

REPORT

Heteromyopia and the spatial coexistence of similar competitors

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Abstract

Most spatial models of competing species assume symmetries in the spatial scales of dispersal and interactions. This makes analysis tractable, and has led to the conclusion that segregation of species in space does not promote coexistence. However, these symmetries leave parts of the parameter space uninvestigated. Using a moment-approximation method, we present a spatial version of the Lotka–Volterra competition equations to investigate effects of removing symmetries in the distances over which individuals disperse and interact. Some spatial segregation of the species always comes about due to competition, and such segregation does not necessarily lead to coexistence. But, if interspecific competition occurs over shorter distances than intraspecific competition (heteromyopia), spatial segregation becomes strong enough to promote coexistence. Such coexistence is most likely when the species have similar dynamics, in contrast to the competition–colonization trade-off that requires large competitive differences between species.

Keywords

Coexistence, competition, dispersal distance, interaction distance, Lotka–Volterra, moment dynamics, spatial structure.

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INTRODUCTION

Opinions differ on how space affects coexistence of competing species. Traditionally, spatially localized competition and dispersal are thought to make it easier for species to coexist. One reason is that conspecifics tend to develop into clusters segregated from other species, thereby increasing the importance of intraspecific competition relative to interspecific competition (Weiner & Conte 1981; Pacala & Levin 1997; Pacala 1997; Murrell *et al.* 2001). Pacala (1997, p. 553) called coexistence generated in this way the spatial segregation hypothesis. Another reason is that weaker competitors may compensate by exploiting gaps through better colonization, the so-called competition–colonization trade-off (Hutchinson 1951; Skellam 1951; Levins & Culver 1971; Horn & MacArthur 1972; Hastings 1980; Tilman 1994; Holmes & Wilson 1998).

However, the role of spatial segregation in promoting coexistence has been challenged (Takenaka *et al.* 1997; Neuhauser & Pacala 1999; Neuhauser 2001). In particular, a mathematical analysis of two competing species on a spatial lattice has led to the surprising conclusion that coexistence is harder to achieve than in the non-spatial case (Neuhauser

& Pacala 1999; Neuhauser 2001). A possible reason is that, although species separate into clusters, the clusters are dynamic, and events at cluster boundaries may determine the outcome, irrespective of the fact that most contacts are with conspecifics (Chesson & Neuhauser 2002). Even if spatial processes do promote coexistence, there remains a question as to how important these processes are relative to other non-spatial ones (Adler & Mosquera 2000; Chesson & Neuhauser 2002). For instance, coexistence of an unlimited number of species due to a competition–colonization trade-off (Tilman 1994) stems from a stepwise asymmetric model of competition rather than from space (Adler & Mosquera 2000); the number of coexisting species is greatly reduced by making the competition function smooth (Geritz *et al.* 1999; Adler & Mosquera 2000).

One reason for the continuing debate about space is the great complexity of spatial dynamical systems: to describe neighbourhood-dependent dispersal and competition between two species, six independent spatial functions are needed in addition to the usual non-spatial parameters (Law & Dieckmann 2000; see also below). Faced with such complexity, ecologists and mathematicians understandably make simplifying assumptions to achieve analytical results

and thereby uncover no more than part of the potential behaviour. Common assumptions are that parameters of neighbourhoods over which individuals compete are the same, irrespective of species, or that dispersal and competition neighbourhoods are the same size (Bolker & Pacala 1999; Neuhauser & Pacala 1999). Similar assumptions apply in a variety of lattice models of single species and two competing species; these often have interactions among adjacent cells, and dispersal that is either global to all cells or local to adjacent cells (e.g. Weiner & Conte 1981; Harada & Iwasa 1994; Takenaka *et al.* 1997).

Removing neighbourhood symmetries may have profound consequences. For instance, an exploratory simulation suggested that coexistence could then occur as a direct result of the spatial structure generated by competition (Murrell *et al.* 2002). This paper examines in more detail some effects of removing neighbourhood symmetries on the outcome of competition between two species. In particular, we offer a solution to opposing viewpoints about the spatial segregation hypothesis by showing that space can promote coexistence, but only if the distance over which individuals sense their heterospecific neighbours is shorter than the distance over which they sense their conspecific neighbours. Building on the metaphor of the plant's-eye view of the community (Turkington & Harper 1979), we propose the term *heteromyopia* for individuals that are 'short-sighted' in sensing neighbours of other species relative to their own.

MODEL

To build on familiar ground, we take a spatial extension of the well-known, two-species, Lotka–Volterra competition equations, with mean-field dynamics

$$\dot{N}_1 = (b_1 - d_1)N_1 - d'_{11}N_1^2 - d'_{12}N_1N_2 \quad (1a)$$

$$\dot{N}_2 = (b_2 - d_2)N_2 - d'_{21}N_1N_2 - d'_{22}N_2^2, \quad (1b)$$

where N_i is the mean density (first spatial moment) of species i . Here b_i and d_i are density-independent per capita rates of, respectively, birth and death of species i , and $d'_{ij}N_j$ is an additional per capita death rate of species i caused by species j at its current density [it would be equally possible for there to be a neighbour-dependent effect on fecundity (e.g. Bolker & Pacala 1999)]. This slightly unfamiliar birth–death parameterization is used because, in a spatial model, such as the one below, births and deaths can affect spatial structure in quite different ways.

Our spatial extension of the Lotka–Volterra model involves a large homogeneous, two-dimensional, spatially continuous landscape (rather than a lattice). Individuals of two species occur at points in this space; competition is confined to individuals within some neighbourhood, and

individuals disperse over limited distances at birth. In such a setting, spatial structure can change over time as individuals disperse and interact. To deal with these changes, at the very least, one needs to track second-order spatial structure as well as the mean densities; for this purpose we use a spatial covariance function of species i and j , known as the pair density function or second spatial moment, and written as $C_{ij}(\xi)$ for the density of pairs with j displaced in space from i by an amount $\xi = (\xi_1, \xi_2)$ in two-dimensional space [see the Appendix for a formal definition of $C_{ij}(\xi)$]. A dynamical system of the first and second moments has been derived from a stochastic individual-based model (IBM) (Dieckmann & Law 2000), and a similar model with density-dependent fecundity was described and analysed by Bolker & Pacala (1999). The dynamical system gives the rate of change of average densities and spatial structure in so far as this is described by the second spatial moments. We refer to the dynamical system as the spatial Lotka–Volterra (SLV) model. With the second-order information, the dynamics of the system below are close to those of the underlying spatial stochastic process (but the reader should bear in mind that spatial structures needing higher-order moments could still be needed in other circumstances).

