

How species with different regeneration niches coexist in patchy habitats with local disturbances

Sandra Lavorel and Peter Chesson

Lavorel, S. and Chesson, P. 1995. How species with different regeneration niches coexist in patchy habitats with local disturbances. – *Oikos* 74: 103–114.

We used a two-species simulation model to study mechanisms of coexistence of annual plants in patchy habitats with local disturbances. In habitats with nested scales of patchiness, short dispersal is advantageous because favorable habitat tends to be aggregated. The invasion of a resident population with short dispersal distance by a species with longer-range dispersal was simulated for combinations of habitat pattern, disturbance frequency and germination strategies. A germination strategy was defined by the type of response to disturbance (“disturbance-broken” when disturbances trigger germination, “risk-spreading” when germination is insensitive to disturbance) and the dormancy fraction at dispersal. Simulations estimated the long-term low-density growth rate of the invader, the mean local crowding (number of competing seeds per invader seed at each site) and the effective fecundity of each species (the mean number of seeds successfully dispersed per adult plant). Crowding increased with habitat suitability and decreased with increasing dormancy fractions for the resident. Effective fecundity in a landscape can be taken as a measure of competitive ability. The short-dispersing resident invariably had higher effective fecundity, but this difference decreased with increasing suitability, i.e. competitive differences decreased. Coexistence depended on both habitat suitability and disturbance frequency. Maximum coexistence was obtained for habitats of intermediate suitability with moderately frequent disturbances. General linear modelling of the long-term low-density growth rate showed that coexistence results from a reduction in local crowding. This growth rate also increased for increasing habitat suitability and connectivity, and for a higher dormancy fraction of the resident species. The effects of disturbance frequency and of invader’s dormancy fraction depended on the type of dormancy of the resident species. The analysis showed that 2 different mechanisms are involved in the coexistence of species with different niches. Differences in regeneration niches permit coexistence through competitive equivalency with trade-offs between dispersal and germination traits, but for a limited range of habitat pattern and disturbance conditions. On the other hand, coexistence through density fluctuations of a disturbance-broken species and storage effects can be achieved for a broad range of environmental conditions and species germination strategies. Species coexistence thus results from the combination of two mechanisms. Evidence from natural communities is discussed. Our results also demonstrate the importance of detailed attention to spatial patterns and dispersal because of the complexity of spatial effects. Further, spatial pattern and disturbance frequencies need to be considered jointly to understand the dynamics of diversity.

S. Lavorel and P. Chesson, Research School of Biological Sciences, Australian National Univ., Canberra ACT 0200, Australia (present address of SL: Centre d'Ecologie Fonctionnelle et Evolutive, C.N.R.S. BP 5051, F-34033 Montpellier Cedex, France).

Accepted 27 February 1995

Copyright © OIKOS 1995
ISSN 0030-1299

Printed in Denmark – all rights reserved

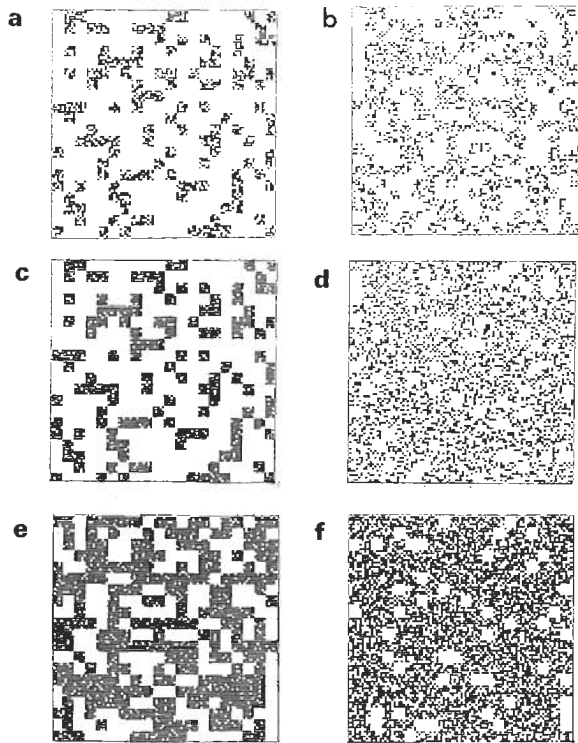


Fig. 1. Habitat maps for (a) $p_2=0.32$, $p_3=0.60$, (b) $p_2=0.60$, $p_3=0.32$. (c) $p_2=0.32$, $p_3=0.88$, (d) $p_2=0.88$, $p_3=0.32$, (e) $p_2=0.60$, $p_3=0.88$, (f) $p_2=0.88$, $p_3=0.60$.

Recent theoretical and experimental work has demonstrated the role of environmental spatio-temporal variability for species coexistence (Chesson 1986, Chesson and Case 1986, see reviews by Silvertown and Law 1987 and Wilson 1990). Chesson and Huntly (1989) proposed to unify a diversity of hypothesized mechanisms by showing that the common feature is an interaction between species biology and environmental fluctuations. The key mechanism is "storage effects" (Chesson 1983) whereby, as a result of their biologies, species which are favored differentially in time and/or space can store the demographic benefits obtained under favorable conditions and outweigh the losses in unfavorable conditions. This requires: 1) that when a species is favored by the environment it causes more competition (has a greater competitive effect, *sensu* Goldberg 1990) 2) that some trait of their biology (e.g. seed dormancy, overlapping generations) allows them to store the demographic benefits. In particular, these mechanisms would apply in the case of differences of regeneration niches (Grubb 1977), i.e. species differing in their requirements of the establishment of a new generation (Chesson 1991).

Spatial variability due to environmental heterogeneity and to disturbances is recognized as an important type of variability underlying the dynamics of species diversity (Levin 1976, Chesson 1981, 1985, Pickett and White

1985, Pacala 1989, Kareiva 1994). Species coexistence has been explained by several mechanisms leading to the spatial segregation of competitors. These mechanisms fall into two broad categories. Firstly, environmental patchiness with conditions locally suitable to different species leads to spatial niche partitioning (Whittaker and Levin 1977, Shmida and Ellner 1984, Chesson 1985, Comins and Noble 1985). Secondly, spatial segregation can result from chance colonization followed by a local build-up of propagules favoring the species that arrived first (Levin 1974, Yodzis 1978, Shigesada et al. 1979, Comins and Noble 1985, Pacala 1986a). Recently, the advances of spatially-explicit models have allowed more detailed insight into these mechanisms (see the review by Czárán and Bartha 1992). Such models have allowed deeper understanding of the role of habitat spatial pattern (Green 1989, Milne 1992, Palmer 1992), dispersal distances (Comins and Noble 1985, Pacala 1987, Molofsky 1994) and population distributions (Czárán and Bartha 1989, Silvertown et al. 1992).

Spatially-explicit simulations of community dynamics for 2 annual plant species characterized by their mean dispersal distance and their dormancy strategy (i.e. response of germination to disturbances and fraction dormant seeds at dispersal) showed that coexistence is possible in patchy habitats with local disturbances in spite of a competitive difference determined by dispersal capacities (Lavorel et al. 1994a). These results validated the hypothesis that differences in regeneration niches can lead to coexistence (Grubb 1977). However, further investigation is needed to identify the details of the mechanisms of coexistence.

We used a development of that model to address the following questions: 1) What are the specific effects on species coexistence of environmental spatial and temporal variability, resulting from habitat pattern and local disturbance respectively? 2) What differences between species regeneration niches are required for stable coexistence? 3) Is coexistence explained by competitive lottery and storage effects?

