Selection for restraint in competitive ability in spatial competition systems

Craig R. Johnson^{1*} and Ingrid Seinen²

¹*School of Zoology, University of Tasmania, GPO Box 252-05, Hobart, Tasmania 7001, Australia*

²*Department of Zoology, University of Queensland, Queensland 4072, Australia*

The absence of 'super competitors' in nature is usually attributed to organisms facing trade-offs in resource allocation. Here we identify another mechanism, dependent on indirect interactions among species and non-random spatial organization, in which selection favours restraint in competitive ability. In simple spatial models of a three-species intransitive network, indirect interactions favour slower growth and selection limits the difference in growth rate among species. The mechanism involves a trade-off between selection at the individual level, which selects for increased growth rate, and at the community level, which acts to limit growth rate to less than the maximum possible. If the difference in growth rates among species becomes too large, then the community becomes unstable and collapses to a monoculture of the slowest growing species. The mechanism requires both the intransitive network structure and self-organized spatial structure in the system. Similar behaviours arise in more complex systems of more than three species, and where there are reversals in interaction outcomes between species pairs. The work suggests that spatial self-structuring, indirect interactions and selection acting on community properties can be important in evolution. It provides a partial explanation of the high level of species coexistence and apparent restraint in interspecific interactions evident in some assemblages of sessile marine colonial organisms.

Keywords: competition; indirect interactions; spatial self-structuring; coexistence; community-level selection; cellular automata

1. INTRODUCTION

In communities of subtidal sessile marine benthic invertebrates and algae growing on hard substrata, such as some coral reef and marine fouling assemblages, competition for space is intense because unoccupied space is rare. Patterns of interspecific interactions in these communities manifest important characteristics that raise several questions about the importance of spatial context and indirect interactions in the evolution of species' traits in complex systems. First, interaction networks of many subtidal hard-bottom marine benthic communities are rich in intransitive 'loops' (e.g. where $S_1 > S_2$, $S_2 > S_3$, $S_3 > S_1$; $S_x > S_y$ indicates that species X competitively displaces species Y), which arise in part because reversals in competitive outcomes are common (e.g. Buss & Jackson 1979; Kay & Keough 1981; Russ 1982; Buss 1986, 1990; Rinkevich *et al.* 1993; Tanner 1993). This contrasts strongly with terrestrial systems in which intransitive interaction pathways occur rarely, if at all (Grace *et al.* 1993; Shipley 1993). Second, as interaction networks in these systems are maximally connected (because each species potentially interacts with every other species), the total number of possible indirect interactions among species greatly exceeds the number of direct interactions. For every direct interaction between species S_A and S_B in an S -species system there are $\sum_{i=1}^{S-2} (S-2)!/(S-2-i)!$ indirect interactions between S_A and S_B . Third, spatial context is critically important because growth, survivorship and other aspects of the fitness of an individual organism or colony depend in large

part on the identity and morphology of its immediate neighbours (e.g. Kay & Keough 1981; Russ 1982; Keough 1984; Buss 1990). A final important feature of this type of competition system is that, like many other spatial systems (e.g. Boerlijst & Hogeweg 1991; Hassel *et al.* 1991; Comins *et al.* 1992; Nowak & May 1992; Dieckmann *et al.* 2000), they have a strong tendency to spatially self-organize, which generally acts to enhance system stability (Johnson 1997; Johnson & Boerlijst 2002).

These features raise two important questions about the dynamics of this type of community and the evolution of species' traits and interspecific interactions in them. First, in highly connected spatial systems with intransitivities, by what mechanism is spatial self-organization realized, and how does it affect the stability of the system? Second, does the apparent importance of indirect interactions (Stone & Roberts 1991; Wootton 1994; Menge 1995) and spatial organization in complex networks influence the evolution of species' traits and interspecific interactions as has been suggested (Miller & Travis 1996)?

Here we use probabilistic cellular automaton (CA) models of spatial competition among sessile colonial organisms to examine these questions. Our initial model is the simplest (three species) intransitive system in which $S_1 > S_2$, $S_2 > S_3$, $S_3 > S_1$, where ' $>$ ' indicates overgrowth.

2. THE MODELS

(a) *Three-species models*

Two rule structures were compared initially to examine the robustness of behaviours to the precise form of the updating algorithm, *viz.* a 'standard' model in which rates of overgrowth are equivalent to the growth rates of the

* Author for correspondence (craig.johnson@utas.edu.au).

Figure 2. Selection on growth rates to show (a) 'Red Queen' dynamics and (b) selection for restraint in growth.

