Spatially realistic plant metapopulation models and the colonization–competition trade-off

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Summary

1 Results from patch-occupancy metapopulation models indicate that a trade-off between competitive and colonization abilities is necessary for species to coexist in patchy environments. However, such models are often based on unrealistic ecological assumptions, such as global dispersal and no local population dynamics.

2 We develop a plant metapopulation model that allows us to sequentially relax unrealistic assumptions about dispersal and local population interactions. We use our model to examine the extent to which the conclusions of analytical, patch-based coexistence models depend on their assumptions.

3 We found that the need for an inferior competitor to be a superior colonizer was reduced by using a dispersal kernel to distribute seeds, and totally removed by relaxing the assumption of instantaneous competitive displacement. These results hold for annual or perennial plants with or without seedbanks, for global, local and stratified dispersal, for delayed competitive exclusion, two-way competition and neighbourhood competition, and for landscapes where habitat patches are either adjacent or disjunct.

4 We conclude that the results of patch-occupancy metapopulation models differ greatly from results of models that incorporate more realistic assumptions about dispersal and local population dynamics. As a result it may be premature to base biodiversity management and policy on the results of patch-occupancy models.

Key-words: dispersal, long-distance seed dispersal, local population dynamics, competition, landscape connectivity

Introduction

A major goal of ecology is to understand factors that determine the diversity of species within communities. For sessile organisms, a trade-off between competitive ability and colonization ability has long been suggested as a mechanism that promotes the coexistence of species in patchy environments (Skellam 1951; Hutchinson 1951; Levins & Culver 1971). Among such competition-colonization trade-off models, the hierarchical, patch-occupancy model developed by Hastings (1980), Nee & May (1992), Tilman (1994) and others (hereafter referred to as the occupancy model) has been particularly influential (Kareiva & Wennergren 1995; McCarthy et al. 1997; Eriksson & Kivimaki 1999; Lindenmayer 1999). Insights from competition-colonization models have influenced how ecologists view a wide range of theoretical and conservation issues, including species coexistence, limiting similarity, species packing, successional dynamics and the loss of species due to habitat destruction.

The occupancy model follows the dynamics with which two or more competitive species occupy a large set of patches. Two important assumptions are made that allow the development of a simple and elegant model. First, it is assumed that the environment is homogeneous and that there is complete mixing of the populations. This assumption allows the spatial arrangement of patches to be ignored. Because this assumption also means that dispersal is equally likely among patches, we refer to it as the assumption of global dispersal. Secondly, it is assumed that within-patch population dynamics do not influence the outcome of metapopulation dynamics. Specifically, this assumption means that competition is absolute and instantaneous,
that is, inferior competitors cannot persist, reproduce or establish in the presence of superior competitors. Equilibrium solutions of the occupancy model reveal that an inferior competitor can coexist with a superior competitor, provided that $c_i > c_s/e$ (where $c_i$ and $c_s$ are the colonization rates of the inferior and superior species and $e$ is the rate at which all occupants are removed from a patch (Hastings 1980; Tilman 1994).

Results from occupancy models indicate that a trade-off between colonization and competition is necessary for species coexistence, but such trade-offs are imperfect or absent (Banks 1997). Several observations support the existence of colonization-competition trade-offs in plants. Trade-offs have been found between allocation to roots (leading to high competitive ability) and allocation to reproduction (leading to high colonization ability) (Tilman 1990; Tilman & Wedin 1991a, b). Other evidence comes from correlations with seed size: small-seeded species tend to produce smaller seedlings and have lower establishment success (Westoby et al. 1996), and they tend to be competitively inferior to larger seeded species (Rees 1995). Small seeds also have low descent velocities and therefore may have better dispersal abilities (Okubo & Levin 1989), and small-seeded species tend to produce more seeds (Jakobsson & Eriksson 2000) and therefore may be better colonizers. However, it should be noted that many vertebrate-dispersed seeds are widely dispersed despite being large. Seed mass and seed morphology also often correlate poorly with a species' long-distance dispersal ability (Webb 1986; Wilkinson 1997), the primary determinant of colonization ability (Clark 1998; Cain et al. 1998; Higgins & Richardson 1999). Moreover, competitive ability as a seedling may have little bearing on adult competitive ability (Saverimuttu & Westoby 1996). Indeed, empirical studies suggest that colonization-competition trade-offs are imperfect or absent (Banks 1997).