Methods

The model

The model is an extension of the simulation model by Lavorel et al. (1994a).

Habitat maps

The algorithm generates hierarchically structured habitat maps (O'Neill et al. 1992, Lavorel et al. 1993) consisting of a matrix of zeros and ones, indicating unsuitable and suitable sites for plant establishment, respectively. Three level maps are generated by a top-bottom procedure subdividing the map into blocks of ($g_i \times g_i$) sites at level i , ($i=1, 2, 3$), and randomly setting the suitability of each block with a probability p_i of encountering a suitable site

within a cell at hierarchical level i . The total number of suitable sites for plant establishment, SS , will be $(g_1 \times g_2 \times g_3)^2 (p_1 \times p_2 \times p_3)$. Different combinations of p_1 , p_2 and p_3 can produce the same total fraction of suitable sites, but will result in distinctly different landscape patterns (O'Neill et al. 1992, Lavorel et al. 1993).

Seven different random landscapes, all having the same values of g_i and p_1 , but different combinations for p_2 and p_3 were used in the simulation experiments. The successive levels within the maps were fixed at $g_1=4$, $g_2=5$ and $g_3=5$, resulting in square maps with 100 sites on a side ($g_1 \times g_2 \times g_3 = 100$). These grids may be thought of as 10×10 m plots with 10000 10×10 cm sites each representing the basal area that a herbaceous plant would cover. The larger subblocks of 2.5×2.5 m represent the area within which a herbaceous plant might be expected to deposit most of its seeds. The fraction of suitable sites at the coarser scale, p_1 , was assumed to be 1.0 for all maps, reflecting a potential vegetation cover of 100%. At finer scales, variation in microtopography, soils, nutrients and historical patterns of disturbance will affect the degree of site suitability. This variation was modelled by setting the partial probabilities (p_2) lower than 1.0 at the level of 5×5 (i.e. 50×50 cm) patches. Finally, microenvironmental conditions determine the suitability of sites at the scale of the individual plant (p_3). A single map with $p_2=p_3=1.0$ was used to create a solid homogeneously suitable landscape. Combinations of p_2 and p_3 were varied in the other maps at values of 0.32, 0.6, or 0.88, producing three pairs of maps (Fig. 1a) with the same percent suitable sites, SS , but different levels of patchiness. In each pair of maps, the landscape with the higher level of fine-scale suitability ($p_2 < p_3$) has a higher level of mean cluster size and is referred to as "aggregated" (vs "disaggregated" for the map with $p_2 > p_3$) (Lavorel et al. 1993).

Simulating population dynamics

Each suitable map site represents a place where one individual plant can germinate, establish, grow and reproduce – a 'safe site' sensu Harper et al. (1961). Density-dependent competition for establishment is simulated by a lottery process (Chesson and Warner 1981), with each species having a probability of establishment proportional to the number of viable seeds present at that site. Interference competition for space is assumed to summarize species interactions at a particular point in space (Yodzis 1986). Once a seed germinates, growth and survival to a reproductive adult will occur, and all adults will produce a fixed number of seeds each year. For the simulations presented here, fecundity of both species was set at 10 viable seeds per plant.

Seeds are dispersed by an isotropic stochastic process. A random angle and distance from the parent plant are selected and each seed is moved to a new map site. Seeds that are dispersed beyond the edge of the map are lost (i.e., the map boundaries are absorbing). The standard exponential distribution (Johnson and Kotz 1970) was

used to generate dispersal distances. An important species characteristic is mean dispersal distance. We expressed the dispersal distance in numbers of sites from the parent plant in order to scale dispersal in relation to plant sizes. For example, if a site represents an area of 10×10 cm, for a decreasing exponential to a mean of 2 sites, 90% of the seeds will land within a radius of 5 sites or 50 cm. For a mean dispersal distance of 10 sites this radius would be 2 m.

Dormancy strategy is characterized by dormancy fraction and type. The dormancy fraction (*dorm*) gives the probability of newly dispersed seeds becoming dormant. Seed survival from one year to the next was set equal to 0.2. Germination response to disturbance can be described as either 'disturbance-broken', i.e., disturbances induce the germination of all seeds present, or 'risk-spreading', i.e., disturbances do not modify the germination timing of dormant seeds (Grubb 1988). These two kinds of sensitivity to disturbance will be addressed as 'dormancy types'. The seed bank at each site is composed of an 'active' seed bank, containing readily germinable seeds, and the 'dormant' seed bank. Newly dispersed seeds join the dormant seed bank with probability *dorm*, else they are available in the active seed bank for germination at the next generation. If the species follows a risk-spreading strategy, the fraction of seeds already in the dormant seed bank which break dormancy and join the active seed bank each year is assumed to equal $(1.0 - \textit{dorm})$. If the species follows a disturbance-broken strategy, all seeds from the dormant seed bank of a given site will join the active seed bank after having been activated by a disturbance at that site.

Disturbances

Local disturbances were produced every generation in the same hierarchical pattern used to generate the maps. The disturbance pattern is generated hierarchically with the same values of g_1 , g_2 , and g_3 as the habitat maps, and is independent of the distribution of the safe sites and of the plants. Examples of such disturbances are frost heaving, digging or trampling by animals. An individual at a site is affected by disturbance by failing to reproduce that year, and the seed banks of both species for the next generation will be modified according to their types of dormancy. Disturbances were generated at the intermediate scale (g_2) of the 5×5 subblocks, i.e., $p_1=p_3=1.0$. Disturbance frequency, the proportion ($p_2 = \textit{dis}$) of sites disturbed at the intermediate level, was varied. In a spatio-temporal context, disturbance frequency represented both the extent of disturbance in any particular generation and the temporal frequency of disturbance at any particular site. In the terminology of Chesson (1985), disturbances imposed in this way represent spatio-temporal environmental variation, while the pattern of suitable sites represents pure spatial variation. There is no component of pure temporal variation, which would be temporal variation that is perfectly synchronised (perfectly correlated) over space.

Table 1. Factorial design of analysis of the variations of the low-density growth rate.

Variable	Levels
<i>SS</i> Habitat suitability	1920, 2816, 5280, 10000
<i>dis</i> disturbance frequency	0.04, 0.08, 0.16, 0.24, 0.32
dispersal distance	2, 5
dormancy type	Risk-spreading, Disturbance-broken
<i>dorm</i> dormancy fraction	0.2, 0.8

Invasion analysis

Our analysis of the mechanisms of species coexistence was based on the use of invasion analysis (Turelli 1981). Invasion analysis, identified as the only reliable technique to determine coexistence stability and strength, is a well-established technique in analytical modelling but under-utilised in simulations (Chesson and Ellner 1989). It focusses on the geometric growth rate (sometimes called the finite rate of increase) of a species introduced at low density into a stable resident population. This geometric growth rate is calculated as the ratio of the total number of seeds of a species in suitable sites at one time to the total for the previous time. A stable value of this growth rate is obtained by first allowing the invading species to achieve a stable pattern of distribution over suitable sites, apart from spatio-temporal fluctuations due to disturbances, and then calculating the growth rate. As all the environmental variation in the system is a mixture of spatial and spatio-temporal variation, with no purely temporal variation, environmental variation does not lead to large temporal fluctuations in total seed populations for the system. The dynamics of these total seed populations come from arithmetic averages over space of local population dynamics including dispersal (Chesson 1985). In this respect, the implementation of the invasibility analysis for systems dominated by spatial and spatio-temporal variation is different from that in systems dominated by temporal variation, where a geometric mean over time is taken, or equivalently, an arithmetic mean of the log of the geometric growth rate forms the basis of the analysis (Turelli 1981, Chesson 1994).

