

A novel theory to explain species diversity in landscapes: positive frequency dependence and habitat suitability

Jane Molofsky^{1*} and James D. Bever²

¹*Department of Botany, University of Vermont, Burlington, VT 05405, USA*

²*Department of Biology, Indiana University, Bloomington, IN 47405, USA*

Theories to explain the diversity of species have required that individual species occupy unique niches and/or vary in their response to environmental factors. Positive interactions within a species, although common in communities, have not been thought to maintain species diversity because in non-spatial models the more abundant species always outcompetes the rarer species. Here, we show, using a stochastic spatial model, that positive intraspecific interactions such as those caused by positive frequency dependence and/or priority effects, can maintain species diversity if interactions between individuals are primarily local and the habitat contains areas that cannot be colonized by any species, such as boulders or other physical obstructions. When intraspecific interactions are primarily neutral, species diversity will eventually erode to a single species. When the landscape is homogeneous (i.e. does not contain areas that cannot be colonized by any species), the presence of strong intraspecific interactions will not maintain diversity.

Keywords: intraspecific interactions; stochastic spatial model; positive frequency dependence; priority effects; species coexistence; landscape patterns

1. INTRODUCTION

Understanding mechanisms whereby species can coexist in landscapes has been a subject of great interest and controversy in ecology (Ricklefs & Shluter 1993). Explanations have either required that individual species occupy unique niches and/or individual species vary in their response to environmental factors (Ricklefs & Shluter 1993; Chesson 2000). Neutral models of species diversity have also been proposed but these models will not maintain species indefinitely (Hubbell 2001). In neutral models, diversity is maintained by the balance between migration of new species into the community and the loss of species due to extinction (Hubbell 2001). In niche-based models, diversity is maintained when the increase in the density of the more common species favours the rare species, as happens in niche differentiation between species (Levins 1974; May 1974). In this case, the presence of conspecifics creates a negative feedback on a species' own abundance, allowing a less common species to increase. In circumstances in which overall density within a competitive guild is at or near the carrying capacity for the environment, negative feedback on density is equivalent to negative feedback on frequency. The importance of negative frequency dependence as a mechanism maintaining diversity has been widely recognized (Clarke 1969; Ayala 1971; May & Anderson 1983; Antonovics & Kareiva 1988).

Interspecific interactions, whereby the common species increases at the expense of a rare species (positive frequency dependence), are also common in communities. Examples include interactions between plants and their pollinators in which the common species receives more

pollen, interactions between plants and host-specific root mutualists in which common plant species benefit from higher densities of mycorrhizae (Ronsheim 1996; Bever 1999; Ronsheim & Anderson 2001), and priority effects in marine intertidal and plant communities where once a species establishes it has an advantage over less abundant species (Wilson & Agnew 1992; Petraitis & Latham 1999). Predictions from models of positive frequency dependence predict the loss of diversity (Levins 1974; May 1974). In sessile organisms such as plants and many intertidal animals, interactions can occur over small spatial scales (Ronsheim 1996; Molofsky 1999; Petraitis & Latham 1999). The local spatial scale of the interactions can have a profound influence on dynamics (Durrett & Levin 1994; Pacala & Levin 1997). For example, the inclusion of spatial structure can result in several novel and distinct behaviours in frequency-dependent systems (Molofsky *et al.* 1999, 2001). Here, we demonstrate that positive frequency-dependent interactions can maintain species diversity if interactions occur locally and if landscapes contain locations that cannot be colonized by any species. Because areas that cannot be colonized are common in communities, positive frequency-dependent interactions may be an important, but under-appreciated, mechanism for maintaining species diversity.

2. THE MODEL

The model is developed for 10 species competing on a two-dimensional grid. Each location on the grid can contain one of the 10 species or be unsuitable for colonization by all species. The dynamics develop from the application of a transition rule in concert over the entire grid. The transition rule depends upon the proportion of each species in its surrounding neighbourhood. The probability of a species establishing into a particular location is either

* Author for correspondence (jmolofsk@zoo.uvm.edu).

directly proportional to its representation in the local neighbourhood or its probability is enhanced relative to its representation in the local neighbourhood. To implement this rule, we consider f_1 , the proportion of species 1 in the target cell and the adjacent cells over the nine-square neighbourhood, and h_1 , where h_1 represents the probability of establishment of an individual of species 1 into a given location and includes all the processes from reproduction from one generation to the next (i.e. fecundity, birth and survival), and is calculated as:

$$h_1 = 0.5 + a(f_1 - 0.5). \quad (2.1)$$

The parameter a represents the strength of positive intraspecific interactions. Positive intraspecific interactions (as compared with the neutral case) occur when $a > 0$. We only examine cases where $0 \leq a \leq 1$. The probability of establishment of species 1 in a given location is then calculated by the weighted frequency of that type.