We concentrate on equations for the dynamics of mean densities below; the full dynamical system also requires equations for dynamics of pair densities (eqn A3), as well resolving a technical issue of a moment closure, as described in the Appendix. The rates of change of the mean densities are written as

$$\dot{N}_1 = (b_1 - d_1)N_1 - d'_{11}I_{11} - d'_{12}I_{12} \quad (2a)$$

$$\dot{N}_2 = (b_2 - d_2)N_2 - d'_{21}I_{21} - d'_{22}I_{22}, \quad (2b)$$

where $I_{ij} = \int w_{ij}(\xi) C_{ij}(\xi) d\xi$ is an integral over all displacements ξ describing how, on the average, the density of species j appears to species i (see also Bolker & Pacala 1999, equations 3 and 4). The integral depends first on the spatial structure given by the pair density $C_{ij}(\xi)$, and second on the attenuation of competition with increasing separation ξ of j from i , given by a function $w_{ij}(\xi)$, a so-called competition kernel (Bolker *et al.* 2000, p. 392). Competition kernels are normalized to make $\int w_{ij}(\xi) d\xi = 1$, and give the *relative* weight of an individual of j displaced by ξ from i ; thus, the faster the attenuation of competition with distance, the greater the relative importance of competition with close neighbours. The integration then adds up the contributions made by neighbours at all distances.

Equations 2 differ from the mean-field eqn 1 only in having the integrals I_{ij} carrying all the information needed to determine how (second-order) spatial structure affects the winners and losers of competition. If $I_{ij} > N_i N_j$, spatial structure amplifies the effect of j on i ; if $I_{ij} < N_i N_j$, spatial structure has the reverse effect. 'Stirring' the community to

remove all spatial structure, gives $I_{ij} = N_i N_j$, and returns the dynamics of the mean-field Lotka–Volterra equations. Thus the integrals deal only with effects of spatial structure and are quite distinct from the parameter d'_{ij} which describes how deleterious the effect of a j individual is on an i individual.

The four competition kernels $w_{ij}(\xi)$ ($i, j = 1, 2$) affect spatial structure, but do not fully determine it: spatial structure also depends on the distances over which offspring disperse, given by two dispersal kernels $m_i(\xi)$ ($i = 1, 2$). These kernels are not in eqns 2, because they do not lead to change in density (they simply redistribute individuals across space), but they do appear in the dynamics of the pair densities (see Appendix eqn A3), and can ultimately have important effects on the mean densities through the integrals in eqns 2. The kernels must be made explicit for numerical analysis; we use bivariate Gaussian functions:

$$w_{ij}(\xi) = \frac{1}{W_{ij}} \cdot \exp\left(-\frac{|\xi|^2}{2(s_{ij}^w)^2}\right) \quad (3a)$$

$$m_i(\xi) = \frac{1}{M_i} \cdot \exp\left(-\frac{|\xi|^2}{2(s_i^m)^2}\right), \quad (3b)$$

each with one parameter that determines the width of the function; together there are then six spatial parameters (s_{ij}^w , s_i^m for all i, j), counterparts of the six non-spatial parameters in eqns 1. A small value of s_{ij}^w means that competition is concentrated in small neighbourhoods (compare Figs 1a,b); a small value of s_i^m means that most offspring disperse only a short distance from their parents. The kernels are truncated at three times the parameter value (the effect this has on the dynamics is very small), and normalized so that their integrals are one; W_{ij} and M_i are the normalization constants.

Below, it helps to understand that local competition and dispersal operate on spatial structure in opposing ways. On the one hand, local intraspecific competition acts to reduce the occurrence of conspecifics at short distances, because the death rate increases the closer they are together (making $C_{ii}(\xi)$ smaller for small $|\xi|$); in the same way, local interspecific competition makes $C_{ij}(\xi)$ smaller for small $|\xi|$. On the other hand, local dispersal of individuals of species i acts to increase aggregation of i because offspring tend to occur close to their parents (local dispersal makes $C_{ii}(\xi)$ larger for small $|\xi|$). Within species ($i = j$), these opposing forces lead eventually to a characteristic spatial structure which may be aggregated or overdispersed (Law *et al.* 2002). But there is no force corresponding to local dispersal holding the different species together ($i \neq j$) – instead they drift apart to some extent. This tendency for separation is both important and problematic: important because spatial segregation is implicated in the spatial coexistence of species

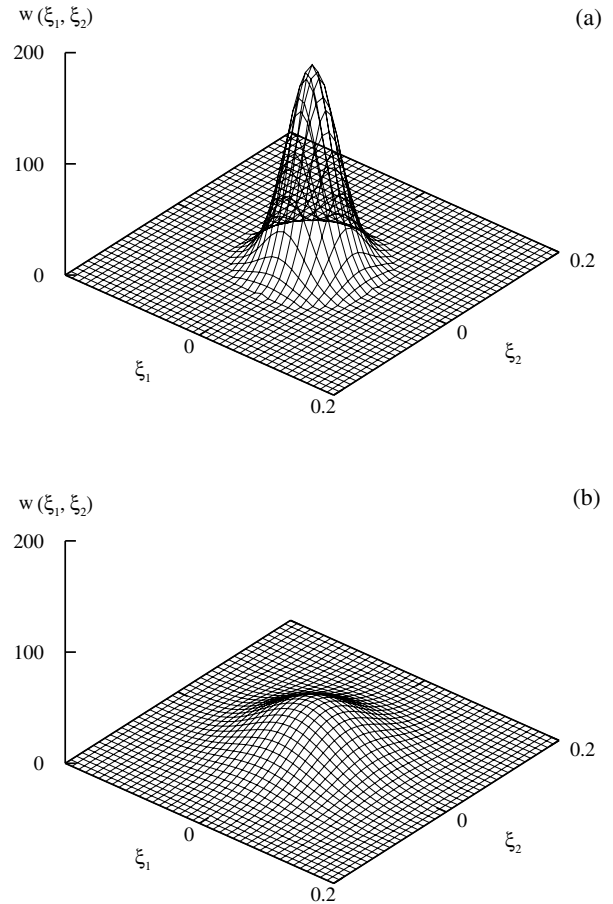


Figure 1 Two competition kernels with contrasting parameter values: (a) $s^w = 0.06$, (b) $s^w = 0.03$.

(Pacala & Levin 1997; Pacala 1997), and problematic because large-scale spatial correlations may develop, making numerical results from stochastic processes and deterministic approximations unreliable.

To avoid numerical errors, we use an invasion analysis to test for coexistence and exclusion, rather than trying to examine the state of the community after a long time period has elapsed. The analysis uses numerical integration of eqns 2 and A3, and proceeds as follows. (1) Allow the resident species i to get close to equilibrium density \tilde{N}_i and spatial structure $\hat{C}_{ii}(\xi)$. (This presupposes that there is a single nontrivial equilibrium; extensive simulations give no grounds to doubt this, but a formal proof is not available.) (2) Introduce a low density of the other species j at random over space. (3) Determine j 's fate by numerical integration of eqns 2 and A3, where sufficient time is allowed for j to relax from its initial random pattern to its spatially structured state.