According to the invasibility criterion for spatial variation or spatio-temporal variation, a species persists in a community if its geometric growth rate at low density is greater than 1. It is then able to increase from low density. More importantly, this tendency to increase from low density prevents a species from getting extinct once it is present in a community. Conversely, if the low-density growth rate is less than 1, the invader is excluded by the resident. The species in a community have a long-term coexistence if they can each invade the community consisting of the other. The case where species have geometric growth rates equal to 1, however, has an ambiguous outcome. The species have a neutral coexistence, with no stabilizing tendency, or there may be some stabi-

lizing or destabilizing effect at high densities. Experience in this particular system implied that when both species have low-density growth rates equal to 1, coexistence is neutral: the relative abundances of the species undergo a very slow random walk, with no tendency of one species to dominate on average.

Previous simulations (Lavorel et al. 1994a) showed that, in competition for living space, a species with shorter dispersal (e.g. 1 or 2 sites) has an advantage over a species with longer dispersal (e.g. 5 or 10 sites) such that coexistence of these species required the existence of seed banks and local disturbances. Preliminary invasion simulations indicated that any species with a mean dispersal distance of 2 sites can invade any resident population with a mean dispersal distance of 5 sites. Therefore, our analysis focussed on the invasion of a resident with a mean dispersal of 2 sites by an invader with a mean dispersal distance of 5 sites.

Simulations with the resident species alone were run for 50 generations necessary to establish a spatially patterned adult and seed bank population. Then, the invading species was introduced with *SS*/100 initial seeds. This density was determined as sufficiently small to limit density-dependent effects but large enough for popula-

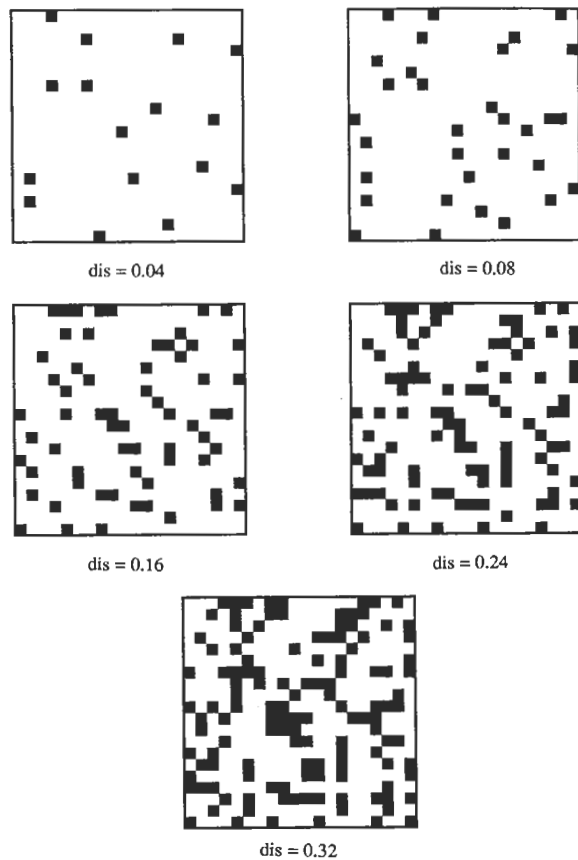


Fig. 2. Disturbance maps for (a) *dis*=0.04, (b) *dis*=0.08, (c) *dis*=0.16, (d) *dis*=0.24, (e) *dis*=0.32.

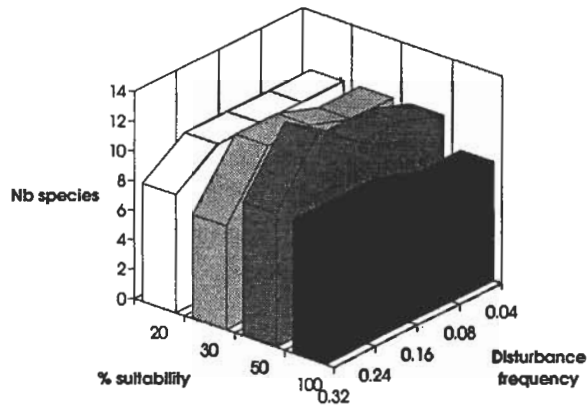


Fig. 3. Variations of number of potential two-species communities depending on habitat suitability and disturbance frequency.

tion persistence. In order to properly address coexistence in a patterned habitat, the invader was kept at low density by, at each generation, reducing its total seed density to a total of $SS/100$ but retaining the spatial distribution. This was achieved by reducing the seed number at each site proportionally to its relative contribution to the total seed density over the entire map. The invasion was run for an initial 50 generations to allow for a stable spatial distribution to be reached, then the growth rate was measured at each time step for 50 generations.

We investigated the mechanisms of coexistence by examining the low-density growth rate for combinations of species and system properties varied in a factorial design (Table 1) with 7 habitat map types representing 4 levels of suitability (Fig. 1), 5 disturbance levels (Fig. 2), 2 types of dormancy response to disturbance (risk-spreading and disturbance-broken) and 2 levels of dormancy fraction. Five simulations with 50 time steps of growth rate measures were run for each parameter set.

In order to examine the hypothesis of lottery competition more specifically, local competition at the scale of the individual site was quantified by a crowding index (*crowd*) calculated as the mean number of resident seeds competing at each site with invader seeds for establishment (i.e. the weighting factor in the lottery for establishment). The competitive differences between species with different mean dispersal distances were also estimated by calculating the ratio of their effective fecundities, defined as the mean number of seeds per plant of a species dispersed to a suitable site at each generation.

Statistical analysis

Variations of invasibility with local competition, environmental variables (number of suitable sites SS , and disturbance frequency dis), and dormancy characteristics (dormancy type and fraction) were analyzed using general linear models of the logarithm of the low-density growth rate. Preliminary analyses showed the absence of

temporal autocorrelation in the low-density growth rate. The analyses were then carried out on a subset of the growth-rate data sampled every 10 generations. Linear relationships were graphically identified between the log of the low-density growth rate ($\log GR$) and the logarithms of the crowding index and of the number of suitable sites. Linear models of the covariation of $\log GR$ with $\log SS$ and $\log crowd$, with disturbance frequency (dis) and dormancy rates ($dorm1$ and $dorm2$ for the resident and invader respectively) as co-factors were fitted using the software package GENSTAT 5.0 (NAG 1987).

Results

Patterns of species coexistence

We first look at landscape properties in terms of the total number of alternative two-species communities that could exist there. Simulations showed that the number of species pairs showing coexistence in a particular landscape (Fig. 3) varied with landscape suitability (ANOVA $F(3, 19) = 2.134$, $p = 0.018$) and disturbance frequency ($F(4, 19) = 1.863$, $p = 0.021$). The lowest numbers of potential two-species communities were observed for habitats of low suitability with very frequent disturbances and for highly suitable habitats with infrequent disturbances. The highest number of communities corresponded with intermediate levels of both habitat suitability and disturbance frequency, for which all species could coexist. Habitats of low suitability with infrequent disturbance and highly suitable habitats with very frequent disturbances exhibited intermediate numbers of potential communities.