$$P_1 = h_1 f_1 / (h_1 f_1 + h_2 f_2 + h_3 f_3 + h_4 f_4 + h_5 f_5 + h_6 f_6 + h_7 f_7 + h_8 f_8 + h_9 f_9 + h_{10} f_{10}). \quad (2.2)$$

The probability of establishment can be adjusted to take into account physical obstructions or unsuitable habitat in the landscape. To simulate unsuitable habitat, a fixed proportion of sites are randomly designated uninhabitable at the start of the simulation and the location of these sites remains fixed throughout each simulation.

Although this model greatly simplifies ecological interactions, analytical solutions are still not possible. However, we can quantitatively investigate the probability of long-term coexistence by simulating multiple initial conditions using a spatially explicit stochastic model in which the probability of species 1 establishing at a given square is determined by the probability calculated by equation (2.2) for that square. To calculate the local transition probabilities the nine-square neighbourhood was used (the centre and eight adjacent squares). Our model applies equally well to different species within a community or different asexually reproducing genotypes within populations. For clarity, we only discuss the model with respect to different species.

Each simulation is initiated with 10 species randomly positioned on a 100×100 grid with absorbing boundaries. Each cell either contains one of the 10 species or is considered uninhabitable. Subsets of simulations were performed using a torus boundary condition. In the torus, the border on one side wraps around to the opposite side, which generates a doughnut. In addition, for a subset of the simulations, we also included the effect of random disturbance. By disturbance, we mean the probability d that a given site will be unoccupied in each generation. To implement disturbance, at the start of each simulation, we removed a set fraction of individuals from random locations within the grid. The probability of establishment for each species is then adjusted by this as follows:

$$P'_i = (1 - d)P_i, \quad (2.3)$$

where P'_i is the adjusted probability of establishment of species 1. Calculations of the neighbourhood values for each target cell remain as described above. Note that increasing our disturbance parameter has the effect of reducing the overall density within the grid.

We used our model to investigate a variety of different scenarios. First, we describe what happens for two species subject to positive intraspecific interactions in a homogeneous landscape. Next, we examine what happens within a multispecies community where each species experiences strong positive intraspecific interactions ($a = 1$) in both a homogeneous landscape and a landscape that contains increasing amounts of unsuitable habitat (20% and 40%, respectively). To better understand the role of positive intraspecific interactions in generating our results, we compare the results of simulations carried out on a homogeneous landscape and one with unsuitable habitat (40% uninhabitable) subject to neutral ($a = 0$), and strong ($a = 1$) local positive intraspecific interactions (i.e. the nine-square neighbourhood). In addition, we compare the number of species that can coexist in landscapes with unsuitable habitat when the positive intraspecific interactions are not local, but occur at the scale of the entire landscape. Finally, by varying the amount of unsuitable habitat and the strength of the interactions simultaneously, we investigate the interacting effects of the strength of positive intraspecific interactions and the amount of unsuitable habitat in the landscape. To ensure that our results were not specific to simulation details, we performed a factorial comparison with two boundary conditions (absorbing and torus) with and without random disturbance (0 and 10% disturbance) under strong positive interactions ($a = 1$) with 40% unsuitable sites.

3. RESULTS

To understand the interacting effects of habitat suitability and positive intraspecific interactions, it is instructive to first understand what happens on a homogeneous landscape. With two species living in a homogeneous landscape, single-species patches are created from a random initial placement of both species on the landscape because each species does better when surrounded by conspecifics. In a homogeneous landscape, the larger patches engulf the smaller patches resulting in one species overtaking the whole landscape. However, it is possible for both species to coexist, if intraspecific patches coalesce to form a continuous band across the landscape (Molofsky *et al.* 2001). Once such a straight band is created, the positive interactions prevent the penetration of either species into the other's territory and in this case, the two species may coexist indefinitely. In a homogeneous landscape, if we start with 10 species, the eventual outcome is the same as in the two species case (figure 1a), unless we imagine a landscape that contains areas that cannot be colonized because of physical obstructions such as boulders or even other species in the landscape that do not interact with the focal species and form clumps in the landscape (figure 1b,c). Patches of uninhabitable space create boundaries in the landscape where pairs of species end up in a standoff with neither species able to advance into the other's territory, as occurs for the band straightening in the two species case. Standoffs occur because obstructions in the landscape create narrow passageways that a species can enter but not easily penetrate beyond. Penetration up and through the passageway is difficult because the advancing species becomes a local minority as it crosses through to the other species' territory, which halts further advance.

