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The interplay of positive and negative species interactions across an environmental gradient: insights from an individual-based simulation model

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Positive interspecific interactions are commonplace, and in recent years ecologists have begun to realize how important they can be in determining community and ecosystem dynamics. It has been predicted that net positive interactions are likely to occur in environments characterized by high abiotic stress. Although empirical field studies have started to support these predictions, little theoretical work has been carried out on the dynamic nature of these effects and their consequences for community structure. We use a simple patch-occupancy model to simulate the dynamics of a pair of species living on an environmental gradient. Each of the species can exist as either a mutualist or a cheater. The results confirm the prediction: a band of mutualists tends to occur in environmental conditions beyond the limits of the cheaters. The region between mutualists and cheaters is interesting: population density here is low. Mutualists periodically occupy this area, but are displaced by cheaters, who themselves go extinct in the absence of the mutualists. Furthermore, the existence of mutualists extends the area occupied by the cheaters, essentially increasing their realized niche. Our approach has considerable potential for improving our understanding of the balance between positive and negative interspecific interactions and for predicting the probable impacts of habitat loss and climate change on communities dominated by positive interspecific interactions.

Keywords: mutualism; facilitation; competition; range limits; dispersal; spatial structure

1. INTRODUCTION

Positive interactions (mutualisms and facilitation) have been observed in many different ecosystems, including salt marshes, deserts, arctic tundra and alpine systems. It is increasingly realized that these positive interactions may be as important as negative interactions (e.g. competition and predation) in determining community dynamics and ecosystem processes, especially in severe environments (see reviews by Bertness & Callaway 1994; Callaway 1995; Brooker & Callaghan 1998; Bruno *et al.* 2003).

There is a large body of theoretical literature devoted to understanding the consequences of negative interactions for community dynamics (e.g. Amarasekare 2003 and references within; Murrell & Law 2003). Considerable potential exists for applying similar analytical and simulation methods to the study of mutualistic interactions, and indeed some progress has been made in this area (Wilson & Nisbet 1997; Amarasekare 2004). Several studies have developed relatively simple spatial models for looking at the dynamics of altruists of a single species (Matsuda 1987; Taylor 1992; Wilson *et al.* 1992). Recently, Yamamura *et al.* (2004) extended this approach to investigate the dynamics of mutualists and cheaters in a spatial model incorporating simple costs and benefits of being a mutualist. Their results confirmed those of previous studies in showing that mutualists can persist only if dispersal is limited (Yamamura *et al.* 2004). However, with limited dispersal, mutualists can invade a population of cheaters if the ratio of cost to benefit is low. They also demonstrate that mutualists are more likely to become established if the intrinsic reproductive rate is low. This impinges on an important question: under what environmental conditions should we expect positive interactions to be most prevalent?

Simple verbal models have suggested that positive interactions should be more important in very severe environments because of the proposed positive relationship between the ameliatory impact of neighbours and the severity of the environment, as well as the reduced importance of negative interactions in systems where the abiotic environment dominates success (Brooker & Callaghan 1998). By developing more advanced model systems we are able to examine the dynamic impact of interactions through time, and test our current predictions concerning the long-term success of different interaction 'strategies' at different positions across the environmental gradient in a way that would be virtually impossible through field experimentation.

2. THE MODEL

Our model is similar to that described by Yamamura *et al.* (2004), except that we introduce an environmental gradient. We represent the landscape as a two-dimensional lattice. At any point in time each cell may be empty, occupied by an individual of just one species, or occupied by an individual of each species. Both species can occur as mutualists and non-mutualists (or cheaters). We use A_M and A_N to represent the frequencies of mutualists and non-mutualists of species A, and B_M and B_N to represent the frequencies of mutualists and non-mutualists of species B. A_E and B_E are the frequencies of sites not occupied by individuals of species A and B. Conceptually it may be easiest to imagine two parallel lattices: one populated by individuals of species A, and the other by individuals of species B. This dual-lattice description was suggested by Doebeli &

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Knowlton (1998) and used by Yamamura *et al.* (2004). We will adopt a similar notation here, and like Yamamura *et al.* (2004), we have the following identities for the two lattices:

$$A_M + A_N + A_E = 1 \tag{2.1a}$$

and

$$B_M + B_N + B_E = 1. \tag{2.1b}$$

Individuals of species A benefit from being in the presence of a mutualist of species B. Similarly, individuals of species B benefit from occupying the same site as a mutualistic individual of species A. Here, we assume that the benefit gained by being associated with a mutualist is an increased reproductive rate. Other potential benefits that we do not consider here include reduced mortality or greater dispersal ability. We assume that all mutualists incur a cost of being mutualistic, and that this cost takes the form of reduced reproductive potential.