Effective fecundities

An ANOVA showed that the ratio of effective fecundities of species with different mean dispersal distances (Fra -

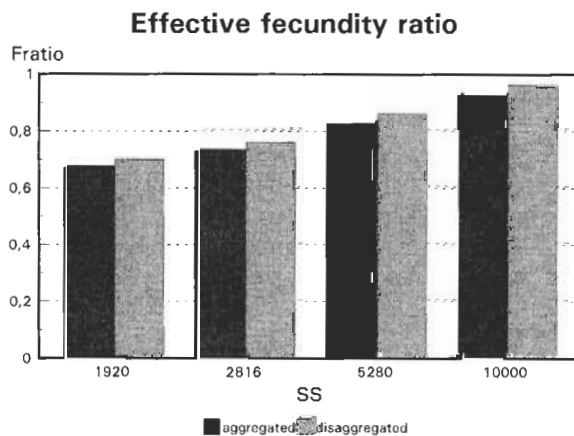


Fig. 4. Effect of landscape pattern (suitability and clumping) on the ratio of effective fecundities.

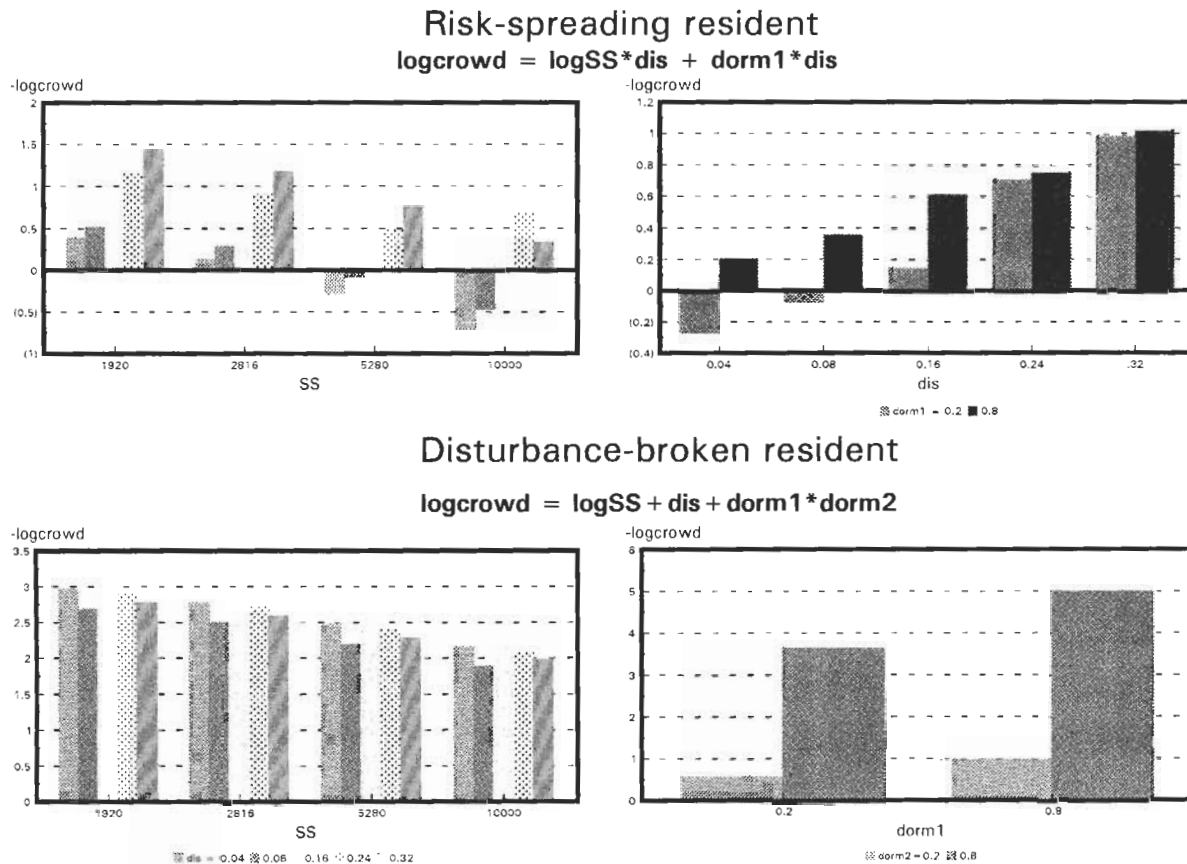


Fig. 5a. Effect of habitat suitability and disturbance on the crowding index. b. Effect of dormancy fraction on the crowding index.

tio) was independent of disturbance frequency ($p=0.305$) but depended significantly on habitat pattern described by suitability ($p < 0.001$) and clumping nested within suitability ($p < 0.001$). The species with a shorter dispersal distance had a greater dispersal advantage over the species with a larger mean dispersal distance in poorly suitable and thus disconnected habitats than in more suitable and more connected habitats (Fig. 4). This advantage disappeared for a homogeneously suitable habitat map. These patterns result from the fact that for the habitat structures used, the probability of dispersing into a suitable site close to the mother plant is greater than random and thus greater than for a larger dispersal distance (see the discussion by Lavorel et al. 1995).

Local crowding

Linear modelling of $\log\text{crowd}$ showed that the crowding index was determined in two very different manners depending on the dormancy type of the resident (risk-spreading or disturbance-broken). In both cases, the crowding increased for increasing habitat suitability (SS) and decreased for increasing resident dormancy fraction (*dorm1*) (Fig. 5). However, disturbance frequency had a significant effect only in the risk-spreading case. This is

possibly because disturbance would only decrease fecundity for a risk-spreading species, while its effects on fecundity (negative) and recruitment (positive) would compensate for a disturbance-broken species. On the other hand, in the disturbance-broken case crowding also depended on the invader's dormancy fraction (*dorm2*) because a disturbance-resident can fall locally to very low densities. On average, crowding was higher for a risk-spreading ($\mu=0.65$) than for a disturbance-broken resident ($\mu=0.077$).

Invasion growth rate

Initial analyses of the variations of the low-density growth rate with local crowding and environment for each pair of species showed a qualitative difference in the behavior of the invader's growth rate depending on the dormancy type of the resident. Then, sets of runs with the 2 different types of residents were analyzed in 2 separate groups and we present the resulting linear models separately.

As a general feature, the logarithm of the low-density growth rate ($\log GR$) for a risk-spreading resident ($\mu = 0.0588$) was lower than for a disturbance-broken resident ($\mu = 2.556$). A risk-spreading resident was hard to invade