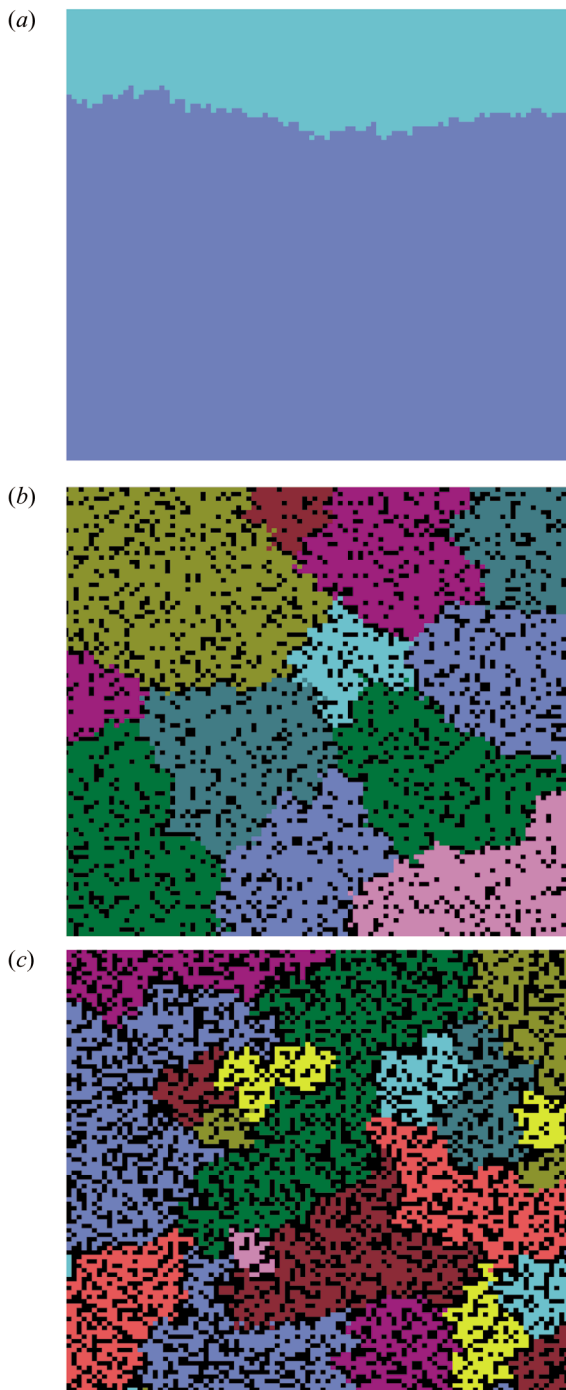


Figure 1. Results from the simulation of one random initial condition when simulations are started with 10 different species randomly placed on a 100×100 grid at equal frequencies after 100 000 generations for the case of strong positive frequency dependence ($a = 1$) with: (a) no unsuitable habitat; (b) 20% unsuitable habitat; and (c) 40% unsuitable habitat. Different colours denote different species. Black denotes areas that are not suitable for colonization.

Even the presence of few obstructions in the landscape can act to increase diversity that would otherwise erode over time.

For diversity to be maintained, local positive intraspecific interactions and unsuitable habitat are required. In the absence of positive interactions (i.e. the neutral case of drift (Wright 1943; Holley & Liggett 1975)) with or without the presence of unsuitable habitat, species persist in