The probability of a non-mutualist of either species reproducing is r in the absence of a mutualist of the other species, and $r+b$ if a mutualist of the other species is present. The probability of a mutualist reproducing is $r-c$ in the absence of a mutualist of the other species, and $r+b-c$ in the presence of a mutualist of the other species. When reproduction occurs, a propagule, identical to the parent, is dispersed to one of the cells in the parent's neighbourhood. The neighbourhood is defined as the nearest four cells (Von Neuman neighbourhood). Propagules only establish at the site to which they disperse when the site is currently unoccupied by that species. During a single time-interval, all individuals suffer the same probability of death, d.

We extend the simulation model described by Yamamura *et al.* (2004) by introducing an environmental gradient. We assume that in a harsh environment the basic probability of reproduction (r) is lower. For each run of the simulation we define $r_{\max}$ and $r_{\min}$. $r_{\max}$ represents the habitat quality at the right edge of the lattice and $r_{\min}$ the quality at the left edge. A linear gradient is used to determine the quality of sites along the length of the lattice. For simplicity, we assume that the probability of mortality is the same across the gradient. We also assume that b and c remain constant across the gradient.

3. RESULTS AND DISCUSSION

When an environmental gradient is imposed on the landscape it frequently results in the coexistence of

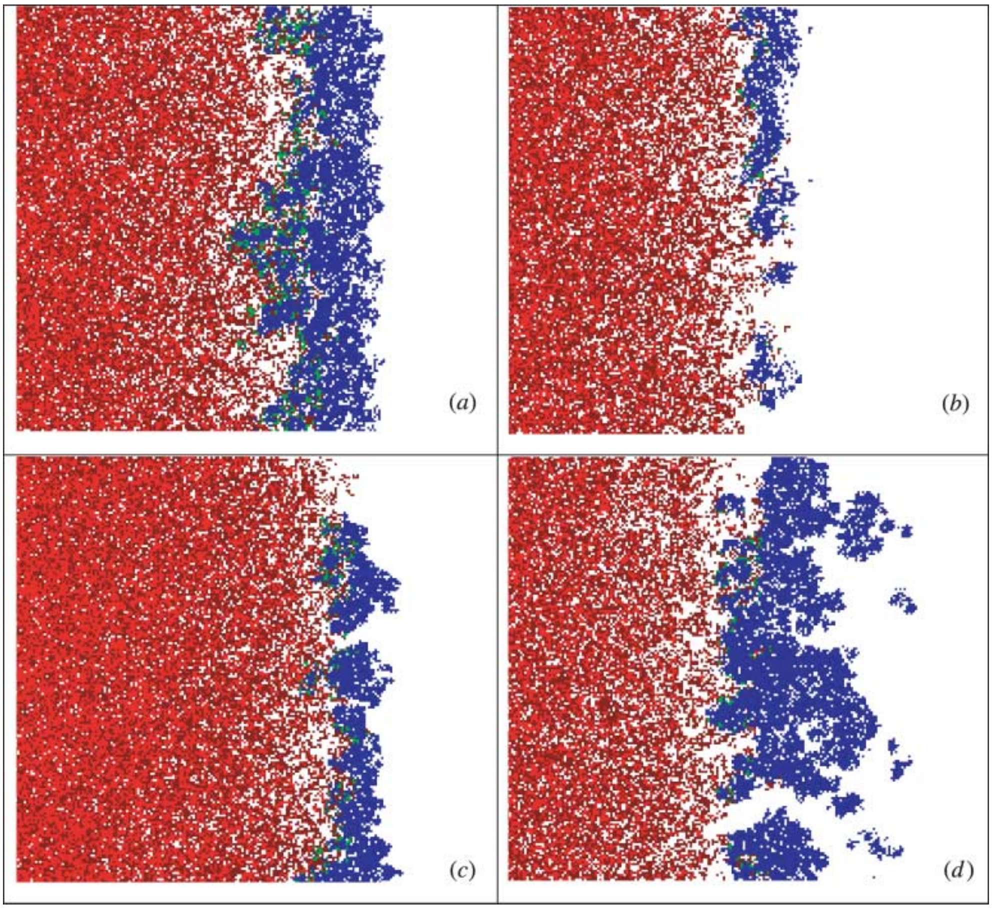