Risk-spreading resident

logSS+logcrowd*dis+dorm1*dorm2*dis



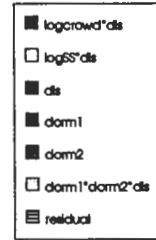
$r^2 = 0.902$

Disturbance-broken resident

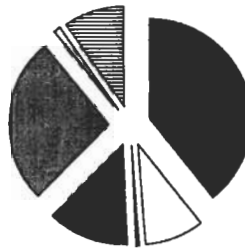
logSS*dis+logcrowd*dis+dorm1*dorm2*dis



$r^2 = 0.978$



Fratio*dis+logcrowd*dis+dorm1*dorm2*dis



$r^2 = 0.893$

Fratio*dis+logcrowd*dis+dorm1*dorm2*dis



$r^2 = 0.975$

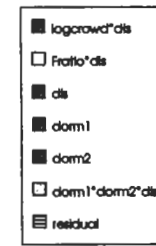
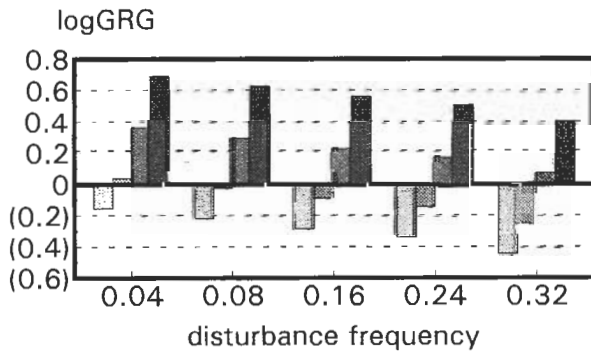
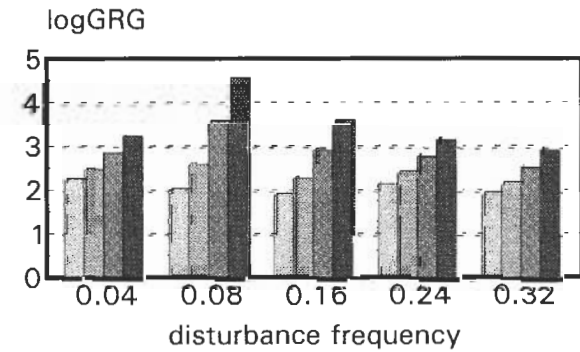


Fig. 6. Results of the linear modelling analysis of the low-density growth rate.

R-resident



D-resident



SS = 1920 2816 5280 10000

Fig. 7. Effect of habitat suitability and disturbance on the low-density growth rate.

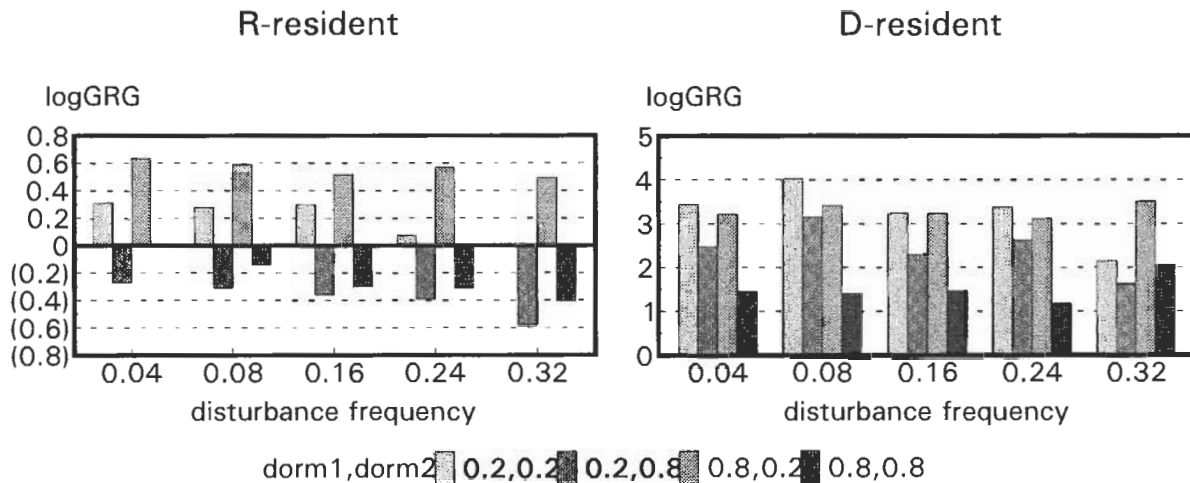


Fig. 8. Effect of dormancy fractions on the low-density growth rate.

(negative or small positive values of $\log GR$), while disturbance-broken residents were easy to invade by any other species (positive values).

In both cases, we were able to explain a highly significant portion of the variance of the low-density growth rate with the design variables (Fig. 6, r^2 values). The crowding index explained the largest part of the variance. Negative regression slopes (-0.75 for a risk-spreading resident and -1.30 for a disturbance-broken resident) showed that coexistence resulted from a decrease of local competition. This effect was much stronger for a disturbance-broken resident than for a risk-spreading resident.

The contribution of habitat suitability was larger for a risk-spreading resident than for a disturbance-broken resident (Fig. 6). In both cases, the slope of the regression was positive (0.51 and 0.61, respectively), showing that coexistence becomes easier as habitat suitability increases (Fig. 7). Such results are consistent with the trends observed for the ratio of effective fecundities.

In both cases the effect of disturbance frequency, although significant, was rather weak and mainly in interaction with other variables (Fig. 7). For a risk-spreading resident, however, there was no significant interaction with habitat suitability, and increasing disturbance frequency demoted coexistence with lower low-density growth rates. For a disturbance-broken resident, the response of the low-density growth rate to disturbance was bell-shaped, and dependent on level of habitat suitability, with a maximum at $dis=0.08$ for $SS \geq 2816$, and a minimum at $dis=0.16$ for $SS=1920$. Sensitivity to disturbance increased with increasing habitat suitability and maximum sensitivity to habitat suitability occurred for $dis=0.08$.

In both cases, the effect of the invader's dormancy fraction was negative (Fig. 8), because a larger dormancy leads firstly to a higher seed mortality through time, secondly to a lower availability of seeds for competition

during establishment. On the other hand, the effect of the resident's dormancy fraction depended on its dormancy type. The slope was positive for a risk-spreading resident but negative for a disturbance-broken resident. In fact, the low-density growth rate was determined by the combined effects of dormancy fractions of both species and of disturbance (Fig. 6). Invasion success was determined more by the invader's dormancy fraction for a risk-spreading resident, but more by the resident's dormancy fraction for a disturbance-broken resident, which can be interpreted as a dominant effect of the dormancy fraction of the disturbance-broken species.

Discussion

Using invasion analysis, we demonstrated the complexity of mechanisms underlying coexistence of species with different regeneration niches. Invasibility has been shown to relate closely to long-term stochastic coexistence (e.g. stochastic boundedness: long-term stable density fluctuations for all species in a community; Chesson and Ellner 1989). Our results support its use, as the values of long-term low density growth rate were consistent with coexistence results in previous runs (Lavelle et al. 1994a). In the past, simulations have often used time to extinction as a variable characterizing stability of coexistence (e.g. Caswell 1978). But time to extinction displays a high variance and may require very long simulations to determine its value. The low-density growth rate is a useful variable for quantitative analysis of the strength of species persistence, and will often have much better statistical properties than the time to extinction.

Mechanisms of species coexistence

We found that dispersal distance is of primary importance in the ability of a species to invade a resident population. A species with a mean dispersal distance of two sites could always invade a population of a species with a mean dispersal distance of five sites. Pacala (1986a) also found dispersal distance to be determinant of the outcome of plant competition. Hobbs and Hobbs (1987) simulated and observed in the field that the response of species dominance rankings to gopher disturbances was determined by dispersal distances. Such a result would not be expected in a homogeneous habitat, but in a heterogeneous habitat presumably reflects the risk of spreading to an unsuitable site, which increases with dispersal distances (see the discussion by Lavorel et al. 1995; see also the mother site theory for desert plants, Ellner and Shmida 1981). We did not investigate the optimal dispersal distance, although work of others suggests that it should not be zero (Levin et al. 1984, Cohen and Levin 1991). However, our simulations showed that a disadvantage in dispersal can be compensated for by germination characteristics, allowing a long dispersal species to invade and coexist with a short dispersal species.