Overall therefore we do not find the empirical evidence for colonization-competition trade-offs compelling. In a modelling context, this leads us to ask, under which conditions is a trade-off between colonization and competitive ability necessary for coexistence? We address this question by developing a discrete analogue of the occupancy model and then sequentially relaxing its assumptions; this procedure allows us to examine whether predictions from occupancy models hold when we no longer assume global dispersal and instantaneous competition. Relaxing these assumptions opens a Pandora’s box of potentially overwhelming biological detail. Notably, when we no longer assume global dispersal we need to specify whether patches are adjacent or disjunct and specify a kernel that distributes seeds between patches. The dispersal kernel could either restrict seeds to the local environment or allow some long-distance dispersal (a stratified dispersal kernel; Cain et al. 2000; Nathan & Muller-Landau 2000). Similarly, relaxing the assumption of no within-patch population dynamics forces us to specify which demographic processes (seed production, seed dormancy, recruitment, mortality) operate within the patch, and how they are influenced by competition and the size of the neighbourhood over which the competitive interactions operate. Consideration of within-patch dynamics also means that we need to separate the effects of catastrophe (‘patch mortality’) from longevity (‘individual mortality’) on mortality rates. In other words, we are forced to be explicit about whether the patch is occupied by a population of plants or by an individual plant. In the former case the model may be thought of as a metapopulation model, in the latter as an individual-based model.

Many studies have relaxed some of the assumptions of the occupancy model. In a study that relaxed global dispersal to neighbourhood dispersal (dispersal only to neighbouring cells in a discrete lattice) and immediate competitive exclusion to delayed competitive exclusion, Tilman et al. (1997) found the patch occupancy model’s predictions regarding the sequence of species extinction following habitat loss to be robust. Neuhäuser (1998) also examined the sequence of species extinctions following habitat loss, and found that the occupancy model’s predictions were robust for most patterns of habitat loss investigated. Adler & Mosquera (2000) show that the nature of competitive advantage assumed in the occupancy model is sufficient to predict coexistence. Furthermore, Yu & Wilson (2001) relaxed the assumption of absolute and instantaneous competitive exclusion, and found that the competition-colonization trade-off was insufficient to generate coexistence. Bolker & Pacala (1999) provide another perspective; they explored the effects of local dispersal kernels and local competitive neighbourhoods in homogeneous spatial environments and showed that a trade-off between colonization and competition was not needed for coexistence. Similarly, Holmes & Wilson (1998) showed that a colonization-competeition trade-off was not necessary for coexistence when the inferior competitor dispersed globally and the superior competitor was rare and dispersed locally.

Collectively these seemingly conflicting results suggest that the predictions of the occupancy model may not be robust. Our aim is to examine the consequences of assumptions made regarding plant life-history, competition, dispersal and patch arrangement on the predictions of the occupancy model. At the occupancy model’s predictions regarding the sequence of species extinctions following habitat loss were to be robust. Our aim is to examine the consequences of assumptions made regarding plant life-history, competition, dispersal and patch arrangement on the predictions of the occupancy model. At the occupancy model’s predictions regarding the sequence of species extinctions following habitat loss were to be robust. Our aim is to examine the consequences of assumptions made regarding plant life-history, competition, dispersal and patch arrangement on the predictions of the occupancy model. At the occupancy model’s predictions regarding the sequence of species extinctions following habitat loss were to be robust. Our aim is to examine the consequences of assumptions made regarding plant life-history, competition, dispersal and patch arrangement on the predictions of the occupancy model.
the stratified nature of dispersal, catastrophic disturbance, the spatial location of each patch, and the plant life-history type. We use our model to explore the conditions under which an inferior competitor can coexist with a superior competitor when the assumptions of the patch-occupancy model are relaxed in a sequential manner. Although the model can simulate the ecological processes listed above it can also be parameterized to represent a discrete analogue of the analytical occupancy model. This allows us to systematically add detail to the model and thereby explore the consequences of two fundamental assumptions of the occupancy model (global dispersal and no local population dynamics).