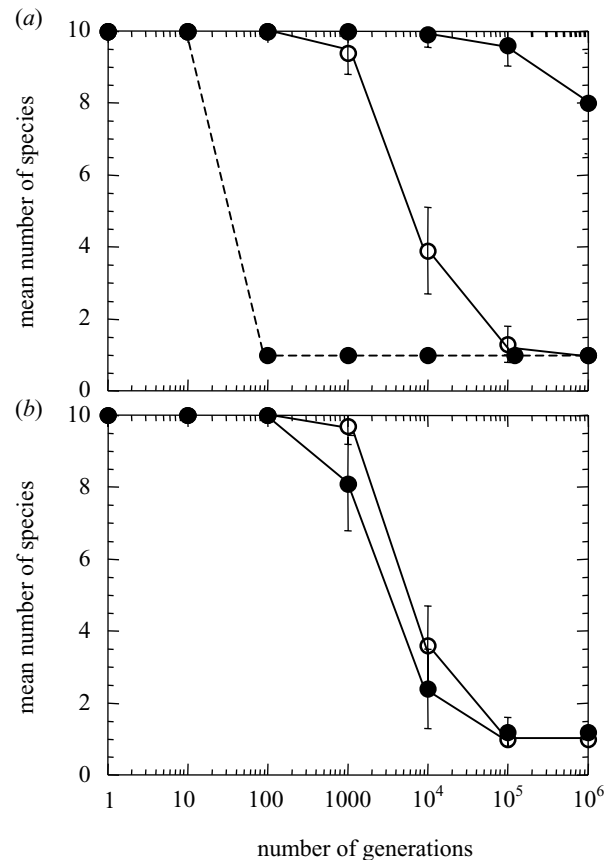


Figure 2. (a) Coexistence of species in a complex habitat (40% unsuitable sites) under drift ($a = 0$), strong local positive frequency dependence ($a = 1$) and under strong global positive frequency dependence ($a = 1$). Open circles represent drift ($a = 0$); filled circles represent strong positive frequency dependence ($a = 1$). Dashed line represents strong global positive frequency dependence ($a = 1$). (b) Coexistence of species in a homogeneous habitat (0% unsuitable sites) under drift ($a = 0$) and strong local positive frequency dependence ($a = 1$). Open circles represent drift ($a = 0$); filled circles represent strong positive frequency dependence ($a = 1$). Plotted in each panel are the mean and one standard error for 30 different random initial conditions initiated with equal frequency of the 10 species.

the landscape over many generations but eventually all but one will be lost (figure 2a,b). If strong positive intraspecific interactions occur at the scale of the entire grid, with or without the presence of unsuitable habitat, rapid extinction of all but one species occurs within 100 generations (figure 2a). Furthermore, if strong positive interactions occur at a local scale, but the landscape is homogeneous then at most two of the 10 species will persist as described above for the two species case (figure 2b). However, when both strong local positive intraspecific interactions and unsuitable habitats are present, 95% of the species present remain at 100 000 generations and close to 80% at one million generations (figure 2a).

The interdependence of positive intraspecific interactions and unsuitable habitat is illustrated by systematically varying the strength of positive interactions and the amount of unsuitable habitat (figure 3). The stronger the degree of positive interactions and the greater the amount of unsuitable habitat, the more species can be maintained in the landscape. However, even weak positive interactions

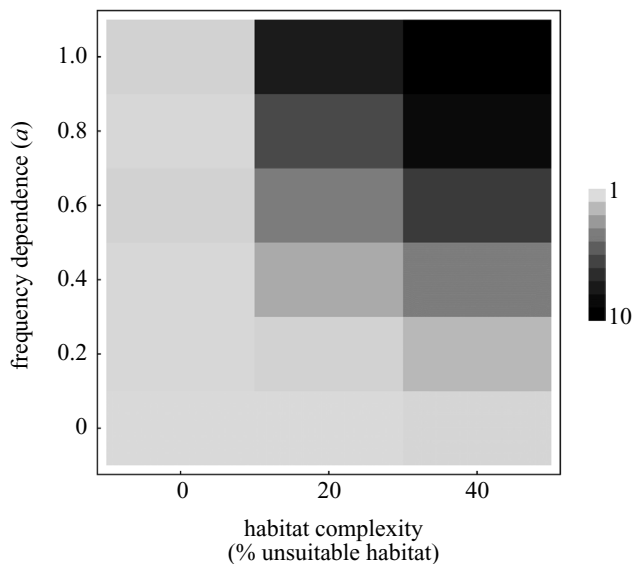


Figure 3. Coexistence of species as a function of the strength of frequency dependence and the amount of unsuitable habitat over 100 000 generations. Plotted is the mean of 30 different random initial conditions initiated with equal frequency of the 10 species.

and moderate values of unsuitable habitat can maintain greater diversity than either the neutral process of drift or homogeneous landscapes (figure 3).