The analysis showed that stable coexistence is achieved under environmental and biological conditions that decrease local relative densities of the more effectively dispersing species. Coexistence is known to be facilitated by an increase of intraspecific relative to interspecific competition (MacArthur 1972). Pacala (1986a) and Czárán and Bartha (1989) also explained coexistence of species with short dispersal distances by this mechanism.

The existence of significant effects on low-density growth rate of other variables once the effect of local crowding has been accounted for, indicates that local crowding does not fully capture local competition and is only one of the factors of coexistence in the context of a structured landscape with local disturbances. Lower relative densities of the resident are in fact achieved in 2 ways: reduced crowding and decreased advantage in effective fecundity. Crowding is reduced in habitats of low suitability which, for the maps used, support low population densities (see Lavorel et al. 1995), and for higher resident dormancy fractions. Reduction of the resident's advantage in effective fecundity occurs as habitat suitability increases. Various factors in life-history and environment (habitat pattern and disturbance) will modify the way effective fecundity and local competition combine to yield the actual growth rate. Our analysis showed that the mechanisms of coexistence differ depending on the type of germination response to disturbance of the species with shorter dispersal distance. The following interpretation is proposed. Risk-spreading dormancy allows a species to maintain continuous competition pressure in time and space. Only low fluctuations in densities will result from spatio-temporal variability in seed production due to disturbances and spatial variability in effective fecun-

dity due to habitat pattern. On the other hand, a disturbance-broken strategy leads to large spatio-temporal fluctuations in local density. The mean local density pressure is less than that imposed by a risk-spreading species. Although such a resident might still be competitively superior on average (as a result of the ratio of effective fecundities), density fluctuations in time and space mean that it is not always locally superior (realized competition). Recent work has emphasized that species coexistence often results from the combination of several processes rather than a single mechanism (Chesson 1994). As a summary of the two cases, we propose that decrease in local competition and coexistence are achieved in 2 complementary ways.

With differences in regeneration niches, coexistence is promoted by a trade-off between the capacity to disperse to a suitable site and the capacity for establishment determined by the germination strategy. This means that the species are very nearly equal on average, so that small regeneration niche differences are sufficient for a stable coexistence (Chesson 1991). Important in such average equality are the conditions that lead to a decrease in the competitive advantage of the species with more effective dispersal. For example, increasing habitat suitability decreases the difference in effective fecundities and thus facilitates coexistence. Dormancy increases seed loss through mortality in the seed bank, and thus higher dormancy fractions of the resident and lower dormancy fractions of the invader will favor coexistence. This mechanism was detected in both resident cases. The growth rates close to 1 ($\log GR \approx 0$) obtained in the risk-spreading case indicate that such mechanisms offer rather limited scope for coexistence in terms of environmental conditions as well as of compatible species. Pacala (1986b) and Geritz et al. (1987) also observed coexistence as a result from a trade-off between effective fecundity and seed dormancy, expressed as the life time germination success. Similarly, Liljelund et al. (1988) demonstrated coexistence of species with equivalent life time fecundities resulting from a trade-off between longevity (equivalent to our dormancy fractions) and annual seed set (equivalent to our effective fecundity). Extensive literature has addressed trade-offs between dispersal and dormancy traits within species (e.g. Venable and Brown 1988; see the review by Westoby et al. 1992) which could be extended to species coexistence. Further investigations of the effects of annual seed set and on possible trade-offs with dispersal and dormancy need investigation for our model. Finally, coexistence of unlimited numbers of species can result from trade-offs between dispersibility and competitive ability (Tilman 1994).

The second mechanism, evidenced in the case of a disturbance-broken resident and for the combined effects of resident and invader dormancy fractions (Fig. 8), is based on fluctuations in performances. These result in the existence of times and places where the invader is more favored than the resident. For example, the germination probability of the disturbance-broken resident depends on

whether or not the site is disturbed. At a given generation, all the undisturbed sites are free of competition from the resident and can be colonized by a risk-spreading invader. Disturbed sites will be colonized either by the resident or by a disturbance-broken invader depending on local seed availabilities and chance. Conditions favoring coexistence are those which either amplify these fluctuations (e.g. a lower dormancy fraction of the resident) or decrease the difference in effective fecundities (e.g. a higher suitability). The mechanisms involved are likely to be storage effects, where the resident fluctuations allow some "windows of opportunity" for invaders with a wide range of dormancy strategies. As opposed to simple differences in regeneration niches, such mechanisms of competitive lottery permit coexistence of numerous species under a wide range of environmental conditions.

These results support the claim that neither interspecific differences in regeneration niches nor environmental variability are enough in themselves to fully account for coexistence (Chesson 1991). Regeneration niche differences need to be such that the environmental fluctuations affect species differentially and that the storage effect can operate. Grubb (1988) discussed coexistence mechanisms for species within only a single dormancy type. Consistent with our findings, he proposed that different disturbance-broken species are favored at different places and times. The coexistence of risk-spreading species would result from shifting clouds of abundance (Grubb 1984, 1986), i.e. spatio-temporal density fluctuations such that interspecific competition would be avoided. Our results do not allow to test this assertion on the details of the spatio-temporal population dynamics. Further investigations need to analyze the variability of densities in time and space.

Coexistence of species with different regeneration niches, and in particular with different germination responses to disturbance, has been documented for a number of communities, such as chalk grasslands (Verkaar et al. 1983, Grubb 1986), Mediterranean annual grasslands (Grubb and Hopkins 1986, Rice 1989, Hobbs and Mooney 1991), oldfields (Armesto and Pickett 1985, Gross 1987, Lavorel et al. 1994b), desert annuals (Shmida and Ellner 1984, Venable et al. 1993, Huntly and Chesson unpubl.), and dune communities (van der Meijden et al. 1985), as well as for some marine communities (Butler and Chesson 1990). Our interpretation is consistent with experimental data for Mediterranean old fields in southern France. Model predictions that communities dominated by annual grasses (with low risk-spreading dormancy) tend to be harder to invade and with lower species richness than, for example, communities dominated by annual legumes (with strong disturbance-broken dormancy) match patterns observed through succession (Escarré et al. 1983, Debussche et al. unpubl.) and for recolonization of experimental disturbances (Lavorel et al. 1994b). In desert annuals, there is considerable evidence that species differ in germination responses to weather and time of the rain that occurs (Shmida and

Ellner 1984, Venable et al. 1993, Chesson and Huntly unpubl.), allowing for more complex differences between species than germination in response to disturbance. Coupled with between-year seed dormancy, such weather-determined regeneration niches theoretically allow coexistence of many species (Ellner 1984, Chesson 1994).

Effects of habitat spatial pattern

The detailed analysis of the effects of habitat suitability suggests that the effects of spatial patterns can be complex. *SS* had a positive effect on growth rate directly, but an indirect negative effect through local crowding, making overall effects hard to predict. As a result of these opposite trends, maximum species coexistence was obtained at intermediate levels of suitability (Fig. 3). Habitat spatial pattern was shown to critically affect species coexistence in several ways. Firstly, the magnitude of competitive differences between species determined by their dispersal distances was highly sensitive to landscape pattern. Secondly, in the case of a risk-spreading resident, a switch from exclusion to coexistence occurred for a map suitability of 5280. This threshold corresponds with a threshold in connectivity of the structured habitat maps (Lavorel et al. 1993), making dispersal differences no longer critical.