The model is a coupled map lattice model, that is, it considers the dynamics of a series of spatially linked populations (Fig. 1). The model landscape is a two-dimensional grid of \( d \times d \) cells, each cell is potentially a patch of habitat that can be occupied by \( K \) plants of each of two competing species (\( N_x, N_y \)). The size of the competitive neighbourhood (\( w \)) relative to the patch sizes (\( d \)) defines the level of competitive mixing in each patch. In the simulations below we consider two levels of competitive mixing (Fig. 1). In mixed patches (\( w = d \)) competition is between all individuals in the patch, whereas in neighbourhood patches (\( w < d \)) competition is only between individuals in the local neighbourhood. By varying the size of the landscape (\( h \)) we can simulate different interpatch distances (we use 100 patches for all simulations). When \( h \) is appropriately small a system of adjacent patches is represented, when \( h \) is large a system of disjunct patches is represented (Fig. 1). When patches are disjunct they are arranged at random locations in the landscape. The boundaries of the landscape are assumed to be periodic.

Each iteration (1 year) of the model sequentially simulates catastrophes, seed production, seed dispersal, adult mortality, germination and establishment, and seed decay (Fig. 1). The sequence of simulating these processes is important: simulating catastrophes before seed production ensures that local extinction can occur, while simulating mortality before recruitment, but after seed production and dispersal, ensures that short-lived plants produce seeds before dying and that space is released by death for new recruitment. Where appropriate we denote these different time intervals as: \((t)\), current year; \((t + \Delta 1)\), after catastrophe; \((t + \Delta 2)\), after mortality; and \((t + 1)\), next year.

Catastrophes are modelled as:

\[
N_x(j, t + \Delta 1) = N_x(j, t) - e_j N_x(j, t), \quad \text{eqn 1}
\]

Here \( N_x(j, t + \Delta 1) \) is the size of the population in the \( j^{th} \) patch of species \( x \) after the catastrophe (i.e. at time \( t + \Delta 1 \)). The frequency of catastrophe (\( e \)) defines whether a catastrophe occurs; \( e \) is the outcome of a Bernoulli trial for patch \( j \). We assume that catastrophes affect species equally and patches independently.

The seed production of the \( j^{th} \) patch of species \( x \) (\( SP_x \)) is

\[
SP_x = r_x N_x(j, t + \Delta 1) \left[ 1 - \frac{\beta_y N_y(j, t + \Delta 1)}{K} \right], \quad \text{eqn 2}
\]

where \( r_x \) is the fecundity of species \( x \), \( K \) is the carrying capacity and \( \beta_y N_y(j, t + \Delta 1) \) is the effect of interspecific density on seed production. The term in brackets in equation 2 is constrained to be positive. We assume that intraspecific competition does not influence seed production, this allows a population at carrying capacity (\( K \)) to produce the maximum number of seeds.
This assumption is consistent with the occupancy model and seems appropriate for plants, as seed production is not prevented in closed monospecific stands even though such stands recruitment may be non-existent in the absence of adult mortality. Effects of intraspecific competition are included at the recruitment stage (equation 5). To simulate the occupancy model’s assumption that the inferior competitor cannot reproduce in patches occupied by the superior competitor we set $K = 1$, and $\beta_j = 1$ if species $y$ is the superior competitor and $\beta_j = 0$ if species $x$ is the inferior competitor.

For simulations where we assume global dispersal, every patch has an equal probability of receiving seeds and all seeds land in a patch; this assumption matches the assumption of the occupancy model. For kernel dispersal we use a mixture of exponential distributions to describe the distance ($\text{disp}$.; metres) that seeds are dispersed from each source habitat as:

$$f(s) = p_{1h_1} \exp\left( -\frac{s}{h_1} \right) + p_{2h_2} \exp\left( -\frac{s}{h_2} \right), \text{eqn 3}$$

where $p_1$ is the proportion of seeds that are dispersed short distances, $\lambda_1$ is the mean of short-distance dispersal (metres); $p_2$ is the proportion of seeds dispersed long distances (where $p_2 = 1 - p_1$), and $h_2$ is the mean of long-distance dispersal (metres). For local dispersal we set $p_1$ to 1 (and $p_2$ to 0). Dispersal is implemented by using a distance (randomly drawn from the above distribution) and a random direction to calculate the position of each dispersed seed in the two-dimensional landscape. All seeds are dispersed from the centre of the competitive neighbourhood (see Fig. 1). Seeds that land in habitable patches are added to the seedbank ($\text{SB}_{xj}$) and are available for recruitment.