The steps above amount to finding numerically the sign of the per capita rate of increase f_j of species j ; from eqns 2, this is

$$f_j = b_j - d_j - \frac{d'_{ji}\tilde{I}_{ji}}{N_j} - \frac{d'_{jj}\tilde{I}_{jj}}{N_j}. \quad (4)$$

where $\tilde{I}_{ji}, \tilde{I}_{jj}$ the integrals are evaluated after spatial structure of species j has developed. The last two terms on the right hand side are death rates that depend on the density of neighbours; unlike the mean-field model, interactions among individuals of j matter even when j is rare, because aggregations may develop at an early stage due to limited dispersal. Interpretation of the per capita rates of increase follows the standard form:

$f_1 > 0, f_2 > 0$ implies coexistence
 $f_1 < 0, f_1 < 0$ implies founder control
 $f_1 > 0, f_1 < 0$ implies species 1 excludes species 2
 $f_1 < 0, f_2 > 0$ implies species 2 excludes species 1.

Although it may be debated as to whether the term 'coexistence' is appropriate for two species which may be separating out in space, the spatial structure within areas occupied by each species would nonetheless remain invisable by the other species. Note also that a formal proof that invasion behaviour is enough to decide the dynamics in between is not available but, in the case of exclusion, our checks by numerical integration are consistent with the invasion inequalities above.

In view of the large number of parameters involved in the SLV model (six non-spatial and six spatial parameters), we give the species the same parameter values, except those under investigation; this makes it possible to see the direct effect of particular parameters in tilting the balance towards coexistence or exclusion of species. We check robustness of the results by making small random perturbations to all parameter values.

RESULTS

Heteromyopia and coexistence

Tests using numerical invasion analysis show that coexistence of two competing species is achieved if heterospecifics interact over shorter distances than conspecifics. To demonstrate this, we hold the non-spatial parameters of the species and their dispersal kernels at the same values ($b_i = b$, $d_i = d$, $d'_{ij} = d'$, $m_i(\xi) = m(\xi)$, for all i and j), allowing only the parameters of the competition kernels to differ such that $s''_{11} = s''_{22} = s''_c$, $s''_{12} = s''_{21} = s''_h$. The condition for species j eventually to increase when rare is then, from eqn 4:

$$\frac{\hat{I}_{ii}}{\hat{N}_i} > \frac{\tilde{I}_{ji} + \tilde{I}_{jj}}{N_j}. \quad (5)$$

The term on the left-hand side of inequality 5 is the average density of neighbours of an individual of the resident species i ,

after allowing for the weight attached to neighbours at different displacements; when species j is sufficiently rare, this weighted local density is unaffected by j . The term on the right-hand side is the average density of neighbours of an individual of the introduced species j . Both species i and j can contribute to this density: species i because it is common, and species j because local dispersal generates clusters of conspecifics, even though its average density is low.

The outcome of the invasion analysis is very simple. As shown in Fig. 2(a), inequality 5 holds for both species, i.e. the species coexist, as long as $s''_h < s''_c$. We suggest the term *heteromyopia* for this difference in the competition kernels, because individuals in some way 'see' neighbours of other species over shorter distances than those of their own species. It is important to realize that coexistence achieved in this way depends solely on how spatial structure affects neighbourhood densities: throughout the effect of a given density of neighbours on j 's per capita death rate remains unchanged at the value d' . The mechanism by which coexistence is achieved is therefore quite different from that of the mean-field model, although in both cases the effect is to make intraspecific competition stronger than interspecific competition. Coexistence caused by heteromyopia is robust in the sense that it remains when small random changes are made to other parameters of the SLV model; it is therefore not dependent on the exact symmetry used in Fig. 2.

To illustrate the dynamics, some paths of population density with different parameter values of the competition kernel are shown in Figs 2(b,c,d). All three planes show a rapid relaxation of paths towards a manifold of intermediate population density. If $s''_h = s''_c$ (Fig. 2b), the community has no tendency to move one way or the other close to the manifold. If $s''_h < s''_c$ (Fig. 2c), the trajectories are drawn towards an interior state, permitting the species to coexist. If $s''_h > s''_c$ (Fig. 2d), the trajectories move out to one or other boundary, and the winning species is determined by the initial densities, i.e. there is founder control, as in the mean-field Lotka–Volterra model. Notice that, because the paths are projections of a higher-dimensional dynamical system on to a two-dimensional plane in this figure and the ones below, it is quite possible for paths to cross one another.

The dynamical system is an approximation to a stochastic IBM in which individuals give birth, disperse and die at rates that depend on their neighbourhoods. [The stochastic process was described in Law & Dieckmann (2000).] As an independent check on coexistence by heteromyopia, we ran 100 realizations of the stochastic process with parameters and initial values as in Figs 2(c,d). The average of the stochastic realizations are given in Figs 2(e,f), respectively. Although the ecological signal is quite weak close to the manifold, coexistence clearly applies in Fig. 2(e) and founder control in Fig. 2(f). For the most part, paths of the dynamical system approximate closely to the IBM, although