Figure 1. Positive interactions dominate the harsher environmental conditions, but are absent where conditions are more favourable. The spatial patterns shown in these four plates are typical of those observed for a wide range of parameter space. Dark red and dark blue indicate patches where a single 'cheater' species and a single 'mutualist' species occur, respectively. Bright red and bright blue indicate patches where both 'cheater' species and both 'mutualist' species occur, respectively. Patches occupied by one 'cheater' and one 'mutualist' are shown in green. (*a*) $r_{\max}=0.3$, $d=0.07$, $b=0.3$ and $c=0.02$. (*b*) $r_{\max}=0.15$, $d=0.04$, $b=0.13$ and $c=0.02$. (*c*) $r_{\max}=0.3$, $d=0.05$, $b=0.3$ and $c=0.05$. (*d*) $r_{\max}=0.1$, $d=0.03$, $b=0.2$ and $c=0.05$. The landscape is 200×200 patches.

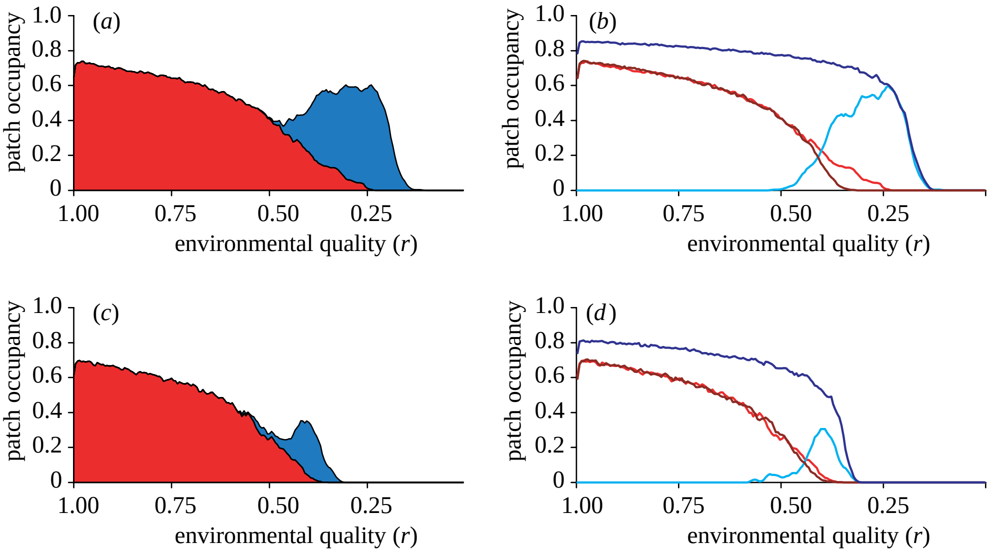

Figure 2. Mean rates of patch occupancy along the gradient. (*a*) and (*c*) show the results when cheaters and mutualists are both present. (*b*) and (*d*) illustrate the effect that one species has on the other. In (*a*) and (*c*), red shading shows the abundance of cheaters and blue shading the abundance of mutualists. In (*b*) and (*d*), light blue lines show the patch occupancy obtained by mutualists in the presence of cheaters, and dark blue lines their occupancy in the absence of cheaters. Similarly, paler red lines show the occupancy obtained by cheaters in the presence of mutualists and darker red lines their occupancy in the absence of cheaters. The model was run for 2500 time-steps and average patch occupancy over the final 500 time-steps was calculated. (*a*) and (*b*) use the same parameter values as figure 1*a*; (*c*) and (*d*) use the same parameter values as figure 1*b*.