(a) Results of three separate runs of the 'catalyst' model (the 'standard' model shows similar behaviour). The graph shows: 'single species', a single species in the landscape, initial mean growth rate 0.45, range 0.4–0.5 (dotted line); 'low v ', three-species system, all with initial mean growth rates 0.45 with low variance, range 0.4–0.5 (heavy lines); 'high v ', three-species system, all with initial mean growth rates 0.5 with high variance, range 0–1.0 (light lines). (b) Results of four separate runs in which g_2 and g_3 are fixed at either 0.2, 'standard' model (heavy line) or 0.6 'catalyst' model (light line), but where selection can act on g_1 . Mean growth rate of S_1 is initially either the same as the fixed growth rates of S_2 and S_3 (i.e. at 0.2 with range 0.1–0.3 for the 'standard' model, or at 0.6 with range 0.4–0.8 for the 'catalyst' model) or well above the eventual asymptotic rate (for 'standard' model at 0.4 with range 0.2–0.6; for 'catalyst' model at 0.85 with range 0.7–1.0). In all cases, the growth rate evolves to an asymptote well below the maximum possible.

Figure 1. 'Standard' (a,d) and 'catalyst' (b,c) cellular automaton models of a three-species intraspecific network ($S_1 > S_2$, $S_2 > S_3$, $S_3 > S_1$; S_1 , blue, S_2 , red, S_3 , yellow) show similar spatial (a,b,c; time-step $t=200$) and temporal (d) self-organization. The scale of spatial organization (mean colony size) is smaller in the 'standard' (a) than in the 'catalyst' (b) model. Within each system the scale of spatial organization is independent of initial cover and spatial arrangement, but dependent on relative growth rates (g_i , growth rate of species i). Slowly growing species either codominate with the faster growing species ((e) 'standard' model, $g_1 = 0.66$, $g_2 = g_3 = 1.0$); (f) 'catalyst' model, $g_1 = 0.15$, $g_2 = g_3 = 0.3$), or dominate space ((c,g) 'catalyst' model, $g_1 = 0.66$, $g_2 = g_3 = 1.0$), and in all cases the species overgrown by the slowest grower is least abundant. Colonies of all species are of a similar size and are similarly abundant when growth rates are equal ((a,b) $g_1 = g_2 = g_3 = 1.0$). Persistence stability (*sensu* Johnson & Mann 1988) depends on the magnitude of the difference in relative growth rates (h). Although coexistence does not depend on equal growth rates, if the difference in growth rates among species becomes too large, there is increasing likelihood of the system collapsing to a monoculture of the slowest-growing species ($g_2 = g_3 = 1.0$ and fixed; results in (h) are from Monte Carlo simulations of 1000 runs each of 200 time-steps; diamond, 'standard' initial cover 100%; circle, 'catalyst' initial cover 20%; triangle, 'catalyst' initial cover 50%; plus sign, 'catalyst' initial cover 100%).

Figure 3. Spatial dynamics of the three-species system ($S_1 > S_2$, $S_2 > S_3$, $S_3 > S_1$, 'catalyst' model) from three different initial configurations (*a,b,c*) showing that the fast growing (black) genotype (fast, $g_1 = 1.0$) of S_1 is often lost from the system in the presence of the slowly growing (blue) genotype of S_1 (slow, $g_1 = g_2 = g_3 = 0.5$), irrespective of initial cover and spatial configuration. A similar behaviour is evident in the 'standard' model providing there is a large difference in $g_{i,slow}$ and $g_{i,fast}$, but the rate of decline of the rapid growing genotype is slower than in the 'catalyst' model. Note that while these particular simulations show total loss of the fast-growing genotype, in both model models it is possible that the rapid growing genotype may persist at very low levels for more than 25 000 time-steps. The important result is that the superior competitor locally (the fast-growing genotype) is always driven to very low levels or to extinction.

overgrowing species, and a 'catalyst' model in which the rate of overgrowth of one species by another is slightly enhanced by the local presence of the third species. In the 'standard' model, an identified potential 'winner' in the von Neumann neighbourhood (i.e. neighbouring cells to the north, south, east and west) of an occupied cell C_x at time t overgrows C_x at $t + 1$ with a probability proportional to the number of von Neumann neighbours of C_x that are the identified 'winner'. In the 'catalyst' model, the potential winner overgrows C_x with a probability proportional to the number of occupied cells in the von Neumann neighbourhood not in the same state as C_x . In both models, growth into empty cells with at least one occupied neighbour is determined by selecting the state of a neighbour at random. Overgrowth probabilities so determined are multiplied by the growth rate of the potential winner (maximum = 1.0) to determine the actual probability of overgrowth. CA landscapes are toroidal (zero boundary

conditions), 200×200 cells in dimension, and updating of the landscape is synchronous.

We examined selection on growth rates (a key component of competitive ability) by assigning all initial recruits (colony size = one cell) in the CA landscape a 'genotype' that defines their growth rate. As colonies grow and produce propagules they replicate their genotype exactly in new modules (from growth) and recruits (from propagules), except for mutations in a proportion of propagules that either increase or decrease the growth rate by a small amount (0.02 relative growth units of a maximum possible growth rate = 1.0) with equal probability. Disturbance creates patches of bare space on the landscape at random into which propagules can establish. The genotypes of propagules reflect the distribution of genotypes on the landscape. For our three-species model, the likelihood of disturbance per cell was 0.0001, individual disturbance events cleared one cell and the likelihood of

mutation was 0.001. Qualitative behaviours were not greatly sensitive to these parameters.