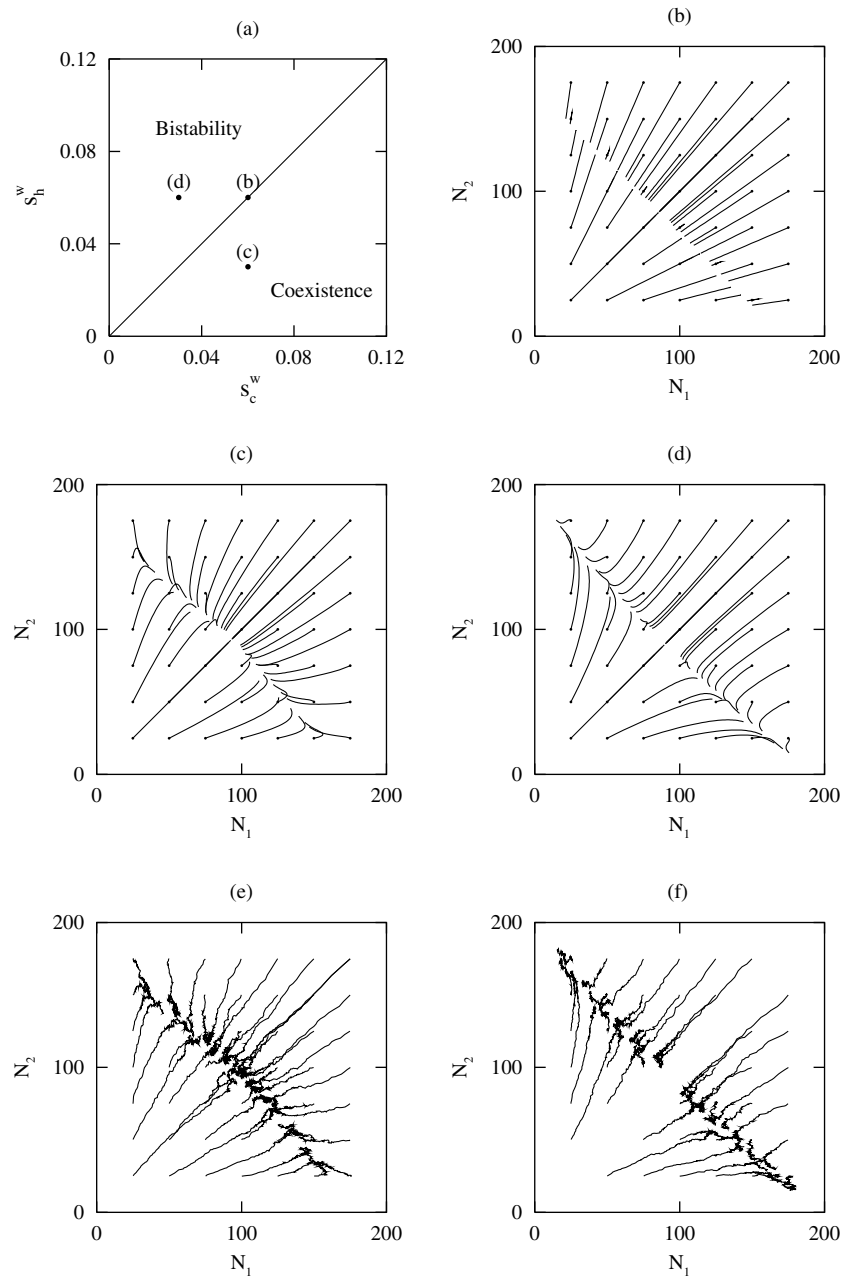


Figure 2 Effect of varying intra- and inter-specific competition kernels on coexistence of two species, with $s_c^w = s_{11}^w = s_{22}^w$, and $s_h^w = s_{21}^w = s_{12}^w$. (a) Regions of the parameter space permitting different outcomes of competition found by numerical invasion analysis; circles mark combinations of parameter values used in constructing phase diagrams: (b), (c), (d). The phase diagrams are projections of paths on to planes of population density, the paths being found by numerical integration of the dynamical system eqns 2, A3, for a period of 30 time units, short enough to avoid build-up of large-scale spatial structure. Initial values for N_1 , N_2 shown as dots, and initial pair densities set as $C_{ij}(\xi) = N_i N_j$ for all i, j and ξ corresponding to complete spatial randomness. (e), (f) Paths of population density obtained by averaging over 100 realizations of a stochastic individual-based model with parameter values corresponding to (c) and (d), respectively. Parameter values held constant throughout: $b_1 = b_2 = 0.4$, $d_1 = d_2 = 0.2$, $d'_{11} = d'_{22} = d'_{21} = d'_{12} = 0.001$, $s_1^w = s_2^w = 0.06$.

there is a small deviation from the stochastic process close to the manifold.

Figure 3 shows that heteromyopia achieves coexistence by creating small 'holes' in a landscape occupied by a common species (species 1), sufficiently devoid of the common species, for a rare species (species 2) to spread. To see this, consider a reduction ε in the interspecific kernel parameter from neutrality $s_h^w = s_c^w$ to $s_h^w = s_c^w - \varepsilon$. The change has two consequences. (1) The competitive effect $w_{21}(\xi)$ of species 1 on 2 becomes concentrated in a smaller neighbourhood around individuals of 2 (Fig. 1). (2) As time

goes on, the greater mortality in this smaller neighbourhood means that species 2 is less likely to occur close to 1 (in Fig. 3(a), $C_{21}(\xi)$ has been normalized such that a value of one would indicate independence, and a value less one segregation of the species). These holes make the integral I_{21} smaller and, as a result, reduce the per capita death rate $D_{21} = d'I_{21}/N_2$ in species 2 due to 1 (Fig. 3b). The neighbour-dependent death rate is now lower than that under neutrality, and the rare species increases in density (Fig. 3c). Notice that it is only the rare species that can benefit from this because almost all interactions of the common species

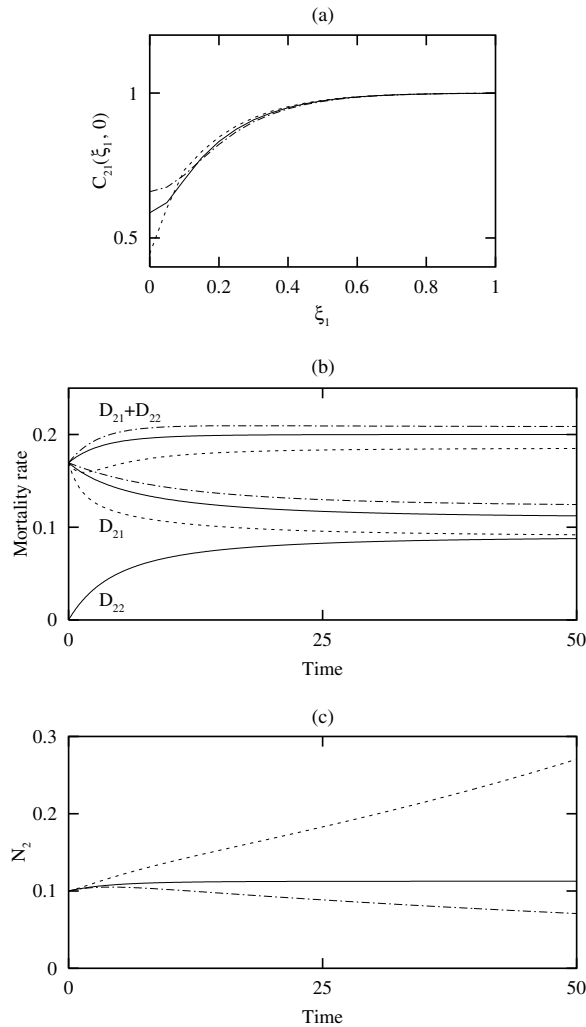


Figure 3 Effect of three interspecific competition kernels on spatial structure and success of a rare species 2 introduced into a landscape dominated by its competitor, species 1. Kernels set at: neutrality $s_{21}'' = s_{12}'' = 0.06$, continuous lines; heteromyopia $s_{21}'' = s_{12}'' = 0.03$, dotted lines; founder control $s_{21}'' = s_{12}'' = 0.09$, dash-dotted lines. Species 1 is allowed to get close to its equilibrium density and spatial structure, prior to introduction of species 2 uniformly at a density 0.1 per unit area. (a) Radial sections through the normalized spatial cross-covariance functions, after integration with both species over 50 time units; (b) changes over time in per capita mortality rates in species 2 due to neighbours; (c) changes over time in population density of species 2. Per capita mortality rates are $D_{21} = d'I_{21}/N_2$ (the lines decreasing with time) and $D_{22} = d'I_{22}/N_2$; the kernels have rather little effect on D_{22} and only one line is shown; when $D_{21} + D_{22} \rightarrow 0.2$, neighbour-dependent mortality balances the intrinsic vital rates, and the density of the rare species becomes constant over time. Parameter values held constant throughout: $b_1 = b_2 = 0.4$, $d_1 = d_2 = 0.2$, $d'_{11} = d'_{22} = d'_{21} = d'_{12} = 0.001$, $s_1''' = s_2''' = 0.06$, $s_{11}''' = s_{22}''' = 0.06$.

are with conspecifics. The argument above is reversed making an increment ε from neutrality, in which case the rare species cannot invade.