Mortality is simulated before recruitment, this allows space vacated by mortality to be used for recruitment. The number of adults surviving to time $t + \Delta t$, $N_{xj}(t + \Delta t)$, is

$$N_{xj}(t + \Delta t) = s_x N_{xj}(t + \Delta t)\left[1 - \frac{1}{K} N_{yj}(t + \Delta t)\right], \text{eqn 4}$$

where $s_x$ is the survivorship rate of species $x$, $\gamma_y$ is the effect of species $y$ on the survivorship of species $x$, $K$ is the carrying capacity and $N_{yj}(t + \Delta t)$ is the size of the $j$th population of species $x$ after the catastrophe ($t + \Delta t$). The term in brackets in equation 4 is constrained to be positive. The inclusion of the density-dependent term in equation 4 allows the presence of an interspecific competitor to increase the mortality rate of the other species. This is perhaps unrealistic for many plant interactions, but it allows us to simulate the occupancy model’s assumption that the superior competitor can immediately displace the inferior competitor (by setting $K = 1$, and $\gamma_x = 1$ if species $y$ is the superior competitor and $\gamma_x = 0$ if species $x$ is the inferior competitor). Further, the occupancy model only considers mortality due to catastrophes (equation 1), for this reason survivorship ($s$) is set to 1 when representing the occupancy model.

Recruitment of seeds into the adult population determines the population size in the next iteration $N_{xj}(t + 1)$:

$$N_{xj}(t + 1) = N_{xj}(t + \Delta t) + G_x, \text{eqn 5a}$$

$$G_x = g SB_{xj} \left[1 - \frac{N_{xj}(t + \Delta t) + \alpha_x N_{yj}(t + \Delta t)}{K}\right], \text{eqn 5b}$$

Here $G_x$ is the number of seeds germinating, ($SB_{xj}$) is the seed density of species $x$ at patch $j$ and $g_x$ is the germination rate of species $x$ (for all simulations presented here we assume $g = 1$); the term in brackets allows intraspecific ($N_{yj}(t + \Delta t)$) and interspecific ($\alpha_x N_{yj}(t + \Delta t)$) densities to influence germination (this term is constrained to be positive). To simulate the occupancy model’s assumption that the inferior competitor cannot recruit in patches occupied by the superior competitor we set $K = 1$, and $\alpha_x = 1$ if species $y$ is the superior competitor or $\alpha_x = 0$ if species $x$ is the inferior competitor.

Seeds that do not germinate decay at rate $u_y$:

$$SB_{yj}(t + 1) = SB_{yj} - u_y [SB_{yj} - G_y], \text{eqn 6}$$

**SIMULATION EXPERIMENTS**

**Long-distance dispersal and colonization rates in metapopulations**

We first perform a simulation experiment that aims to determine the factors that define colonization rates. In the occupancy model the colonization (seed arrival) rate equals the rate of seed production (that is, all seeds land in suitable habitat). To facilitate comparison between models we define colonization rate as the mean number of seeds arriving per habitat patch per year. We use a factorial experimental design to quantify the effect of fecundity ($r$), the proportion of long-distance dispersal ($p$), the local dispersal ability ($\lambda_x$), the long-distance dispersal ability ($\lambda_y$), and the inter-patch distance (the linear dimension of the square landscape, $h$, was varied to create different interpatch distances) on the observed colonization rate. A 2$^4$ design was used: each of five factors was assigned a high and a low level (Table 1). The parameter levels were selected to be consistent with values reported in the literature. The complete factorial was replicated 10 times. Each run was initiated with a single species (at an initial density of half $K$, $K = 10 000$) occupying all habitat patches and run for 1000 years; the colonization rate (mean number of seeds arriving in a habitat patch per year) was recorded from each run.