(b) *Models of more than three species*

Because the behaviour of the two rule structures is qualitatively identical, all models involving more than three species used the 'standard' rule structure. Thus, in updating the landscape, each cell C_x chooses a random neighbour C_y in its von Neumann neighbourhood, and C_y overgrows C_x with the probability $P[C_y > C_x] g_y$, where $P[C_y > C_x]$ defines the interaction outcome as the probability of S_y winning in an encounter with S_x , and g_y is the growth rate of S_y .

3. THREE-SPECIES INTRANSITIVE NETWORK: SELF-ORGANIZATION AND STABILITY

Regardless of initial cover and the spatial arrangement of recruits, both models self-organize to form colonies (groups of juxtaposed cells of identical state) at a characteristic scale (figure 1a,b). Although growth is indeterminate, colony size is asymptotic and defined by a dynamic balance between the interacting perimeter and non-interacting 'interior' (the perimeter : area ratio) of colonies and relative rates of overgrowth. Groups of adjacent colonies form incipient spirals, and there is a predictable temporal sequence of species at any point in space (figure 1d). The characteristic colony size is larger in the 'catalyst' model (figure 1b) than in the 'standard' model (figure 1a). This occurs because growth rates at the point where colonies of all three species meet are, on average, slightly accelerated in the 'catalyst' model, which exaggerates the incipient spiral and generates longer colony perimeters at these sites, which then propagate as larger colonies.

Contrary to early views (Buss & Jackson 1979), coexistence does not depend on equal growth rates and, moreover, the slowest grower eventually either codominates ('standard' model, figure 1e; 'catalyst' model, figure 1f) or dominates ('catalyst' model, figure 1c,g) the landscape. The behaviour whereby the slowest-growing species dominates or codominates space is a function of the indirect interaction in the intransitive network. If S_1 is the slowest-growing species then S_1 has a relatively small limiting effect on S_2 , allowing S_2 to more frequently overgrow and limit S_3 with a net positive, but indirect, effect on S_1 . More formally, the non-spatial form of the 'standard' CA model without disturbance is closely represented by difference equations of the form

$$N_{1,t+1} = \frac{N_{1,t}}{K} [K + g_1(K - N_{1,t} - N_{3,t}) - g_3 N_{3,t}],$$

with similar equations for N_2 and N_3 , where K is the total number of cells or 'carrying capacity' of the landscape, g_i is the growth rate of species i in the interval $t + 1$ and $N_{i,t}$ is the population size of species i at time t . As at equilibrium

$$N_1 = \frac{g_2}{g_1 + g_2 + g_3} K, N_2 = \frac{g_3}{g_1 + g_2 + g_3} K \text{ and } N_3 = \frac{g_1}{g_1 + g_2 + g_3} K,$$

it follows that if a species' growth rate decreases, its equilibrium population size will increase (and vice versa). A simi-

lar result can be derived from the Lotka–Volterra three-species model of competition (Gilpin 1975; May & Leonard 1975) and related mean-field models (Freaan & Abraham 2001).

Coexistence of species (i.e. persistence stability *sensu* Johnson & Mann (1988)) for a variety of growth rates and population sizes depends on spatial self-organizing in the system. In the non-spatial model, non-trivial equilibria are unstable (Johnson 1997) and depend on satisfying

$$\frac{g_1}{g_3} = \frac{N_{3,t}}{N_{2,t}}, \frac{g_2}{g_1} = \frac{N_{1,t}}{N_{3,t}}, \frac{g_3}{g_2} = \frac{N_{2,t}}{N_{1,t}}.$$

If the mean-field behaviour is simulated in the cellular model by randomizing the positions of each cell between each iteration of the model, then the cellular model is similarly unstable. Clearly, self-organizing to form colonies stabilizes the system. When cells of the same species S_i are aggregated into colonies, the portion of the colony margin where S_i is overgrowing its 'inferior' competitor is protected from being overgrown by its 'superior' competitor. Along this margin, the colony perimeter is protected on one side by other cells of the colony and on the other by the presence of the inferior competitor of S_i (as the inferior of S_i overgrows the superior of S_i).

While equal growth rates are not required for coexistence of species in the spatial models, these models become unstable if the differential in growth rates between fastest- and slowest-growing species becomes too large (figure 1h). The likelihood of coexistence of all three species decreases as the relative growth of the slowest grower declines below a critical threshold, which is *ca.* 50–60% of that of the fast-growing species (S_2, S_3) in the 'catalyst' model and 15–20% of the fast-growing species in the 'standard' model. Most importantly, the fast-growing S_3 that overgrows the slow-growing S_1 is always the first to go extinct because, given the pattern of self-organizing on the landscape, in overgrowing S_1 , S_3 is likely to meet its nemesis in S_2 . Once S_3 is lost from the system, the dynamic must always move to a monoculture of S_1 .