Dispersal and trade-offs

Heteromyopia is the only condition we have been able to find under which coexistence comes about simply as a result of space, i.e. through varying the parameters of the competition and dispersal kernels.

For instance, coexistence cannot be achieved simply by varying the dispersal kernels: an invasion analysis (Fig. 4a) shows that the species with longer dispersal always wins. To illustrate this, Figs 4(b,c) give some paths of population density with contrasting dispersal kernels. The reason why the species with greater dispersal wins appears to be that it develops a neighbourhood density of conspecifics lower than that of the other species, and the spatial separation of the species reduces the density of neighbours still further. Figure 4(a) shows additionally that, if the dispersal distance of a species is short enough, the species dies out whether or not there is competition with another species (Etheridge 2002; Law *et al.* 2002); this is because offspring are unable to disperse far enough for both the parents and offspring to survive.

However, coexistence can be achieved from combinations of both spatial and non-spatial parameters. For instance, Fig. 5 illustrates coexistence in the presence of the well-known competition–colonization trade-off (Hastings 1980; Tilman 1994). Greater colonization can be achieved by a greater birth rate and by greater dispersal distances s''' (Holmes & Wilson 1998); we use dispersal distance to keep in place a direct dependence on a spatial parameter. In this figure, species 2 is a weaker competitor than species 1, i.e. $d'_{12} \leq d'_{21}$, all parameters other than d'_{12} and s_2''' being held equal and constant. At the top, where $d'_{12} = d'_{21}$, there is no coexistence: as in Fig. 4(a), species 2 invades and replaces species 1 if it disperses over longer distances than species 1. As the competitive ability of species 2 is made smaller, an intermediate region of coexistence opens out. Notice however, that dispersal over long distances creates a strong advantage, and the competitive ability of species 2 has to be reduced a lot to obtain a substantial parameter space in which coexistence occurs.

Effect of initial spatial pattern

For certain parameter combinations, the mean-field Lotka–Volterra competition model shows founder control, such that the species rarer at the start is eventually excluded by the more common species. This dependence on initial conditions also applies in the SLV model, as is evident in Fig. 2(d).

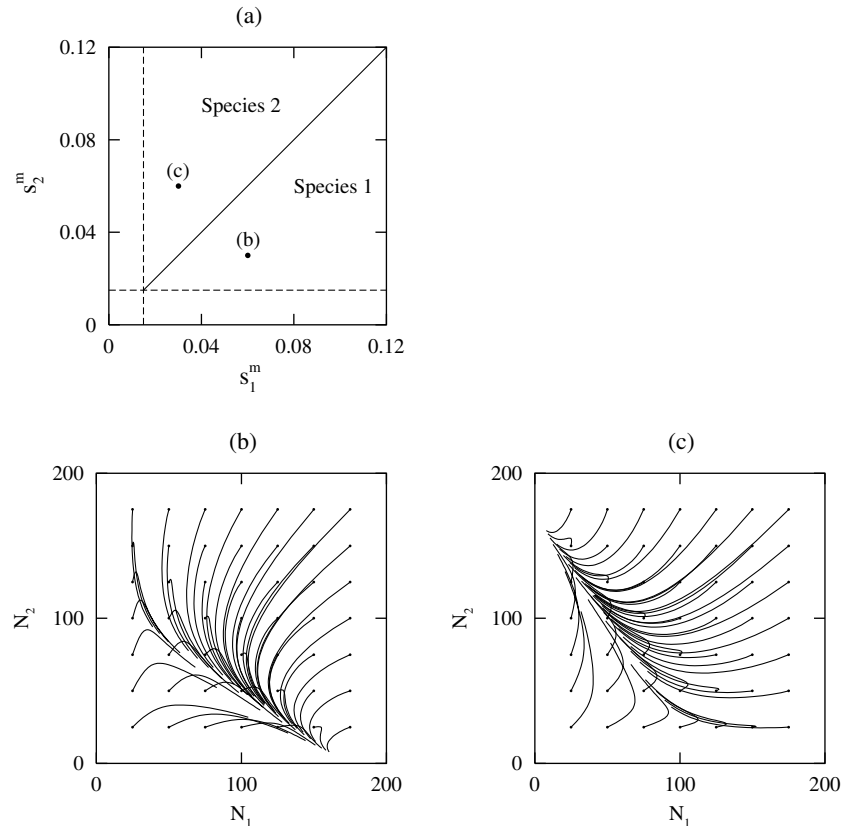


Figure 4 Effect of varying dispersal kernels on the outcome of competition between two species. (a) Regions of the parameter space permitting different outcomes of competition found by numerical invasion analysis; circles mark combinations of parameter values used in constructing phase diagrams: (b), (c). In regions closer to the boundary than the dashed lines, the species excluded would die out, irrespective of the presence of the other species; close to the origin both species die out. Diagrams (b) and (c) obtained as described in Figure 2. Apart from the dispersal kernels, the species have identical parameter values: $b_1 = b_2 = 0.4$, $d_1 = d_2 = 0.2$, $d'_{11} = d'_{22} = d'_{21} = d'_{12} = 0.001$, $s'_{11} = s'_{12} = s'_{21} = s'_{22} = 0.06$.

In addition, the SLV model has a feature that the winning species can be determined by the initial spatial structure irrespective of which species is more common at the start (Fig. 6). The numerical integrations here were carried out in exactly the same way as those in Fig. 2(d), except that species 2 was started with an aggregated spatial structure, and therefore experienced greater density-dependent mortality from a higher density of conspecific neighbours at the beginning of the integration. Thus, while relaxing to its natural spatial structure, species 2 was relatively unsuccessful, especially when starting at high density (this is why the paths in Fig. 6 are 'pulled' downwards near the start more than those in Fig. 2d). Overall, there is a region close to the diagonal of equal initial density where one or other species may win depending solely on the initial spatial pattern.

DISCUSSION

The analysis above disaggregates spatial structure from the direct effects of competition on death of individuals. It is clear from the analysis that competition always causes the species to separate out in space to some extent. Whether this separation results in coexistence of similar competing species, rests on an intricate coupling of spatial segregation to the neighbourhoods over which individuals compete. It is

quite possible for local spatial segregation to be insufficient to permit coexistence, in keeping with results of Takenaka *et al.* (1997) and Neuhauser & Pacala (1999). However, in the case of heteromyopia, where heterospecifics compete over shorter distances than conspecifics, local spatial segregation is great enough to create an advantage for the rare species, and thereby to enable the species to coexist.