**Competition, local population dynamics, dispersal and coexistence in metapopulations**

The second simulation experiment investigates interactions between superior and inferior competitors in
metapopulations by sequentially relaxing two important assumptions of the occupancy model: no local population dynamics and global dispersal. These simulations cover a broad range of assumptions one could make when simulating dispersal, competition, patch configuration and life histories of plants.

For dispersal we consider either global dispersal, local dispersal or stratified dispersal. Global dispersal is simulated by allocating seeds to patches with equal probability (i.e. the relative position of source and destination patches does not influence the seed rain and no seeds fail to land in a patch). Global dispersal mimics the dispersal assumptions of the occupancy model. Kernel dispersal (both local and stratified cases) assumes that seed rain declines with distance from source (equation 3) and that seed may fail to land in a suitable patch. The local dispersal case assumes that dispersal is short tailed (\( p_1 = 1 \)), whereas the stratified dispersal case assumes that the dispersal kernel has a longer tail (\( p_1 > 0 \) and \( \lambda_2 > \lambda_1 \)). In this simulation experiment, we parameterize the local and stratified dispersal kernels in such a way that the overall mean dispersal distances of both kernels are equal; this means that the variance of the stratified dispersal kernel is greater than the variance of the local dispersal kernel. The mean dispersal distances used are consistent with values reported by Wilson (1993).

For competition we consider either instantaneous competition (instant competitive displacement), absolute competition (absolute competitive advantage but delayed competitive displacement), two-way competition (reduced competitive advantage), or neighbourhood competition (reduced competitive advantage where competitive effects are restricted to local neighbourhoods). In the instantaneous competition case, a patch can only be occupied by a single species and competition instantaneously favours the superior competitor, i.e. the inferior competitor cannot persist, produce seeds or recruit in the presence of the superior competitor. The instantaneous competition case closely mimics the demographic assumptions of occupancy models, in that local population dynamics do not occur. In the absolute competition case, the inferior competitor remains invisible to the superior competitor but the performance of the inferior competitor is dependent on the density of the superior competitor: when the superior competitor is at high density the inferior competitor cannot persist, produce seeds or recruit. Thus, in effect, competitive exclusion is time-lagged in the absolute competition case.

In the two-way competition case, competitive effects are not absolute or instantaneous and the inferior competitor is not invisible to the superior competitor: although both species experience interspecific competitive effects, the superior competitor has a sufficient advantage to drive the inferior competitor to extinction in a close local population. Neighbourhood competition is the most realistic competition model we consider: here competition is simulated as for two-way competition, but competitive interactions are restricted to the local neighbourhood. That is, the competition neighbourhood (\( w \)) is smaller than the patch size (\( d \), Fig. 1).

To explore the broad effects of life history, we consider either annual plants with seedbanks or perennial plants without seedbanks. These different life histories are simulated by varying adult longevity (\( s \)) from an annual to a long-lived perennial and rates of seedbank decay (\( a \)) from no seedbank to a moderately persistent seedbank. Finally, to explore the effects of landscape configuration we consider either adjacent patches or disjunct patches by varying the size of the landscape (\( h \), Fig. 1).

The four types of competition modes, three types of dispersal, two types of landscape configuration and two life history types yield 48 potential cases of the simulation model. Some (8) of these cases are identical: for global dispersal no distinction between adjacent and disjunct patches can be made. The parameter values in Table 2 define the scenarios. Fecundity (\( r \)) values are varied for each simulation to create a range of colonization rates. For the superior competitor we draw fecundity values from a uniform distribution that spans a range from values that allow persistence in single species cases to values that allow quasi-equilibrium patch occupancies < 1. For the inferior competitor fecundity values are also drawn from a uniform distribution that spans a range from values that allow persistence in single species cases to values that allow quasi-equilibrium patch occupancies of 1. For each simulated case 1000 simulations, each with a different pair of fecundity values, were run. Each simulation was run for 500 years before an outcome (both species persist, both species go extinct, only the superior competitor persists, or only the inferior competitor persists) was assigned. For the catastrophe rates we consider 500 years is long enough for a true outcome to emerge. The outcome, the time it takes to reach the outcome and the colonization rate (mean number of seeds arriving