4. SELECTION FOR RESTRAINT IN GROWTH: TRADE-OFFS IN SELECTION AT THE LEVEL OF THE INDIVIDUAL AND COMMUNITY IN THE THREE-SPECIES SYSTEM

If the optimum strategy to maximize abundance is to grow more slowly than other species in the system, an obvious question is whether selection will act to reduce growth rates. We examined this question by assigning to initial recruits in the CA landscape a 'genotype' that defines their growth rate, allowing mutation of genotypes in the production of propagules (details in § 2) and examining changes in mean genotype for each species. Where a landscape is seeded with a single species, selection increases the mean growth rate (figure 2a, dashed line) by a straightforward process of replacement (i.e. on average, faster-growing genotypes will occupy a greater area of patches created by disturbance). When all species occur in the initial landscape, selection drives a 'Red Queen' dynamic in which the mean growth rates of all species increase to the maximum possible but each remains similar to the other (figure 2a, heavy and light lines). In this case, for a given initial mean growth rate, the rate of selec-

Figure 4. The effect of reversals in interaction outcome on selection for growth rate. Selection of growth rates of S_1 in a three-species system ($S_1 > S_2$, $S_2 > S_3$, $S_3 > S_1$, 'standard' model, 200×200 cells) is examined by initially seeding the landscape with a uniform range of genotypes for g_1 (mutation on $g_1 = 0$, disturbance = 0, recruitment = 0). In all cases $g_2 = g_3 = 0.2$ and is fixed. Each figure shows the change in relative frequency of genotypes of g_1 within 10 growth-rate classes. Relative frequency is indicated by a grey scale where white is 0% and black is 100% of the total individuals of S_1 . In (a) there are no reversals, but in (b) and (c) reversals can occur in interaction outcomes such that $P[S_1 > S_2] = 0.8$, $P[S_2 > S_1] = 0.2$, and similarly for interactions among S_2, S_3 ; S_3, S_1 . Initial genotype ranges are (a) $g_1 = 0.01-1.0$, (b) $g_1 = 0.01-0.7$, and (c) $g_1 = 0.01-0.8$. Selection for intermediate growth rates, as occurs when there are no reversals in interaction outcome (a), also arises when reversals do occur (b), providing that g_1 remains below a critical threshold defined as $\{g_1 P[S_1 > S_3]\} < \{g_3 P[S_3 > S_1]\}$ (in this example $g_3 P[S_3 > S_1] = 0.2 \times 0.8 = 0.16$, so the critical threshold for $g_1 = 0.8$). When this threshold is attained (c), there is rapid selection for the maximum possible values of g_1 .

tion for faster-growing genotypes increases with increasing variance in genotypes (figure 2a) because there are initially more cells with relatively high growth rates than when the variance in growth rate is low.

By contrast, if the growth rate of some species is fixed, selection operates in a different manner and acts to limit differences in growth rate among species (figure 2b). Selection initially increases growth of the unconstrained species, but mean growth is asymptotic at a rate less than the maximum possible. If initial mean growth rates of the unconstrained species are above this level, selection reduces mean growth to the asymptotic rate. This phenomenon reflects a balance between the opposing effects of selection at the individual level that acts to increase growth rates (figure 2a), and selection at the community level that acts to limit the difference between highest and lowest growth rates (figure 1h). Selection occurs at the community level in that different local regions ('sub-communities') of the landscape demonstrate different community-level properties, dependent on local differences in growth rates among species, and there is differential survival of local sub-communities. The community level property that differs among local regions is persistence stability, *sensu* Johnson & Mann (1988). If the magnitude of the difference in growth rates among species becomes too large in local regions of the landscape, these

Figure 5. Species dynamics in a three-species system ($S_1 > S_2$, $S_2 > S_3$, $S_3 > S_1$, 'standard' model, 200×200 cells) but where reversals in interaction outcomes occur with probability $P = 0.2$, i.e. $P[S_1 > S_2] = 0.8$, $P[S_2 > S_1] = 0.2$, and similarly for interactions among S_2, S_3 ; S_3, S_1 . Growth rates $g_2 = g_3 = 0.15$ and fixed, while $g_1 = 0.1-0.2$ and are allowed to evolve with $P[\text{mutation}] = 0.01$ and mutation step $= \pm 0.02$. In this model, disturbance creates empty spaces on the landscape ($P[\text{disturbance}] = 0.0001$, disturbance patch size = four cells) and each species recruits to empty sites with equal probability. Growth genotypes for recruits of S_1 are taken from a uniform distribution over whatever range of genotypes has existed in the system. The phase shift in relative abundances of S_1 and S_3 at ca. 28 000 generations reflects the point where g_1 has evolved to be sufficiently high (in this example where $g_1 > 0.6$) so that, on average, the likelihood of $S_1 > S_3$ ($= P[S_1 > S_3] g_1 = 0.2 g_1$) exceeds that of $S_3 > S_1$ ($= P[S_3 > S_1] g_3 = 0.8 g_3 = 0.8 \times 0.15 = 0.12$).

sub-communities become locally unstable and the fast-growing genotypes are lost (figure 3).