The general pattern of coexistence was not affected by changes in the boundary condition or the addition of random disturbance; however, there were small changes in the number of species maintained. For example, in a factorial comparison of the two boundary conditions and disturbance rates of 0 and 10% under strong positive interactions ($a = 1$) and 40% uninhabitable sites, slightly fewer species coexisted at 100 000 generations with the torus boundary condition ($\bar{x} = 8.4$, s.e.m. = 0.11, $n = 30$) than with the absorbing boundary condition ($\bar{x} = 8.8$, s.e.m. = 0.11, $n = 30$), and fewer species remained with disturbance ($\bar{x} = 8.0$, s.e.m. = 0.11, $n = 30$) than without disturbance ($\bar{x} = 9.2$, s.e.m. = 0.10, $n = 30$).

4. DISCUSSION

Frequency-dependent processes can drive dynamics among species and hence influence the diversity of species in the landscape. However, positive frequency dependence has received less attention than negative frequency dependence because non-spatial models of positive frequency dependence do not permit coexistence. Our study demonstrates that a stochastic spatial model of positive frequency-dependent interactions between species that includes sites unsuitable for species to colonize, such as boulders or other landscape features, can result in the maintenance of species over long time-scales.

When an individual species alters the environment to enhance its own survival, then intraspecific positive interactions can occur (Wilson & Agnew 1992; Weltzin & McPherson 1999; Catovsky & Bazzaz 2000). Positive intraspecific interactions have been documented in a wide range of communities (see Wilson & Agnew 1992; Petraitis & Latham 1999; Weltzin & McPherson 1999; Catovsky & Bazzaz 2000). Priority effects are commonly

found in marine intertidal communities where species are subject to spatial limitations (Petraitis & Latham 1999). In terrestrial communities, specific associations between mycorrhizal fungi and their host plants can lead to species growth being enhanced in the presence of conspecifics (Ronsheim 1996; Bever 1999; Ronsheim & Anderson 2001). The mechanism described here may also explain the high levels of genetic diversity found in clonally reproducing plant conspecifics (Ronsheim 1996; Bever *et al.* 1997; Ronsheim & Anderson 2001; Gifford *et al.* 2002). Once individual clones establish, like sessile marine organisms, they may be difficult to displace and spatial priority effects may overwhelm other environmental factors.

Although the model is developed for species that reproduce each generation (i.e. annuals), changing the model structure to incorporate species that can live for more than one generation should not alter the conclusions (Molofsky *et al.* 2002). In fact, having species remain for more than one generation would only enhance the 'priority effect', and thus prevent another species from moving into the occupied species' territory. This should then increase the stability of borders and increase persistence times of species.

Because this is a finite stochastic model, in the limit of infinity, the only outcome is monodominance of one species. However, reaching that limit could take an infinitely long time, resulting in effective coexistence. The time-scale to complete exclusion, as demonstrated in our stochastic simulations, is more than one million generations for neighbourhood sizes of only nine cells. Neutral community models that incorporate the random removal of species accompanied by replacement in proportion to their relative abundance can also maintain diversity over long time periods (Hubbell 1979, 2001). However, neutral models require continual introduction of new species through either immigration or speciation (Hubbell 2001). In the absence of such mechanisms, diversity eventually erodes. For example, in these simulations, over half the species have been lost by 10 000 generations in the neutral case while virtually all remain for the case of positive frequency dependence and uninhabitable space. The ability to maintain species in the landscape depends critically on the scale of interaction and dispersal. As interaction scales increase, the level of diversity maintained by the presence of uninhabitable space is reduced with the system approaching the result for the global interaction model at neighbourhood sizes of 225 or above.

In most landscapes, areas that cannot be colonized are common. In fact, continued habitat fragmentation may be creating more landscapes similar to the ones modelled here. Moreover, these uninhabitable areas need not be physical obstructions such as boulders or cleared land, but could be patches of non-interactive species such as clumps of trees in grasslands that could not be colonized by competing grasses. As positive interactions are now well documented within communities (see Bronstein 1994; Bertness & Leonard 1997; Callaway & Walker 1997; Hacker & Gaines 1997), the mechanism described here may be common in natural communities and may be an important force in maintaining diversity within landscapes.

Garr Updegraff wrote the original C program. We thank James P. Hoffmann for the use of his computers and Jean-Baptiste Ferdy for help with the figures. The manuscript was improved by the thoughtful comments of N. Buckley, K. Clay, C. Lively, H. Reynolds, L. Rieseberg and M. Tansey. Support for this research was provided by NSF grant DEB-9527986 to J.M. and NSF DEB-0049080 to J.D.B.