<table>
<thead>
<tr>
<th>Factor</th>
<th>Low level</th>
<th>High level</th>
</tr>
</thead>
<tbody>
<tr>
<td>( r )</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>( p_1 )</td>
<td>0</td>
<td>0.01</td>
</tr>
<tr>
<td>( \lambda_1 )</td>
<td>2 m</td>
<td>10 m</td>
</tr>
<tr>
<td>( \lambda_2 )</td>
<td>50 m</td>
<td>500 m</td>
</tr>
<tr>
<td>( h^* )</td>
<td>5 km</td>
<td>20 km</td>
</tr>
</tbody>
</table>

*Landscape size (\( h \), km) is varied to change the interpatch distance (for \( h = 5 \) km interpatch distance is approximately 0.25 km for \( h = 20 \) km interpatch distance is approximately 1 km).
Spatially realistic metapopulation models

in a habitat patch per year) of each species were recorded for analysis.

All the coexistence simulations were initiated with 33% of the patches occupied by the superior competitor. The superior competitor was allowed to reach a quasi-equilibrium occupancy by running the model for 100 years, after which the inferior competitor was introduced to 15% of sites (the superior competitor was removed from the sites where the inferior competitor was introduced). These initial conditions were selected because they represent a relatively strict coexistence criterion where an inferior competitor must invade, from low densities, an established superior competitor.

Results

LONG-DISTANCE DISPERSAL AND COLONIZATION RATES IN METAPOPULATIONS

There was no relationship between mean colonization rate and the overall dispersal distance (mean of both short- and long-distance dispersal) for a range of fecundity, dispersal and landscape connectivity parameterizations (Fig. 2a). This implies that the overall mean dispersal distance, which largely reflects local dispersal abilities, may often be a poor predictor of colonization rates. A more detailed understanding of what constitutes colonization rate is provided by the factorial experimental design described in Table 1. An ANOVA of this design showed that colonization is influenced by fecundity, the proportion of seeds that move long distances, mean distance of long-distance dispersal and interpatch distance ($P < 0.001$ for all factors), but not by the mean distance of local dispersal ($P = 0.504$). In addition, the colonization rate is affected by interactions between all factors, except those involving the mean distance of local dispersal (Fig. 2b). Because interaction effects were often as strong as main effects, one cannot predict colonization ability from information on a single factor alone.

Table 2. Parameter levels used for the different cases of the simulation experiment that explores the conditions under which persistence and coexistence can occur between competing species in metapopulation models. The average interpatch distance for simulations where patches are disjunct is 80 m ($d = 12.15$ km). For all simulations we draw values of $r$ from uniform distributions; the ranges of $r$ are scaled so as to ensure persistence in single species cases.

<table>
<thead>
<tr>
<th>Competition modes</th>
<th>Instantaneous</th>
<th>Absolute</th>
<th>Two-way</th>
<th>Neighbourhood</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameter</td>
<td>Superior</td>
<td>Inferior</td>
<td>Superior</td>
<td>Inferior</td>
</tr>
<tr>
<td>$\beta$</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>1</td>
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<td>1</td>
<td>0</td>
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<td>$\gamma$</td>
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<td>0</td>
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<td>$K$</td>
<td>1</td>
<td>1</td>
<td>81</td>
<td>81</td>
</tr>
<tr>
<td>$c$ (m)</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>$d$ (m)</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
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</table>

Dispersal modes

<table>
<thead>
<tr>
<th>Global</th>
<th>Local</th>
<th>Stratified</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superior</td>
<td>Inferior</td>
<td>Superior</td>
</tr>
<tr>
<td>$p_0$</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>$\lambda_1$ (m)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>$\lambda_2$ (m)</td>
<td>–</td>
<td>–</td>
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</tbody>
</table>