5. SELECTION FOR RESTRAINT IN GROWTH: MORE COMPLEX SYSTEMS

Is the behaviour of selection for restraint in growth more general than the simple three-species system? Relative to more natural systems, the three-species system examined above is over simplistic, in that interaction outcomes are binary (for each species pair there is a consistent 'winner' and 'loser'), and only three species form the interaction network. Spatial competition systems in nature are likely to be more speciose, and interaction outcomes are unlikely to be binary (see references in § 1, also Chornesky (1989) and Lang & Chornesky (1990)). For example, in examining more than 8900 interactions among 173 species in shallow marine benthic assemblages on the Great Barrier Reef (GBR) (Johnson 2002) and more than 6800 interactions among 46 species in a shallow marine temperate fouling community (Dunstan & Johnson 2002a,b), in cases of six or more replicate interactions of a given species pair there was not a single occurrence where one species consistently overgrew another. In this section we consider separately the effect on evolution of growth rates of (a) 'reversals' in interaction outcome and (b) expanding the system to more than three species, before (c) examining selection on growth in systems with both large numbers of species and interaction networks containing reversals.

Figure 6. Examples of selection on growth rate in 5- to 12-species systems without reversals in interaction outcomes ('standard' model). In all cases (a)–(j), growth-rate genotypes of the species of interest is initially uniform over the range 0–1, mutation on growth = 0, growth rates of all other species = 0.2, disturbance = 0, recruitment = 0. The initial spatial distribution of all species is random. Each figure depicts selection on growth rates as the change in relative frequency of genotypes of the species of interest within 10 growth-rate classes (as in figure 4). (a)–(d) are for a five-species system ($S_1 > S_2, S_4$; $S_2 > S_3$; $S_3, S_5 > S_1$; $S_4 > S_5$; landscape 200×200 cells) and show that selection for intermediate growth rates is stronger in S_1 ((a) and (b) are examples from different simulations) than in S_2 ((c); equivalently S_4) and S_3 ((d); equivalently S_5). Selection for intermediate growth is also evident in: (e) which is for a different five-species system ($S_1 > S_2, S_3$; $S_2 > S_3, S_4 \dots S_5 > S_1, S_2$; landscape 200×200 cells) depicting selection in any species S_n ; (f) a seven-species system ($S_1 > S_2, S_3$; $S_2 > S_3, S_4 \dots S_7 > S_1, S_2$; landscape 300×300 cells) depicting selection in a randomly selected species S_n , which in this example goes extinct at ca. 7800 generations; and in (g), another seven-species system ($S_1 > S_2, S_3, S_4$; $S_2 > S_3, S_4, S_5 \dots S_7 > S_1, S_2, S_3$; landscape 300×300 cells) depicting selection in S_n . (h) shows selection in a randomly selected species S_n in a 12-species system ($S_1 > S_2, S_3, S_4$; $S_2 > S_3, S_4, S_5 \dots S_{12} > S_1, S_2, S_3$; landscape 400×400 cells). Selection for intermediate growth does not arise in non-spatial (simulated mean-field), but otherwise identical, versions of these models. The examples in (i) and (j) show rapid selection for the fastest-growing genotypes, leading to rapid extinction, in mean-field simulations of the seven-species systems depicted in (f) and (g), respectively.

(a) The effect of reversals

Selection for intermediate growth can also arise in the three-species system with 'reversals' in interaction outcome (i.e. where $P[S_x > S_y]$ and $P[S_y > S_x] > 0$), but under more limiting circumstances (figures 4 and 5). In this system, the likelihood of an individual of species S_x overgrowing an individual of S_y is the product of the interaction outcome ($= P[S_x > S_y]$) and the growth-rate genotype of that individual of S_x ($= g_x$). In a three-species system with reversals in which $P[S_x > S_y] > P[S_y > S_x]$ (but where $P[S_x > S_y]$ and $P[S_y > S_x] > 0$), selection for intermediate growth rate in S_y (figure 4b) arises in a similar way as occurs in the three-species system without reversals, but only if growth rates do not evolve to the point where the net likelihood of S_y overgrowing S_x exceeds that of S_x overgrowing S_y (i.e. provided that $P[S_x > S_y] g_x > P[S_y > S_x] g_y$). Once this threshold for g_y is exceeded, selection acts to increase growth rate (g_y) to

the maximum possible (figure 4c), and S_y , which was previously relatively uncommon, comes to dominate the landscape (figure 5). Thus, reversals in interaction outcome in the three-species system do not change the qualitative pattern of selection for intermediate growth rates, unless the mutation rate on the growth genotype is elevated to the point where the production of new rapidly-growing genotypes overwhelms the capacity of community-level selection to remove them. If this occurs and the critical growth threshold is attained, the evolutionary attractor changes to become the fastest possible growth rate.