REFERENCES

- Antonovics, J. & Kareiva, P. 1988 Frequency-dependent selection and competition: empirical approaches. *Phil. Trans. R. Soc. Lond. B* **319**, 601–613.
- Ayala, F. 1971 Competition between species: frequency dependence. *Science* **171**, 820–824.
- Bertness, M. D. & Leonard, G. H. 1997 The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* **78**, 1976–1989.
- Bever, J. D. 1999 Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. *Ecol. Lett.* **2**, 52–61.
- Bever, J. D., Westover, K. & Antonovics, J. 1997 Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *J. Ecol.* **85**, 561–573.
- Bronstein, J. L. 1994 Our current understanding of mutualism. *Q. Rev. Biol.* **68**, 31–51.
- Callaway, R. M. & Walker, L. R. 1997 Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**, 1958–1965.
- Catovsky, S. & Bazzaz, F. A. 2000 The role of resource interactions and seedling regeneration in maintaining a positive feedback in hemlock stands. *J. Ecol.* **88**, 100–112.
- Chesson, P. 2000 Mechanisms of maintenance of species diversity. *A. Rev. Ecol. Syst.* **31**, 343–366.
- Clarke, B. 1969 The evidence for apostatic selection. *Heredity* **24**, 347–352.
- Durrett, R. & Levin, S. A. 1994 The importance of being discrete (and spatial). *Theor. Popul. Biol.* **46**, 363–394.
- Gifford, A., Ferdy, J.-B. & Molofsky, J. 2002 Genetic composition and morphological variation among populations of the invasive grass *Phalaris arundinacea*. *Can. J. Bot.* **80**, 779–785.
- Hacker, S. D. & Gaines, S. D. 1997 Some implications of direct positive interactions for species diversity. *Ecology* **78**, 1990–2003.
- Holley, R. A. & Liggett, T. M. 1975 Ergodic theorems for weakly interacting systems and the voter model. *Ann. Probability* **3**, 643–663.
- Hubbell, S. P. 1979 Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* **203**, 1299–1309.
- Hubbell, S. P. 2001 *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.
- Levins, R. 1974 Qualitative analysis of partially specified systems. *Ann. NY Acad. Sci.* **231**, 123–138.
- May, R. 1974 *Stability and complexity in model ecosystems*. Princeton University Press.
- May, R. M. & Anderson, R. M. 1983 Epidemiology and genetics in the coevolution of parasites and hosts. *Proc. R. Soc. Lond. B* **219**, 281–313.
- Molofsky, J. 1999 The effect of nutrients and spacing on neighbor relations in *Cardamine pensylvanica*. *Oikos* **84**, 506–514.
- Molofsky, J., Durrett, R., Dushoff, J., Griffeth, D. & Levin, S. A. 1999 Local frequency dependence and global coexistence. *Theor. Popul. Biol.* **55**, 270–282.
- Molofsky, J., Bever, J. D. & Antonovics, J. 2001 Coexistence under positive frequency dependence. *Proc. R. Soc. Lond. B* **268**, 273–277. (DOI 10.1098/rspb.2000.1355.)
- Molofsky, J., Bever, J. D., Antonovics, J. & Newman, T. J. 2002 Negative frequency dependence and the importance of spatial scale. *Ecology* **83**, 21–27.
- 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* (ed. D. Tilman & P. Kareiva), pp. 204–232. Princeton University Press.
- Petraitis, P. S. & Latham, R. E. 1999 The importance of scale in testing the origins of alternative community states. *Ecology* **80**, 429–442.
- Ricklefs, R. E. & Shluter, D. (eds) 1993 *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press.
- Ronsheim, M. L. 1996 Evidence against a frequency dependent advantage for sexual reproduction in *Allium vineale*. *Am. Nat.* **147**, 718–733.
- Ronsheim, M. L. & Anderson, S. E. 2001 Population-level specificity in the plant–mycorrhizae association alters intraspecific interactions among neighboring plants. *Oecologia* **128**, 77–84.
- Weltzin, J. & McPherson, G. 1999 Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. *Ecol. Monogr.* **69**, 513–534.
- Wilson, J. B. & Agnew, A. D. Q. 1992 Positive-feedback switches in plant communities. *Adv. Ecol. Res.* **23**, 263–336.
- Wright, S. 1943 Isolation by distance. *Genetics* **28**, 114–138.