mutualists and non-mutualists. There is a striking pattern of spatial segregation, with the mutualists occurring in the harshest conditions and the non-mutualists in the more favourable environment (see figure 1). This result supports that of Wilson & Nisbet (1997) who found strong spatial patterns of strategy segregation in similar model systems. They also tie in closely with data from numerous field experiments showing a shift from the general dominance of competition in benign conditions to facilitation in severe conditions (e.g. Choler *et al.* 2001; Callaway *et al.* 2002). Intriguingly, we often find a zone between the mutualists and non-mutualists that has a low rate of occupancy (see figures 1 and 2). This no-man's land represents an area where mutualists would be able to persist in the absence of cheaters, but where cheaters are unable to persist in the absence of mutualists. Mutualists periodically colonize this area, but they are vulnerable to invasion by cheaters from the other side of the zone. After the cheaters invade, both mutualists and non-mutualists are doomed to become locally extinct until the next wave of mutualists moves in. This results in a dynamic boundary that separates the mutualists from the non-mutualists. This is an interesting result. In natural communities we do not observe zones with reduced vegetation cover at such a species interface because additional species may fill the empty space, but we might observe an area of increased turnover of both the cheater and the mutualist. However, this is an output from the model that lends itself to further investigation and which necessitates the collection of suitable field data for validation or refutation. From this simulation we predict that regions with an average net interaction of zero, which result from the balance of positive and negative effects, might be associated with greater rates of community turnover.

In this model, mutualistic interactions permit species to exist in harsher environments than would otherwise be possible. Figure 2 enables a comparison of the environmental conditions that are occupied by mutualists in the absence of cheaters, cheaters in the absence of mutualists, and cheaters and mutualists co-occurring. Unsurprisingly, a positive interaction enables both mutualistic partners to persist in harsher conditions than their cheating counter-parts. It is worth noting that the cheaters can sometimes extend their range into harsher conditions when mutualists are present (figure 2*b*). Our model thus supports the prediction that facilitation might extend the realized niche of species (Bruno *et al.* 2003). Also, for some parameterizations, the mutualists do not occupy as many patches in harsh conditions when cheaters are present (figure 2*d*). This is because the cheaters reduce the abundance of mutualists in better-quality habitats, and this reduces the strength of a mutualist source that supports a mutualist sink in the harsher conditions (figure 2*d*). However, this effect is dependent upon the dispersal capabilities of the mutualists.

We have assumed that being in the presence of a mutualist confers a benefit in terms of an increased probability of reproduction, and that being a mutualist incurs a cost paid through reduced reproduction. However, for some associations it may be that these benefits and costs change the probability of mortality rather than reproduction. Results from a modified model show that all of the results and patterns are qualitatively very similar regardless of whether costs and benefits act on reproduction or mortality.

Models such as the one described in this paper provide considerable scope for future work on positive interactions. We identify a few areas where we feel future work might be valuable. Stanton (2003) emphasized the need for theoretical work that moves beyond the traditional view of a single pair of interacting partner species, and instead considers guilds of mutualistic species on one or both sides of the interaction. Extending the model presented in this paper to incorporate a greater number of species should be relatively straightforward and would enable us to model the impact of changes in interactions on biodiversity. We have not considered any evolution in the strength of the positive interactions. Doebeli & Knowlton (1998) recognized that evolution along a continuum of interaction strengths (with a corresponding trade-off) is likely, and constructed a model that allowed this evolution to occur. It would be interesting to explore the evolutionary impact of interaction strength on an environmental gradient. Predictions for the selective impact of positive interactions in plants from arctic and alpine systems were made by Brooker & Callaghan (1998). They pointed out that such adaptations might already exist in arctic and alpine species. However, in field studies it is not possible to examine whether facilitation alone is capable of producing such adaptations. With such a model system this would be possible.

Here, we have incorporated spatial environmental variability in the form of a simple environmental gradient. In reality, the pattern of spatial variability is likely to be far more complex. Travis & Dytham (2004) presented a method for simulating patterns of habitat availability at species range margins, and these methods offer promise for future work investigating how patterns of habitat availability determine the ability of species and communities (including those with positive interactions) to shift their range in response to climate change (Travis 2003).

We believe that combining modelling and field studies offers considerable promise for improving our understanding of the role of positive interactions in structuring communities. We have demonstrated that models can be used to generate testable predictions. Some empirical studies (Callaway *et al.* 2002; Maestre & Cortina 2004) have already generated the type of data that will allow these models to be validated and refined, but further field-based studies are needed.

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