(b) The effect of increasing species richness

Selection for intermediate growth rates is not a unique feature of the three-species intransitive system, but also arises in other systems containing intransitive structures (examples in figure 6). Depending on the network structure, selection for intermediate (or even low) growth rates

may be stronger for some species than others in the same system (cf. figure 6*a,b* versus *c,d*). Different network structures of the same number of species can yield similar (cf. figure 6*c,d* versus *e*) or dissimilar (cf. figure 6*f* versus *g*) selection patterns. Where there is a large number of 'stand-offs' in the competition network, spatial patterns develop in which groups of species that stand off with each other form spatially stable aggregations. When this occurs, a broad range of genotypes are able to persist locked within static structures on the landscape (figure 6*f,h*).

The effect of emergent spatial structure on these patterns can be removed by randomizing the position of all individuals on a landscape between iterations of the rules. This simulates the mean-field situation. Notably, in non-spatial mean-field counterparts of systems in which selection for moderate growth is evident in the spatial model, selection for restraint on growth never arises. In all mean-field simulations there is rapid selection towards the maximum growth rate, which usually results in rapid extinction of the evolving species (cf. figure 6*f,g* versus *i,j*). It is clear that the phenomenon of restraint in the evolution of growth rates in these systems depends fundamentally on the self-organized spatial structures.

(c) Selection for intermediate growth in speciose systems with reversals in interaction structure

We developed 20-species models in which all species interact with all others, and in which the outcome of interactions between each pair of species S_x and S_y is defined by the probability of a win, loss or stand-off in the interaction. These probabilities are determined randomly and are fixed for each model run. While most species in these systems show selection for rapid growth (figure 7*a*), there are always some species (typically 4–6 of the 20) where selection for intermediate growth rates is clearly evident (figure 7*b*). Given the complex nature of indirect-interaction pathways in these systems, it is not possible to identify the exact mechanism that gives rise to this behaviour as is possible in the three-species system (for each species there are 19 direct interactions and *ca.* 1.74×10^{16} indirect interactions with other species). In marked contrast, for the same species, equivalent mean-field simulations always show rapid evolution towards the maximum possible growth rate, and rapid extinction of the species (figure 7*c*). Notably, extinction rates in systems in which intransitive structures are likely to arise are much lower than in systems with networks tending to a more hierarchical structure (figure 8). Extinction rates are much higher in non-spatial than in spatial versions of these models (figure 8).

6. DISCUSSION AND CONCLUSION

Our results indicate that selection for restraint in growth can arise in complex species-rich systems in which reversals occur in interaction networks, just as arises in simple three-species systems with no reversals in interactions. The phenomenon depends on spatial-self-structuring of species' distributions and, by inference from the mechanism identified in the three-species system, indirect interactions arising from intransitive structures in the interaction network. Spatial self-structuring generates local assemblages or 'sub-communities' on the landscape with different spatial and stability properties on which

Figure 7. Examples of selection on growth rate in a 20-species system where the network topology is determined randomly and reversals are permitted (i.e. each species has a fixed random probability between 0–1 of a win, loss or stand-off in interacting with each other species, such that $P[\text{win}] + P[\text{loss}] + P[\text{stand-off}] = 1$). Growth-rate genotypes of the species of interest is initially uniform over the range 0–1, mutation on growth = 0, growth rates of all other species = 0.2, disturbance = 0, recruitment = 0. The initial spatial distribution of all species is random. Each figure depicts selection on growth rates as the change in relative frequency of genotypes of the species of interest within 10 growth-rate classes (as in figure 4). In spatial models most species show selection for the fast-growing genotypes (*a*), but there are always several species where selection for intermediate growth is evident (*b*) (although in this example a fast-growing genotype is able to persist to 4000 generations). Species that tend to intermediate growth in spatial models (*b*) never show this behaviour in equivalent mean-field models (*c*), in which there is always rapid selection for the fastest-growing genotype until the species goes extinct.

selection may act. The mechanism that limits competitive ability (in this case, growth rate) does not explicitly require trade-offs in resource allocation.

