaments despite the fact that entrants to the second knew about its success in the first. It was later shown that a *TIT-FOR-TWO-TATS* strategy, which would not defect until provoked by two defections from its opponent, could have beaten the original winner had it been entered [2]. However, the real value of the tournament was to show that these strategies could emerge and be evaluated in a meaningful way both in a tournament framework and through simulation.

The natural extension of this simulation framework was to introduce structured populations, making the traditional evolutionary games explicitly spatial. One of the advantages of introducing this kind of spatial structure is that, as with other models, although the structure can be interpreted minimally as a geographic distance, it can also usefully be seen as a demographic structure of any sort that restricts free global interactions between individuals. This is an especially interesting distinction to make in this case since the kind of cooperation that we see outside of humans is often localized or directed towards group members or kin, e.g. [52, 57]. In that way any conclusions that are drawn from the spatial models can be generalized and extended to include restricted interactions between other

sub-groups within the population as a whole and can shed light on the effects of in- and out-groups on the evolution of cooperation.

Spatial effects in the evolution of costly behavior like cooperation are generally thought to increase the likelihood of invasion and maintenance of strategies that would be more open to exploitation in well-mixed populations. However, in the case of cooperation models we find some quite counterintuitive results. While spatial models of the evolution of social learning seem to suggest that space may result in the spread of social learning despite the lowering of the average fitness in the population [48], cooperation is not always supported by spatially structured populations, and is at times hampered by the presence of space, depending on the pay-off structure of the game [10, 13, 14].

Nowak *et al.* [39] show that spatial structure in stochastic simulations of iterated prisoners' dilemmas allowed cooperators to coexist with defectors without the need for complex strategies. This, in part, occurred because the cooperators were able to form spatial clusters, as with the social-learning and niche-construction models, this time avoiding exploitation by defectors. Although the clustering effect in cooperation models is pleasingly intuitive, the effects of spatial structure is in this case are more complex. As we shall see, the impact of space on the maintenance of cooperation in a population is critically sensitive to the underlying update rule, as well as the pay-off functions and structures. In the prisoners' dilemma, for example, the pay-off structure (Table 1(a)) shows that it pays to mirror your opponent's move in any given interaction. This means that individuals in agent-based simulation models naturally congregate and segregate into groups acting in a similar way. The consequence of this grouping is that individuals form spatially explicit clusters dominated by particular strategies, helping the evolution of cooperation in these circumstances. The effects of space in these circumstances are especially strong. In the prisoners' dilemma, the chance of cooperators surviving in the population is independent of the actual number of original cooperators, but depends critically on their ability to form at least 3×3 clusters in space [12, 23, 33]. It remains to be seen to what extent these findings based on clustering are robust to more realistic assumptions about individual dispersal such as those considered by Chen *et al.* [6].

The introduction of space leads to very different results in other strategic settings. We can illustrate this with the snowdrift game, another established window on cooperation. This game can be envisioned as two people trapped either side of a snowdrift. Each has two options, they can dig the snow or they can wait. If both dig, both get past the snowdrift, sharing the cost of digging. If both wait neither gets past. However if one person digs and the other waits, both get past the snowdrift but one shoulders the entire cost of digging the snow. This pay-off matrix (Table 1(b)) leads to quite different dynamics to the better-known prisoners' dilemma. In this case, unlike the prisoners' dilemma, it pays to do the opposite to what your opponent does in any given interaction and the pay-offs follow a slightly

different pattern: Temptation > Reward > Sucker > Punishment. This force opposes the formation of clusters of either cooperators or defectors.

Hauert and Doebeli [13] demonstrate a change in dynamics in the case of the snowdrift game as compared to the prisoners dilemma. In the spatial snowdrift game, the effect of space is to reduce the amount of cooperation sustained in the population compared to the non-spatial model and in some cases cause cooperation to go extinct. The clusters that form in the snowdrift game are diffuse, expanding "dendritic structures" which expand as individuals vie to border those exhibiting a strategy opposite to their own. (Note, the "pays to do the opposite" finding bears some resemblance to the findings of [25] which found that it only pays to niche construct to produce a resource when the manufactured resource is not otherwise available in the environment.)

The patterns that emerge from spatial models of cooperation can be very interesting. They can be chaotic in certain cases with kaleidoscopic patterns emerging from non-stochastic runs of prisoners' dilemma simulations [40] or enter limit cycles of cooperation and defection [15]. Detailed examinations of other strategies that can compete within the hawk/dove or snowdrift type of model show that spatial effects can also support strategies that non-spatial models cannot and that incorporating social learning and cultural transmission of strategies can also support more cooperation in these systems [22].

5. Discussion

Interesting comparisons can be drawn between the spatial models of social evolutionary systems discussed above with regard to the shapes, sizes and processes affecting the clustering of costly behavior. The clusters originate and are maintained by different processes in each case, nonetheless giving rise to strikingly similar structures. The subtle differences in the mechanisms that bring and keep these clusters together can also help to elucidate the differences in the microscopic processes at work in each system. For example, groups of cooperators forming in spatial prisoners' dilemma games are held together by inward evolutionary forces, caused by the advantage to cooperating individuals of having cooperating neighbors. Conversely, social learning clusters are held together by the inability of asocial learners to survive where social learners surround them. Further examining the structure of these clusters could help us to identify the different processes causing successful or unsuccessful invasions of particular strategies into populations [33]. The spatial-niche-construction models restrict the benefits of niche-construction to the immediate locale of the constructor. It would be a natural — and fascinating — extension to consider allowing niche constructors to produce (or deplete) resources for (or produced by) their neighbors. Such an extension potentially takes such models into the sphere of spatial cooperation models and at the same time addresses the concern that models of cooperation have neglected ecological processes [42].

The inclusion of space in models examining the evolution of niche construction and cooperation, in particular, has also enabled more empirical and experimental testing of the models. Many tests have now been performed using bacteria in media allowing or restricting free mixing of individuals and sharing of resources. This paradigm has been used to examine the evolution of cooperation, e.g. [24, 35] and niche construction, e.g. [21] and would have been difficult or impossible to interpret correctly in the light of purely non-spatial models.

The primary advantage of extending models to include the effects of spatial (or demographic) stratification is realism, and therefore, validity. It is abundantly obvious that we live in a spatial world. We interact differentially with individuals who live and work in our neighborhoods, we interact less with those who do not. This is, of course, by no means a strict rule and further generalizations of the models discussed above could usefully look at a more "small world" type of stratification [56] where the likelihood of interacting with distant members of the population is greater than zero or that incorporate levels of dispersal that better capture biological reality. As we add more and more complex interactions in space and demography to our models, we allow the models to capture what is clearly an important effect that previously we may have failed to take into account. The models we have discussed here are simulation models but this does not have to be the case: some spatial systems can be modeled using equations like reaction–diffusion equations or spatially implicit analytical models, e.g. [36]. These models have the advantage of eliminating the problem that spatially explicit agent-based models necessarily disallow continuous time processes. Discrete time and updating rules in these models have been shown to change results of evolutionary simulations considerably [18].

The advantage of using the simulation approach, though, is that it is relatively easy to extend non-spatial, analytical descriptions of different systems to account for the effects of space without redesigning an entire model from scratch and without reducing the ability to compare between spatial and non-spatial results. The fact that the results from spatial models differ, sometimes substantially, from their non-spatial ancestors, coupled with the fact that spatial stratification is observable in most animal systems means that these models may more accurately reflect the environment in which animals, ourselves included, learn and evolve. This, in turn, may mean that the most informative models are by necessity spatially explicit ones.

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