Life history modes

<table>
<thead>
<tr>
<th>Annual with seedbank</th>
<th>Perennial no seedbank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superior</td>
<td>Inferior</td>
</tr>
<tr>
<td>$e$</td>
<td>0.2</td>
</tr>
<tr>
<td>$r^*$</td>
<td>0</td>
</tr>
<tr>
<td>$u$</td>
<td>0.25</td>
</tr>
<tr>
<td>$g$</td>
<td>1</td>
</tr>
</tbody>
</table>

*To mimic the occupancy model when instant competition is simulated $s = 1$. 

strong colonization advantage ($c_i > e_i c_j$), where $c_i$ and $c_j$ are the colonization rates of the inferior and superior species and $e$ is the rate at which all occupants are removed from a patch (Hastings 1980). We devise a statistical test for whether a colonization advantage is needed by the inferior competitor for it to coexist with the superior competitor using the empirical cumulative density function of $c_i - c_j$. If more than 0.1 of the simulations where coexistence is reported have $c_i - c_j < 0$, we conclude that the inferior competitor does not need a colonization advantage to coexist with the superior competitor.

With respect to species coexistence, we showed that an inferior competitor could coexist with a superior competitor under a much broader set of conditions than allowed in patch-occupancy models, such as Hastings (1980) or Tilman (1994). By varying how life history, competition, dispersal and the location of patches were represented in our model, our simulations covered a broad set of cases. We found that local or stratified dispersal reduced the need for an inferior competitor to have a colonization advantage in order to coexist with a superior competitor and that using realistic local competition functions totally removed this need. Overall, our results suggest that results from previous models, but rather were a result of a complex set of interactions also involving other factors. These results indicate colonization rates cannot be predicted from information on a single factor, such as fecundity or mean dispersal distance; data on infrequent long-distance dispersal, fecundity and habitat connectivity are all essential. The interacting set of factors that influenced colonization rates suggests that important information may be lost in applications of models, such as patch-occupancy models, that use a single parameter to describe colonization rates.

Discussion

We constructed a spatially explicit metapopulation model that includes the occupancy model of Hastings (1980) as a special case. We used the model to sequentially relax two important assumptions of the occupancy model, namely no local population dynamics and global dispersal, with the aim of detecting the dependency of the conclusions of the occupancy model on its simplifying assumptions. The occupancy model assumes that fecundity is equal to colonization rate. Colonization rates in the spatially explicit metapopulation model were not related to mean dispersal distance or fecundity in the simple manner suggested by previous models, but rather were a result of a complex set of interactions also involving other factors. These results indicate colonization rates cannot be predicted from information on a single factor, such as fecundity or mean dispersal distance; data on infrequent long-distance dispersal, fecundity and habitat connectivity are all essential. The interacting set of factors that influenced colonization rates suggests that important information may be lost in applications of models, such as patch-occupancy models, that use a single parameter to describe colonization rates.

We found that local or stratified dispersal reduced the need for an inferior competitor to have a colonization advantage in order to coexist with a superior competitor and that using realistic local competition functions totally removed this need. Overall, our results suggest that results from
Spatially realistic metapopulation models

patch-occupancy models concerning species coexistence depended strongly on the assumptions of no local population dynamics and global dispersal, neither of which is realistic.

While our results show that there are many situations in which colonization competitor trade-offs are not needed to explain species coexistence in patchy environments, it is not immediately clear what mechanisms are preventing competitive exclusion. We believe that, in our model, coexistence is promoted by refuges from competition: kernel dispersal creates spatial refuges, whereas local population dynamics create temporal refuges. Under local and stratified dispersal most (all in the case of local dispersal) dispersal is restricted, leading to spatial aggregation amongst populations of a species (i.e. spatial mixing is prevented). The consequent aggregation of local populations means that a population is more likely to have intraspecific than interspecific neighbours, hence effects of interspecific competition become less important than the effects of intraspecific competition. Spatial refuges therefore reduce the need for the inferior species to have a large colonization advantage in order to coexist with a superior competitor. Temporal refuges are created by using competition functions that allow the inferior competitor to persist, albeit sometimes only briefly, in a local patch before being excluded by the superior competitor. This brief period of persistence may be sufficient.
time for the inferior competitor to disperse seeds into a patch where the competitor may be absent.