These findings suggest that in communities of sessile colonial organisms in which complex intransitivities in the interaction network occur, selection may favour moderate competitive abilities. This tenet is supported by our observations of interactions between 173 sessile benthic species on the GBR that did not identify competitively dominant species (Johnson 2002), and is in keeping with other recent results for GBR reefs (Tanner *et al.* 1994, 1996). This notion is contrary to the more established view that competitive dominants will displace other species in the absence of disturbance (Connell 1978). The commonness of intransitivities in marine hard-bottom communities but not terrestrial ones (see § 1) and concomitant restraint in the evolution of competitive abilities may be a partial explanation for the constancy of composition of coral-reef communities over much longer periods in geological time (Jackson 1992; Pandolfi 1996) than occurs in terrestrial communities (cf. Graham & Grimm 1990; Overpeck *et al.* 1991; Webb & Bartlein 1992; Spear *et al.* 1994).

It has been argued that because indirect interactions are so important in the dynamics of many communities (Stone & Roberts 1991; Wootton 1994; Menge 1995), they should have strong effects on the evolution of species' traits and interspecific interactions (Miller & Travis 1996). The simple three-species system presented here shows

Figure 8. Extinction rates in 20-species models with different types of randomly constructed interaction networks. Results are means from Monte Carlo simulations of $n = 20$ runs (each run a different random network). In all cases, growth rates of all species are fixed at the maximum ($= 1.0$) on a landscape size of 400×400 . The network topologies are (i) random with reversals (each species has a fixed random probability between 0–1 of a win, loss or stand-off in interacting with each other species); (ii) random without reversals (each species has a probability of 0 or 1, with equal likelihood, of winning against each other species); and (iii) random hierarchical (each species has a fixed random probability between 0–1 of a win, loss or stand-off in interacting with each other species, but constrained such that in rounding values of $P[\text{win}]$, they describe a linear, or transitive, network hierarchy). Solid lines show results for spatial models, and dotted lines for non-spatial (simulated mean-field) models. In all cases, $P[\text{win}] + P[\text{loss}] + P[\text{stand-off}] = 1$ for each species in its interaction with each other species.

clearly that, provided that the system spatially self-organizes to form multicellular colonies, the evolution of growth rates is dependent on the indirect effects of a third species limiting the population of one species overgrowing another. It is apparent that similar mechanisms arise in the more complex systems. We conclude that the rich array of indirect interactions in complex spatially-organized systems with high levels of intransitivity is likely to yield an important substrate for evolution and show strong interdependencies in the evolution of species' traits.

The trade-off between individual- and community-level selection is an important aspect of the results. In our models, selection at the individual level acts to increase growth rate in all cases, but selection at the community level can limit growth rates to intermediate levels. This phenomenon is community-level selection because the trait on which selection is acting (i.e. persistence stability of the community) is an emergent community-level property, and the result reflects differential survival of local 'sub-communities' on the landscape (see Johnson & Boerlijst 2002). The important point is that restricting growth to intermediate levels imparts no benefit to the individual in its local environment, nor is there any benefit at the population level. The benefit arises only at the community level. Community-level selection has similarly been identified in spatial models of 'communities' of catalytic molecules and in several host-parasite and other consumer-prey systems (reviewed in Johnson & Boerlijst (2002)). In all of these examples, community-level selection is depen-

dent on emergent spatial structure. The models reported here are the first, to our knowledge, to note the phenomenon in competition systems.

We thank Paulien Hogeweg for discussion at the beginning and Maarten Boerlijst, Martin Nowak, Ian Owens and Lewis Stone for comments and discussion at the end. Ling Shi programmed the model, and other technical support was provided by Lorraine Longmore and John McKirdy. The work was supported by an ARC large grant to C.J.