Heteromyopia

So far as we are aware, coexistence through heteromyopia has not been noted before. In particular, it could not have been seen in earlier analytical studies because it only becomes apparent when interaction neighbourhoods of conspecifics and heterospecifics are made different in size (Bolker & Pacala 1999; Neuhauser & Pacala 1999). For simplicity, our own simulations also use certain parameter symmetries; by making small random departures from symmetry in all parameters, we have checked that the phenomenon is robust. Broadly, heteromyopia can trade-off against other parameters to achieve coexistence under circumstances in which the other parameters would themselves lead to exclusion of one species; the stronger the force for exclusion is, the greater heteromyopia has to be ($s_h^w \ll s_c^w$) (unpublished results). We have also checked that coexistence is robust to changes in the

Figure 5 Coexistence and the trade-off between competition d'_{12} and dispersal s_2^m of a weaker competitor, species 2. Regions of the parameter space permitting different outcomes of competition found by numerical invasion analysis. Apart from d'_{12} and s_2^m , the species have identical parameter values: $b_1 = b_2 = 0.4$, $d_1 = d_2 = 0.2$, $d'_{11} = d'_{22} = d'_{21} = 0.001$; $s_1^m = 0.04$; $s_{11}^m = s_{22}^m = s_{21}^m = s_{12}^m = 0.04$.

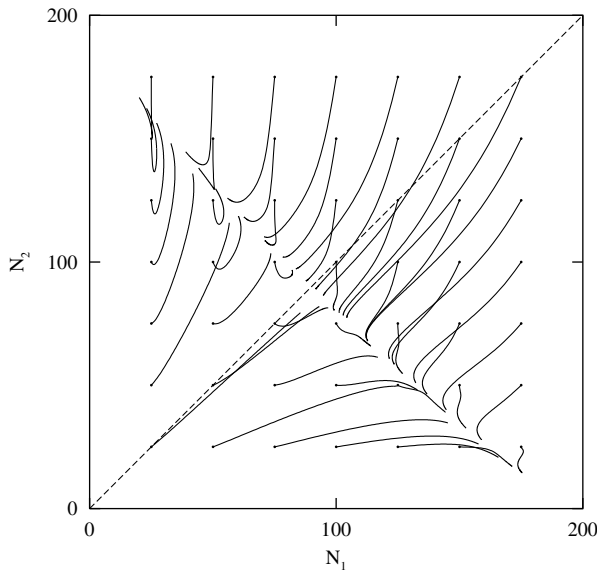
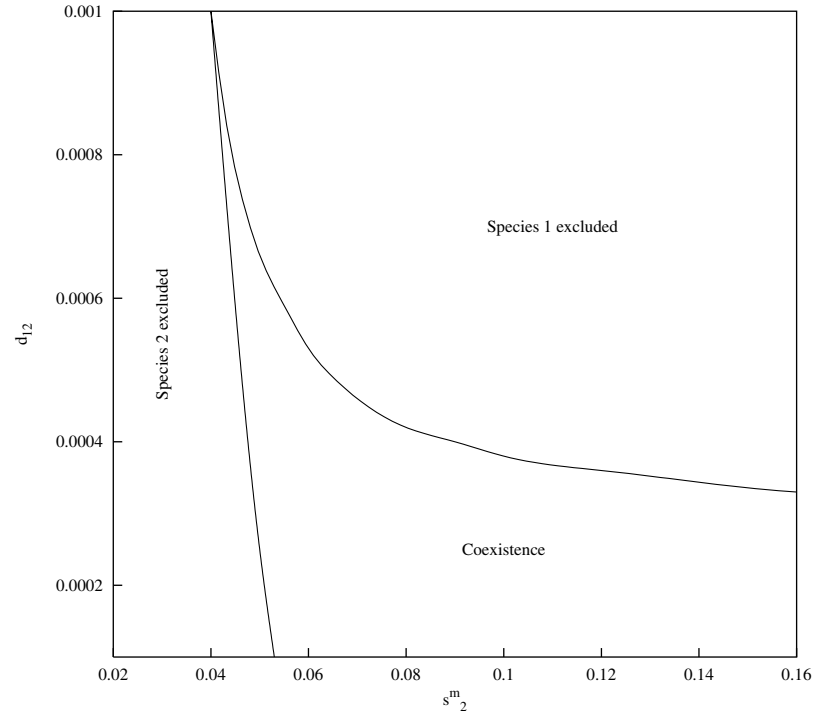


Figure 6 Effect of initial spatial structure on paths of population densities. Conditions identical to those of Figure 2(d), except that species 2 began with a clumped distribution given by $C_{22}(\xi) = N_{22}(1 + 2e^{-30|\xi|})$.

functional form of the competition kernels, using a kernel with a constant positive value up to a fixed distance and zero thereafter. Competition kernels that increase with distance could lead to different results, but would not be realistic (Purves & Law 2002).

Heteromyopia causes coexistence purely through its effect on spatial structure: it lowers the density of a common species enough in the neighbourhood of a rare species to enable the rare species to increase. Segregation occurs at the (local) spatial scale of the competition kernel, and can be thought of as creating small gaps in the distribution of the common species. This effect on coexistence gets weaker the better mixed the community is. Indeed, if the community could somehow be continually stirred to keep individuals randomly distributed over space, the effects of heteromyopia on coexistence would vanish because $I_{ij} = \int w_{ij}(\xi) N_i N_j d\xi = N_i N_j$, since the kernels are normalized to sum to 1 whatever their shape.

There is an obvious parallel between the conditions needed for coexistence of species in the SLV model and those needed in the mean-field model: other things being equal, both require stronger intraspecific than interspecific competition. In the mean-field model, stronger intraspecific competition comes from the interaction parameters, the d'_{ij} terms in eqns 1. In the SLV model, in addition to the interaction terms, stronger intraspecific competition can come from spatial structure generated by competition; this process is much more intricate, because the spatial structure itself changes over time through the process of competition.

Mechanisms for heteromyopia

In general, there is no a priori reason to expect kernels for competition within and between species to be the same.

The overall effect one organism has on another integrates across a range of mechanisms that operate over different distances, such as direct interference, resource competition and sharing of enemies. It would be surprising if kernel shapes emerging from these forces were the same between and within species.

Heteromyopia requires, in addition, that interspecific competition should operate over shorter distances than intraspecific competition; the extent to which this occurs is open to discussion and could be tested empirically. In the case of plants, host-specific enemies, such as specialist herbivores, seed predators and pathogens (Janzen 1970; Connell 1971), could lengthen the distance over which conspecific interactions take place beyond that of heterospecific interactions, more dominated by resource competition. At the same time, the competition kernel of conspecifics could well be higher close to the origin in the presence of such enemies, so the overall effect of these enemies could be to make these kernels more leptokurtic. Another contributing mechanism in plant communities could be allelopathy: it is well established that some plant species produce chemicals that inhibit the growth of heterospecifics (e.g. Ridenour & Callaway 2001), an effect that may only be felt over very short distances (e.g. Sharma *et al.* 2000). This would shorten the distance over which heterospecifics interact, and make heterospecific kernels higher close to the origin.