Other studies have demonstrated the relevance of spatial pattern to species coexistence. Earlier work on lottery models in a spatially variable environment (Chesson 1985, Comins and Noble 1985) showed that spatial variation in species performances, including dispersal rates into habitat patches, is a powerful promoter of species coexistence. However, this early work did not consider any detail of the interaction between habitat pattern and dispersal distance. Recent work demonstrates the necessity to explicitly consider the effects of habitat pattern on dispersal success (Doak et al. 1992, Lavorel et al. 1995) and realized competition (Czárán and Bartha 1989, Silvertown et al. 1992, Bonan 1993). Finally, intraspecific aggregation of propagules has been shown to mediate coexistence of insect (Atkinson and Shorrocks 1981, Ives and May 1985) and plant species (Pacala 1987, Marino 1991, Palmer 1992), provided the mechanism of aggregation leads to greater intraspecific than interspecific aggregation (Ives 1991). Further analysis of adult and seed specific distributions would be needed to test for the existence of such mechanisms in our model.

Effects of disturbance regime

The invasibility analyses highlight qualitative differences in the effects of disturbance for the two types of dormancy leading to a qualitative difference in the mechanism of coexistence. The quantitative effects, although significant, were small and mainly in the form of complex interactions with both habitat suitability and dormancy fractions. This finding indicates that patterns re-

lated to disturbance frequency or extent may be hard to interpret in the real world.

As another complicating factor, disturbance effects were strongly combined with effects of landscape pattern. Stability of coexistence depends not only on the species involved but also on the combined effects of landscape pattern and disturbance frequency. For any given set of species there was always some combination of landscape and disturbance frequency where stable coexistence could be achieved. But conversely, the coexistence of 2 given species will be more or less sensitive to landscape and disturbance, with different species being favored in different situations and more or less sensitive to changes in pattern and/or disturbance depending on their biology. For example, the response of low-density growth rate to disturbance frequency depended on the dormancy type of the resident. The relative roles of dispersal and response to disturbance will also vary between systems. For example, in California serpentine grasslands the community is shaped by disturbance pattern (Hobbs and Hobbs 1987, Moloney et al. 1992), while dispersal is most important in some weed communities (e.g. Czárán and Bartha 1989). It is then essential for studies of the dynamics of diversity or conservation planning to consider landscapes in a dynamic perspective including both spatial pattern and disturbance dynamics (Turner et al. 1993).

Acknowledgements – This work was funded by the Australian National University through a postdoctoral fellowship to the first author. We thank Lindsay Hood and Judy Jenkinson for help with computing, Ross Cunningham for statistical advice, and Karl Grigulis for help with data analysis.

References

- Armesto, J.J. and Pickett, S.T.A. 1985. Experiments on disturbance in old-field plant communities: impact on species richness and abundance. – *Ecology* 66: 230–240.
- Atkinson, W.D. and Shorrocks, B. 1981. Competition on a divided and ephemeral resource: a simulation model. – *J. Anim. Ecol.* 50: 461–471.
- Bonan, G.B. 1993. Analysis of neighborhood competition among annual plants: implications of a plant growth model. – *Ecol. Model.* 65: 123–136.
- Butler, A.J. and Chesson, P.L. 1990. Ecology of sessile animals on sublittoral hard substrata: The need to measure variation. – *Aust. J. Ecol.* 15: 521–531.
- Caswell, H. 1978. predator-mediated coexistence: a nonequilibrium model. – *Am. Nat.* 112: 127–154.
- Chesson, P.L. 1981. Models for spatially distributed populations: the effects of within-patch variability. – *Theor. Popul. Biol.* 19: 288–325.
- 1983. Coexistence of competitors in a stochastic environment: the storage effect. – In: Friedman, H.I. and Strobeck, C. (eds), *Population biology*. Springer, New York, pp. 188–198.
- 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. – *Theor. Popul. Biol.* 28: 263–287.
- 1986. Environmental variation and the coexistence of species. – In: Diamond, J. and Case, T.J. (eds), *Community ecology*. Harper and Row, Cambridge, pp. 240–256.
- 1991. A need for niches? – *Trends Ecol. Evol.* 6: 26–28.
- 1994. Multispecies competition in variable environments. – *Theor. Popul. Biol.* 45: 227–276.
- and Warner, R.R. 1981. Environmental variability promotes coexistence in lottery competitive systems. – *Am. Nat.* 117: 923–943.
- and Case, T.J. 1986. Overview: Nonequilibrium community theories: chance, variability, history, and coexistence. – In: Diamond, J. and Case, T.J. (eds), *Community ecology*. Harper and Row, New York, pp. 229–239.
- and Ellner, S.P. 1989. Invasibility and stochastic boundedness in two-dimensional competition models. – *J. Math. Biol.* 27: 117–138.
- and Huntly, N. 1989. Short-term instabilities and long-term community dynamics. – *Trends Ecol. Evol.* 4: 293–298.
- Cohen, D. and Levin, S.A. 1991. Dispersal in patchy environments: the effects of temporal and spatial structure. – *Theor. Popul. Biol.* 39: 63–99.
- Comins, H.N. and Noble, I.R. 1985. Dispersal, variability, and transient niches; species coexistence in a uniformly variable environment. – *Am. Nat.* 126: 706–723.
- Czárán, T. and Bartha, S. 1989. The effect of spatial pattern on community dynamics; a comparison of simulated and field data. – *Vegetatio* 83: 29–239.
- and Bartha, S. 1992. Spatiotemporal dynamic models of plant populations and communities. – *Trends Ecol. Evol.* 7: 38–42.
- Doak, D.F., Marino, P.C. and Kareiva, P.M. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. – *Theor. Popul. Biol.* 41: 315–336.
- Ellner, S. 1984. Asymptotic behavior of some stochastic difference equation population models. – *J. Math. Biol.* 19: 169–200.
- and Shmida, A. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? – *Oecologia* 51: 133–144.
- Escarré, J., Houssard, C., Debussche, M. and Lepart, J. 1983. Evolution de la végétation et du sol après abandon cultural en région méditerranéenne: étude de la succession dans les Garrigues du Montpelliérais (France). – *Acta Oecol. Ecol. Plant.* 4: 221–239.
- Geritz, S.A.H., Metz, J.A.J., Klinkhamer, P.G.L. and De Jong, T.J. 1987. Competition in safe sites. – *Theor. Popul. Biol.* 33: 161–180.
- Goldberg, D.E. 1990. Components of resource competition in plant communities. – In: Grace, J.B. and Tilman, D. (eds), *Perspectives on plant competition*. Academic Press, San Diego, CA, pp. 27–49.
- Green, D.G. 1989. Simulated effects of fire, dispersal and spatial pattern in competition within forest mosaics. – *Vegetatio* 82: 139–153.
- Gross, K.L. 1987. Mechanisms of colonization and species persistence in plant communities. – In: Jordan, W., Gilpin, M. and Aber, J. (eds), *Restoration ecology: theory and practice*. Cambridge Univ. Press, Cambridge, pp. 173–188.
- Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. – *Biol. Rev.* 52: 107–145.
- 1984. Some growth points in investigative plant ecology. – In: Cooley, J.H. and Golley, F.B. (eds), *Trends in ecological research for the 1980's*. Plenum Press, New York, pp. 51–74.
- 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. – In: Diamond, J. and Case, T.J. (eds), *Community ecology*. Harper and Row, New York, pp. 207–225.
- 1988. The uncoupling of disturbance and recruitment, two kinds of seed bank, and persistence of plant populations at the regional and local scales. – *Ann. Zool. Fenn.* 25: 23–36.
- and Hopkins, A.J.M. 1986. Resilience at the level of the plant community. – In: Dell, B., Hopkins, A.J.M. and La-