REFERENCES

- Boerlijst, M. C. & Hogeweg, P. 1991 Spiral wave structure in pre-biotic evolution: hypercycles stable against parasites. *Physica D* **48**, 17–28.
- Buss, L. W. 1986 Competition and community organisation on hard surfaces in the sea. In *Community ecology* (ed. J. Diamond & T. J. Case), pp. 517–536. New York: Harper and Row.
- Buss, L. W. 1990 Competing within and between encrusting clonal invertebrates. *Trends Ecol. Evol.* **5**, 352–356.
- Buss, L. W. & Jackson, J. B. C. 1979 Competitive networks nontransitive competitive relationships in cryptic coral reef environments. *Am. Nat.* **113**, 223–234.
- Chornesky, E. A. 1989 Repeated reversals during spatial competition between corals. *Ecology* **70**, 843–855.
- Comins, H. N., Hassell, M. P. & May, R. M. 1992 The spatial dynamics of host-parasitoid systems. *J. Anim. Ecol.* **61**, 735–748.
- Connell, J. H. 1978 Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310.
- Dieckmann, U., Law, R. & Metz, J. A. J. 2000 *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge University Press.
- Dunstan, P. & Johnson, C. 2002a Competition coefficients in a marine epibenthic assemblage depend on spatial structure. *Oikos* (In the press.)
- Dunstan, P. K. & Johnson, C. R. 2002b Predicting global dynamics from local interactions: spatial models predict complex features of marine epibenthic communities. *Ecology* (Submitted.)
- Frean, M. & Abraham, E. R. 2001 Rock-scissors-paper and the survival of the weakest. *Proc. R. Soc. Lond. B* **268**, 1323–1327. (DOI 10.1098/rspb.2001.1670.)
- Gilpin, M. E. 1975 Limit cycles in competition communities. *Am. Nat.* **109**, 51–60.
- Grace, J. B., Guntenspergen, G. R. & Keough, J. 1993 The examination of a competition matrix for transitivity and intransitive loops. *Oikos* **68**, 91–98.
- Graham, R. W. & Grimm, E. C. 1990 Effects of global climate change on the patterns of terrestrial biological communities. *Trends Ecol. Evol.* **5**, 289–292.
- Hassell, M. P., Comins, H. N. & May, R. M. 1991 Spatial structure and chaos in insect population dynamics. *Nature* **353**, 255–258.
- Jackson, J. B. C. 1992 Pleistocene perspectives on coral reef community structure. *Am. Zool.* **32**, 719–731.
- Johnson, C. R., Dunstan, P. K. & Wilson, H. B. 2002 Coral reef community structure and species associations predicted from local processes. (In preparation.)
- Johnson, C. R. 1997 Self-organising in spatial competition systems. In *Frontiers in ecology. Building the links* (ed. N. Klomp & I. Lunt), pp. 245–263. Oxford: Elsevier. Also at <http://life.csu.edu.au/esa/esa97/papers/johnson/johnson.htm>.
- Johnson, C. R. & Boerlijst, M. C. 2002 Selection at the level of the community: the importance of spatial structure. *Trends Ecol. Evol.* **17**, 83–90.
- Johnson, C. R. & Mann, K. H. 1988 Diversity patterns of

- adaptation, and stability of Nova Scotian kelp beds. *Ecol. Monogr.* **58**, 129–154.
- Kay, A. M. & Keough, M. J. 1981 Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. *Oecologia* **48**, 123–130.
- Keough, M. J. 1984 Effects of patch size on the abundance of sessile marine invertebrates. *Ecology* **65**, 423–437.
- Lang, J. C. & Chornesky, E. A. 1990 Competition between scleractinian reef corals—a review of mechanisms and effects. In *Coral reefs. Ecosystems of the world*, vol. 25 (ed. Z. Dubinsky), pp. 209–252. Amsterdam: Elsevier.
- May, R. M. & Leonard, W. J. 1975 Nonlinear aspects of competition between three species. *Soc. Ind. Appl. Math. J. Appl. Math.* **29**, 243–253.
- Menge, B. A. 1995 Indirect effects in marine rocky intertidal communities: patterns and importance. *Ecol. Monogr.* **65**, 21–74.
- Miller, T. E. & Travis, J. 1996 The evolutionary role of indirect effects in communities. *Ecology* **77**, 1329–1335.
- Nowak, M. A. & May, R. M. 1992 Evolutionary games and spatial chaos. *Nature* **359**, 826–829.
- Overpeck, J. T., Bartlein, P. J. & Webb, T. 1991 Potential magnitude of future vegetation change in eastern North America: comparisons with the past. *Science* **254**, 692–695.
- Pandolfi, J. M. 1996 Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: constancy during global change. *Paleobiology* **22**, 152–176.
- Rinkevich, B., Shashar, N. & Liberman, T. 1993 Nontransitive xenogenic interactions between four common Red Sea sessile invertebrates. *Proc. 7th Int. Coral Reef Symp.* **2**, 833–839.
- Russ, G. 1982 Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia* **53**, 12–19.
- Shipley, B. 1993 A null model for competitive hierarchies in competition matrices. *Ecology* **74**, 1693–1699.
- Spear, R. W., Davis, M. G. & Shane, L. C. 1994 Late Quaternary history of low- and mid-elevation vegetation in the White Mountains of New Hampshire. *Ecol. Monogr.* **64**, 85–109.
- Stone, L. & Roberts, A. 1991 Conditions for a species to gain advantage from the presence of competitors. *Ecology* **72**, 1964–1972.
- Tanner, J. E. 1993 Experimental analysis of digestive hierarchies in coral assemblages. *Proc. 7th Int. Coral Reef Symp.* **1**, 569–574.
- Tanner, J. E., Hughes, T. P. & Connell, J. H. 1994 Species coexistence, keystone species, and succession: a sensitivity analysis. *Ecology* **75**, 2204–2219.
- Tanner, J. E., Hughes, T. P. & Connell, J. H. 1996 The role of history in community dynamics: a modelling approach. *Ecology* **77**, 108–117.
- Webb, T. & Bartlein, J. 1992 Global changes during the last 3 million years: climatic controls and biotic responses. *A. Rev. Ecol. Syst.* **23**, 141–173.
- Wootton, J. T. 1994 The nature and consequences of indirect effects in ecological communities. *A. Rev. Ecol. Syst.* **25**, 443–466.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.