To evaluate the part heteromyopia plays in coexistence of species requires knowledge of the shape of kernels for interactions within and between species. It is remarkable how little is known about competition kernels compared with kernels for dispersal (but, for plants, see Benjamin 1999; Soares & Tomé 1999; Purves & Law 2002). In plants, matters are complicated by the fact that neighbourhood interactions change as individuals grow: competition kernels may need to be thought of as entities dynamic in their own right (Purves & Law 2002). Spatially referenced data sets of multispecies communities over time are now available, such as the 50 ha plot on Barro Colorado Island (BCI), and could be used to estimate competition kernels within and between species; early indications suggest that conspecifics interact over rather short distances at BCI (Hubbell *et al.* 2001).

Spatial segregation

Initially, it comes as a surprise that competing species with the property of mutual invasibility can become increasingly separated in space as time goes on in spatial dynamical systems. Yet large-scale spatial segregation is a well established phenomenon in the mathematical literature on competition in spatial lattices (Neuhauser & Pacala 1999). Such separation becomes less surprising when it is understood that these dynamical systems have no force, corresponding

to local dispersal of offspring within species, that binds different species together in space.

Although we have avoided complications of the build-up of large-scale spatial segregation by concentrating on invasion and short-term dynamics, there are some interesting questions about the long-term behaviour. For instance, does spatial segregation eventually come to a halt or does it continue to increase over time? Inspection of eqn A3, describing the dynamics of spatial covariances, shows there is one positive term in the flux of the cross-covariance. This could in principle balance the negative terms, and it is possible therefore that the rates of change of the cross-covariances could tend to zero, eventually stopping further spatial segregation.

However, for two reasons we think the gradual, large-scale separation of species is of more mathematical than ecological interest. First, in the case of plants, dispersal kernels are known to have fat tails (Clark *et al.* 1998); in this context it is notable that a low level of uniform dispersal over space can hold spatial segregation in check in simulations of the IBM (unpublished results), because patches of single species still have a spatial structure that allows them to be invaded by the other species. Second, real environments are spatially heterogeneous, and this may limit how far apart species with similar niche requirements can get. In this scenario, species found living together have two properties: (1) mutual invasibility, so that one cannot exclude another, and (2) similar niche requirements, so that they remain together in the spatially heterogeneous environment. Arguably, large-scale spatial segregation may tell us more about ecological processes missing from the dynamical system than about important ecological features of competition in space.

Founder control and dependence on initial spatial structure

Although the numerical results show founder control, Neuhauser & Pacala (1999) conjectured that, in a large enough spatial region, one species should always exclude the other. This is because one species will in general be a stronger competitor than the other and, given enough space, should occur somewhere at a local density great enough to exclude the other species; over time, it then spreads out from this location, eventually driving the other species to extinction. Models such as the one used here deal with dynamics of the average neighbourhood, rather than with variability among neighbourhoods, and are therefore not able to describe such a process.

Founder control is therefore more likely to be a significant feature where the spatial extent of a community is small enough to give a restricted range of initial local densities. Most plant competition experiments have this property (e.g.

Hector *et al.* 1999), and it is important to be aware that the outcome from one generation to the next can be determined by the spatial arrangement chosen at the start of the experiment (Stoll & Prati 2001). A striking application of this is in the use of cereal crop plants to control their weeds: much more effective control can be achieved by switching from the current practice of sowing cereals in rows to sowing them on lattices (Weiner *et al.* 2001).

Caveats

Spatial dynamical systems in nature are very complex. All studies of them should carry a warning about our ignorance of their mathematical properties, and the SLV model in this paper is no exception. We have not proved that there are no other parameter combinations that permit coexistence; when trade-offs between the non-spatial and spatial parameters are put in place, it may well be that other combinations giving coexistence will be found. What the SLV model does do is to provide a framework in which such investigations can be carried out: there is much to learn about its properties.

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REFERENCES

- Adler, F.R. & Mosquera, J. (2000). Is space necessary? Interference competition and limits to biodiversity. *Ecology*, 81, 3226–3232.
- Benjamin, L.R. (1999). A comparison of different rules of partitioning crop growth between individual plants. *Ecol. Modelling*, 115, 111–118.
- Bolker, B.M. & Pacala, S.W. (1997). Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. *Theor. Pop. Biol.*, 52, 179–197.
- Bolker, B.M. & Pacala, S.W. (1999). Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *Am. Nat.*, 153, 575–602.
- Bolker, B.M., Pacala, S.W. & Levin, S.A. (2000). Moment methods for ecological processes in continuous space. In: *The Geometry of Ecological Interactions: Simplifying Spatial Complexity* (eds Dieckmann, U., Law, R. & Metz, J.A.J.). Cambridge University Press, Cambridge, pp. 388–411.
- Chesson, P. & Neuhauser, C. (2002). Intraspecific aggregation and species coexistence. *Trends Ecol. Evol.*, 17, 210–211.
- Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G.A. *et al.* (1998). Reid's paradox of rapid plant migration: dispersal theory and interpretation of paleoecological records. *BioScience*, 48, 13–24.
- Connell, J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of Populations* (eds den Boer, B.J. & Gradwell, G.R.). Centre for Agricultural Publishing and Documentation, Wageningen, the Netherlands, pp. 298–310.
- Dieckmann, U. & Law, R. (2000). Relaxation projections and the method of moments. In: *The Geometry of Ecological Interactions: Simplifying Spatial Complexity* (eds Dieckmann, U., Law, R. & Metz, J.A.J.). Cambridge University Press, Cambridge, pp. 412–455.
- Etheridge, A.M. (2002). Survival and extinction in a locally regulated population. *Ann. Appl. Prob.*, in press.
- Geritz, S.A., van der Meijden, E. & Metz, J.A.J. (1999). Evolutionary dynamics of seed size and seedling competitive ability. *Theor. Pop. Biol.*, 55, 324–343.
- Harada, Y. & Iwasa, Y. (1994). Lattice population dynamics for plants with dispersing seeds and vegetative propagation. *Res. Pop. Ecol.*, 36, 237–249.
- Hastings, A. (1980). Disturbance, coexistence, history and competition for space. *Theor. Pop. Biol.*, 163, 491–504.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G. *et al.* (1999). Plant diversity and productivity experiments in European grasslands. *Science*, 286, 1123–1127.
- Holmes, E.E. & Wilson, H.B. (1998). Running from trouble: long-distance dispersal and the competitive coexistence of inferior species. *Am. Nat.*, 151, 578–586.
- Horn, H.S. & MacArthur, R.H. (1972). Competition among fugitive species in a harlequin environment. *Ecology*, 53, 749–752.
- Hubbell, S.P., Ahumada, J.A., Condit, R. & Foster, R.B. (2001). Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecol. Res.*, 16, 859–875.
- Hutchinson, G.E. (1951). Copepodology for the ornithologist. *Ecology*, 32, 571–577.
- Janzen, D.H. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat.*, 104, 501–528.
- Law, R. & Dieckmann, U. (2000). A dynamical system for neighbourhoods in plant communities. *Ecology*, 81, 2137–2148.
- Law, R., Murrell, D.J. & Dieckmann, U. (2002). On population growth in space and time: spatial logistic equations. *Ecology*, in press.
- Levins, R. & Culver, D. (1971). Regional coexistence of species and competition between rare species. *Proc. Natl. Acad. Sci. USA*, 68, 1246–1248.
- Murrell, D.J., Purves, D.W. & Law, R. (2001). Uniting pattern and process in plant ecology. *Trends Ecol. Evol.*, 16, 529–530.
- Murrell, D.J., Purves, D.W. & Law, R. (2002). Intraspecific aggregation and species coexistence. *Trends Ecol. Evol.*, 17, 211.
- Neuhauser, C. (2001). Mathematical challenges in spatial ecology. *Notices Am. Math. Soc.*, 48, 1304–1314.
- Neuhauser, C. & Pacala, S.W. (1999). An explicitly spatial version of the Lotka–Volterra model with interspecific competition. *Ann. Appl. Prob.*, 9, 1226–1259.
- Pacala, S.W. (1997). Dynamics of plant communities. In: *Plant Ecology* (ed. Crawley, M. J.), Blackwell, Oxford, pp. 532–555.
- Pacala, S.W. & Levin, S.A. (1997). Biologically generated spatial pattern and the coexistence of competing species. In: *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions* (eds Tilman, D. & Kareiva, P.), Princeton University Press, Princeton, New York, pp. 204–232.
- Purves, D.W. & Law, R. (2002). Experimental derivation of functions relating growth of *Arabidopsis thaliana* to neighbour size and distance. *J. Ecol.*, 90, 882–894.