This interpretation of spatial and temporal refuges is consistent with Lavorel et al. (1994) who, in a simulation model of annual plant competition, showed how temporal and spatial storage mechanisms both promoted species coexistence. More formally, a recent analysis of spatial and temporal mechanisms of plant competition (Bolker & Pacala 1999) has shown that spatial and temporal refuges increase the likelihood of coexistence. Bolker & Pacala (1999) used moment closure techniques to derive an analytically tractable model that approximates the spatial aggregation and temporal refuge effects operating in our models. Bolker and Pacala show how spatial aggregation of the superior competitor can increase the space available for the inferior competitor to invade. Similarly, any negative spatial association between the two competitors allows the inferior competitor to avoid competitive confrontations with the superior competitor. Bolker and Pacala also analyse the temporal refuge hypothesis; they show that temporal refuges can be exploited when the inferior competitor has a higher reproductive rate and when the carrying capacity (K) is large. As reproductive and colonization rates are not always correlated (cf. Figure 2b), this temporal refuge can potentially operate independently of differences in colonization rates.

We found that the mechanisms that Bolker & Pacala (1999) identified can explain the qualitative behaviour of our model. This is even true for the cases of our model that consider situations where the analytical approximations used by Bolker and Pacala are not strictly valid (such as disjunct patches). Bolker & Pacala (1999) emphasized the importance of short-distance dispersal for promoting spatial aggregation. However, for landscapes comprised of disjunct patches, local dispersal kernels have the disadvantage (relative to kernels that incorporate long-distance dispersal) that they need to be combined with unrealistically high fecundity rates to ensure that colonization rates exceed extinction rates. In this regard, stratified dispersal kernels hold the advantage in that they allow colonization rates to exceed extinction rates, while maintaining biologically reasonable fecundity parameters. In addition, because stratified dispersal kernels mean that most seeds travel only short distances, stratified dispersal offers the same positive effect that localized dispersals display in allowing individuals to escape interspecific competition. It therefore seems that stratified dispersal offers the advantages of both global dispersal (metapopulation persistence) and local dispersal (interspecific avoidance).

Few studies of species coexistence provide explicit links between empirical systems and theoretical models. Empirical tests of analytical models are rare because of the abstract nature of the models and their parameters. In contrast, simulation models hold the advantage that their parameters can often be estimated directly from empirical systems (e.g. Pacala et al. 1993), although their behaviour can be complex and difficult to interpret. However, new analytical tools allow simulation models to be interpreted with the help of analytical
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approachments (e.g. Bolker & Pacala 1999, Law & Dieckmann 2000). These developments suggest that better links between analytical, simulation and empirical systems are now possible.

To develop links between our model predictions and empirical systems we would need to parameterize our model for a real plant metapopulation and investigate the empirically defined range of behaviours that the model exhibits. Such an enterprise highlights the need to obtain elusive empirical data, such as estimates of the location of suitable habitat (a major challenge as occupied patches may be ‘sinks’ and unoccupied habitat may be suitable but not yet colonized, Eriksson & Kiviniemi 1999), measures of landscape connectivity (Tischendorf & Fahrig 2000) and estimates of long-distance dispersal ability (Cain et al. 2000). Only with such data will we be able to estimate parameters for more realistic metapopulation models, and then use those models with confidence to address important applied issues, such as the response of species to habitat loss, habitat fragmentation and other forms of environmental change.

Finally, as model predictions change greatly depending on how competition and colonization are represented, and as the modes of competition and colonization assumed in patch-occupancy models are highly unrealistic, our results urge caution when interpreting the result of patch-occupancy models in an applied context (McCarthy et al. 1997). Patch-occupancy models have played and can continue to play an important heuristic role, as illustrated by the large impact of Lande (1987) on forest management practices in the United States of America. However, with respect to the details of how habitat destruction affects patterns of species extinction and other important issues, we think it would be premature to base management decisions on results from occupancy models (e.g. Nee & May 1992, Tilman et al. 1994) until those results are confirmed by models that consider more realistic competition and dispersal processes.

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