- mont, B. B. (eds), Resilience in mediterranean-type ecosystems. Junk, Dordrecht, pp. 21–38.
- Harper, J. L., Clatworthy, J. N., McNaughton, I. H. and Sagar, G. R. 1961. The evolution of closely related species living in the same area. – *Evolution* 15: 209–227.
- Hobbs, R. J. and Hobbs, V. J. 1987. Gophers and grasslands: a model of vegetation response to patchy soil disturbance. – *Vegetatio* 69: 141–146.
- and Mooney, H. A. 1991. Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. – *Ecology* 72: 59–68.
- Ives, A. R. 1991. Aggregation and coexistence in a carrion fly community. – *Ecol. Monogr.* 61: 75–96.
- and May, R. M. 1985. Competition within and between species in a patchy environment: relations between microscopic and macroscopic models. – *J. Theor. Biol.* 115: 65–92.
- Johnson, N. L. and Kotz, S. 1970. Distributions in statistics. Continuous univariate distributions. – Houghton Mifflin, Boston.
- Kareiva, P. 1994. Space: The final frontier for ecological theory. – *Ecology* 75: 1.
- Lavorel, S., Gardner, R. H. and O'Neill, R. V. 1993. Analysis of patterns in hierarchically structured landscapes. – *Oikos* 67: 521–528.
- , O'Neill, R. V. and Gardner, R. H. 1994a. Spatio-temporal dispersal strategies and annual plant species coexistence in a structured landscape. – *Oikos* 71: 75–88.
- , Lepart, J., Debussche, M. and Lebreton, J. D. 1994b. Small scale disturbances and the maintenance of species diversity in Mediterranean old fields. – *Oikos* 70: 455–473.
- , Gardner, R. H. and O'Neill, R. V. 1995. Dispersal of annual species in hierarchically structured landscapes. – *Landsc. Ecol.*, in press.
- Levin, S. A. 1974. Dispersal and population interactions. – *Am. Nat.* 108: 207–228.
- 1976. Population dynamics models in heterogeneous environments. – *Annu. Rev. Ecol. Syst.* 7: 287–310.
- , Cohen, D. and Hastings, A. 1984. Dispersal strategies in patchy environments. – *Theor. Popul. Biol.* 26: 165–191.
- Liljelund, L., Ågren, I. G. and Fagerström, T. 1988. Succession in stationary environments generated by interspecific differences in life-history parameters. – *Ann. Zool. Fenn.* 25: 17–22.
- Marino, P. C. 1991. The influence of varying degrees of spore aggregation on the coexistence of the mosses *Splachnum ampullaceum* and *S. luteum*: a simulation study. – *Ecol. Model.* 58: 333–345.
- May, R. M. 1972. Will a large complex ecosystem be stable? – *Nature* 238: 413–414.
- Milne, B. T. 1992. Spatial aggregation and neutral models in fractal landscapes. – *Am. Nat.* 139: 32–57.
- Molofsky, J. 1994. Population dynamics and pattern formation in theoretical populations. – *Ecology* 75: 30–39.
- Moloney, K. A., Levin, S. A., Chiariello, N. R. and Buttel, L. 1992. Pattern and scale in a serpentine grassland. – *Theor. Popul. Biol.* 41: 257–276.
- NAG 1987. Genstat Release 5.0. – Numerical Algorithms Group Ltd.
- O'Neill, R. V., Gardner, R. H. and Turner, M. G. 1992. A hierarchical neutral model for landscape analysis. – *Landsc. Ecol.* 7: 55–61.
- Pacala, S. W. 1986a. Neighborhood models of plant population dynamics. II Multi-species models of annuals. – *Theor. Popul. Biol.* 29: 262–292.
- 1986b. Neighborhood models of plant population dynamics. IV Single and multi-species models of annuals with a seed bank. – *Am. Nat.* 128: 859–878.
- 1987. Neighborhood models of plant population dynamics. III Models with spatial heterogeneity in the physical environment. – *Theor. Popul. Biol.* 31: 359–392.
- 1989. Plant population dynamics theory. – In: Roughgarden, J., May, R. M. and Levin, S. A. (eds), *Perspectives in ecological theory*. Princeton Univ. Press, Princeton, NJ, pp. 54–67.
- Palmer, M. W. 1992. The coexistence of species in fractal landscapes. – *Am. Nat.* 139: 375–397.
- Pickett, S. T. A. and White, P. 1985. The ecology of natural disturbances and patch dynamics. – Academic Press, New York.
- Rice, K. J. 1989. Competitive interactions in California annual grasslands. – In: Huenneke, L. F. and Mooney, H. A. (eds), *Grassland structure and function: California annual grassland*. Kluwer, Dordrecht, pp. 59–71.
- Shigesada, N., Kawasaki, K. and Teramoto, E. 1979. Spatial segregation of interacting species. – *J. Theor. Biol.* 79: 83–99.
- Shmida, A. and Ellner, S. 1984. Coexistence of species with similar niches. – *Vegetatio* 58: 29–55.
- Silvertown, J. W. and Law, R. 1987. Do plants need niches? – *Trends Ecol. Evol.* 2: 24–26.
- , Holtier, S., Johnson, J. and Dale, P. 1992. Cellular automaton models of interspecific competition: the effect of pattern on process. – *J. Ecol.* 80: 527–534.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. – *Ecology* 75: 2–16.
- Turelli, M. 1981. Niche overlap and invasion of competitors in random environments. I. Models without demographic stochasticity. – *Theor. Popul. Biol.* 20: 1–56.
- Turner, M. G., Romme, W. H., Gardner, R. H., O'Neill, R. V. and Kratz, T. K. 1993. A reversed concept of landscape equilibrium: Disturbance and stability on scaled landscapes. – *Landsc. Ecol.* 8: 213–227.
- van der Meijden, E., de Jong, T. J., Klinkhamer, P. G. L. and Kooi, R. E. 1985. Temporal and spatial dynamics of biennial plants. – In: Haeck, J. and Woldendorp, J. W. (eds), *Structure and functioning of plant populations 2*. North-Holland, Amsterdam, pp. 91–103.
- Venable, D. L. and Brown, J. S. 1988. The selective interactions of dispersal, dormancy and seed size as adaptations for reducing risk in variable environments. – *Am. Nat.* 131: 360–384.
- Venable, L., Pake, C. E. and Caprio, A. C. 1993. Diversity and coexistence of Sonoran desert winter annuals. – *Plant Species Biol.* 8: 207–216.
- Verkaar, H. J., Schenkeveld, A. J. and Van de Klashorst, M. P. 1983. The ecology of short-lived forbs in chalk grasslands: Dispersal of seeds. – *New Phytol.* 95: 335–344.
- Westoby, M., Jurado, E. and Leishman, M. 1992. Comparative evolutionary ecology of seed size. – *Trends Ecol. Evol.* 7: 368–372.
- Whittaker, R. H. and Levin, S. A. 1977. The role of mosaic phenomena in natural communities. – *Theor. Popul. Biol.* 12: 117–139.
- Wilson, J. B. 1990. Mechanisms of species coexistence: twelve explanations for Hutchinson's "paradox of the plankton": evidence from New Zealand plant communities. – *N. Z. J. Ecol.* 13: 17–42.
- Yodzis, P. 1978. Competition for space and the structure of ecological communities. – Springer, Berlin.
- 1986. Competition, mortality, and community structure. – In: Diamond, J. and Case, T. J. (eds), *Community ecology*. Harper and Row, New York, pp. 480–491.