- Ridenour, W.M. & Callaway, R.M. (2001). The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. *Oecologia*, 126, 444–450.
- Sharma, N.K., Samra, J.S. & Singh, H.P. (2000). Effect of leaf litter of poplar on *Phalaris minor* weed. *Allelopathy*, 7, 243–253.
- Skellam, J.G. (1951). Random dispersal in theoretical populations. *Biometrika*, 38, 196–218.
- Soares, P. & Tomé, M. (1999). Distance-dependent competition measures for eucalyptus plantations in Portugal. *Ann. For. Sci.*, 56, 307–319.
- Stoll, P. & Prati, D. (2001). Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology*, 82, 319–327.
- Takenaka, Y., Matsuda, H. & Iwasa, Y. (1997). Competition and evolutionary stability of plants in a spatially structured habitat. *Res. Pop. Ecol.*, 39, 67–75.
- Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 685–700.
- Turkington, R.A. & Harper, J.L. (1979). The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. *J. Ecol.*, 67, 201–208.
- Weiner, J. & Conte, P.T. (1981). Dispersal and neighborhood effects in an annual plant competition model. *Ecol. Modelling*, 13, 131–147.
- Weiner, J., Griepentrog, H.-W. & Kristensen, L. (2001). Suppression of weeds by spring wheat *Triticum aestivum* increases with crop density and spatial uniformity. *J. Appl. Ecol.*, 38, 784–790.

APPENDIX

Here we define the second moment, describe its dynamics, and comment on the method of moment closure.

Consider a community of two species living in a continuous, two-dimensional space of area \mathcal{A} . An individual l of species i , located at coordinates $x_{il} = (x_{il1}, x_{il2})$, is denoted by a Dirac delta function $\delta_{x_{il}}(x)$; the spatial pattern of species i at time t is given by the function $p_i(x, t)$, this function being the sum of the delta functions of all individuals of species i . The multispecies spatial pattern collects together the patterns of the two species $p(x) = (p_1(x), p_2(x))$. The second moment $C_{ij}(\xi, p)$ is then the density of pairs of individuals of species i and j , j being displaced by an amount $\xi = x' - x$ from i :

$$C_{ij}(\xi, p) = \frac{1}{\mathcal{A}} \int p_i(x, t) [p_j(x + \xi, t) - \delta_{ij} \delta_x(x + \xi)] dx; \quad (\text{A1})$$

here the delta function removes a degenerate pair in which the same individual would occur twice. If $i = j$, the second moment is a spatial autocovariance function of species i ; if $i \neq j$, the second moment is a spatial cross-covariance function of species i and j .

In a stochastic process, the spatial structure at time t differs from one realization to another, and one can think of a probability density function for pattern p at time t $P(p)$. A

deterministic measure for the pair density averaged over the stochastic realizations is then:

$$C_{ij}(\xi) = \int C_{ij}(\xi, p) P(p) dp, \quad (\text{A2})$$

where, for notational simplicity, the argument t is omitted. We use this measure of second-order spatial structure in the moment dynamics.

The dynamics of the second spatial moment, $C_{ij}(\xi)$, describe the flux in density of neighbours of species j at a displacement ξ around individuals of species i

$$\begin{aligned} \dot{C}_{ij}(\xi) = & \delta_{ij} b_i m_i(\xi) N_i + \delta_{ij} b_j m_j(-\xi) N_j \\ & + b_j \int m_i(\xi') C_{ij}(\xi + \xi') d\xi' \\ & + b_j \int m_j(\xi') C_{ji}(-\xi + \xi') d\xi' - d_i C_{ij}(\xi) \\ & - d_j C_{ji}(-\xi) - \sum_k d'_{ik} \int w_{ik}(\xi'') T_{ijk}(\xi, \xi'') d\xi'' \\ & - \sum_k d'_{jk} \int w_{jk}(\xi'') T_{jik}(-\xi, \xi'') d\xi'' \\ & - \delta_{ik} d'_{ik} w_{ik}(\xi) C_{ik}(\xi) \\ & - \delta_{jk} d'_{jk} w_{jk}(-\xi) C_{jk}(-\xi) \end{aligned} \quad (\text{A3})$$

where $T_{ijk}(\xi, \xi'')$ denotes the third spatial moment, a density of triplets, and δ_{ij} is the Kronecker delta function that takes value 1 when $i = j$ and zero otherwise. The derivation of this equation is technical and is dealt with elsewhere (Dieckmann & Law 2000).

The third moment is a state variable and therefore has its own dynamics, so the dynamical system above is not yet closed. Instead of deriving the dynamics for the third spatial moments (which are functions of yet higher spatial moments) we replace the third moment with an expression involving only the first and second spatial moments: an order-2 closure (e.g. Bolker & Pacala 1997, 1999; Law & Dieckmann 2000; Law *et al.* 2002). The form of moment closure used to generate the above results differs from that used by Law & Dieckmann (2000) and is defined as

$$\begin{aligned} T_{ijk}(\xi, \xi'') = & \frac{1}{5} \left\{ \frac{4C_{ij}(\xi) C_{ik}(\xi'')}{N_i} \right. \\ & + \frac{C_{ij}(\xi) C_{jk}(\xi'' - \xi)}{N_j} \frac{C_{ik}(\xi'') C_{jk}(\xi'' - \xi)}{N_k} \\ & \left. - N_i N_j N_k \right\} \end{aligned} \quad (\text{A4})$$

Previous results for a single-species model have shown this closure to provide a good approximation across a wide range of spatial structures, but especially when there are

aggregations, and also during invasions (Law *et al.* 2002; D.J. Murrell, U. Dieckmann & R. Law, unpublished manuscript).

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