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Patchy disturbance favours longer dispersal distance

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ABSTRACT

Question: How does the spatial pattern of habitat disturbance and availability affect the selection of dispersal distance?

Modelling approach: We use an individual-based simulation model. By looking at the outcome of competition between individuals using different dispersal distances, the model simulates the selection of dispersal distance. Both habitat and disturbance are spatially structured and can range from a purely random pattern, through a fractal to complete aggregation (a solid block).

Conclusions: The disturbance regime affects the selection of dispersal distance more strongly than landscape pattern does. Spatial aggregation of disturbance favours the selection of longer dispersal distances. Lower habitat availability favours shorter dispersal distances. When disturbance is not highly autocorrelated, aggregation of suitable habitat favours shorter dispersal distances.

Keywords: fractals, population model, simulations, spatial autocorrelation.

INTRODUCTION

Local population changes depend on the balance of forces between rates of birth, death, immigration and emigration. A great deal of theoretical attention has long been devoted to the first two of these processes, the so-called 'vital rates' of a population (see, for example, Begon *et al.*, 2005), but the latter two have been the subject of much less discussion until recently. Both immigration rates and emigration rates depend critically on dispersal, and thus the evolution of dispersal should rightfully have a key position in life-history theory. Dispersal is also a key to understanding spatial population processes; indeed, it is the force that allows populations to spread across a landscape, and the connecting tissue of any metapopulation. Thus the study of dispersal is of great theoretical and applied importance. The study of dispersal in the field faces many difficulties and thus relevant studies are few (but see Clark *et al.*, 1999; Clobert *et al.*, 2001; Nathan *et al.*, 2001, 2002). However, many theoretical studies have attempted to explain how dispersal evolved and what its consequences are for the fitness of organisms.

From an evolutionary perspective, three mechanisms have been proposed for the appearance of dispersal:

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- *Avoidance of inbreeding depression*. Juveniles remaining in their natal patch will be more likely to mate with their relatives and thus face a greater danger of inbreeding depression (e.g. Perrin and Mazalov, 1999).
- *Kin selection*. The overall fitness of a genotype increases if the related offspring disperse and do not compete for the same limited resources (Ronce *et al.*, 2000).
- *Temporal and spatial variability of the environment*. In a highly variable environment, the carrying capacity of any patch may decrease unpredictably, and so the local population may face overcrowding. By dispersing to another formerly unsuitable (but now suitable) patch, it will utilize more efficiently the available resources and increase its fitness compared with a species that does not disperse (Fretwell and Lucas, 1970). Moreover, disturbance may lead any local population to extinction, and dispersal allows a population to spread the risk by occupying many habitat patches, increasing the chance that some local populations will persist (Venable and Brown, 1988; Hanski, 1999).

These studies focused on the evolution of dispersal rate, assuming that dispersal was either global (from a well-mixed dispersal pool) or local (from directly neighbouring cells, as stepping stone dispersal). However, in real life dispersal is not only characterized by its rate, but also by the distance that the individuals disperse. Different species disperse at considerably different distances; some only fractions of a metre away from the parent, while others many kilometres away (e.g. Shanks *et al.*, 2003).

Recently, several studies have focused on the evolution of dispersal distance. To examine optimal seed size, Ezoe (1998) tested the hypothesis that as seed size increases, the dispersal distance decreases, increasing the probability of survival and establishment. Savill and Hogeweg (1998) studied the evolution of dispersal distance on a predator–prey system. They found that the dispersal distance of both predator and prey and the scale of interaction increases over evolutionary time, until they exceed the available simulated space. With and King (1999) examined the effect of dispersal distance on dispersal success (the arrival of a propagule on suitable habitat) in landscapes with different spatial distributions of habitat. They showed that when habitat is aggregated, short-range dispersers have a higher probability of successful colonization of vacant patches. Hovestadt *et al.* (2001) studied the evolution of the dispersal kernel on landscapes with spatially structured habitat. They found that spatially autocorrelated habitat distribution favours the selection of fat-tailed dispersal kernels [i.e. most individuals disperse near their natal patch but a small group disperses over long distances (Johnson and Webb, 1989)]. Such distributions raise a number of problems, including the fact that in model analyses the invasion front accelerates without limit. This and other difficulties have been discussed by Clark *et al.* (2001). Rousset and Gandon (2002) showed how dispersal distance may increase to avoid competition among relatives, even if there is a distance-dependent mortality risk. Finally, Murrell *et al.* (2002) found that dispersal distance may evolve as a response to complex population dynamics at the patch level.

Most studies on the evolution of dispersal highlight the fact that dispersal is affected by environmental variability and that it affects a population's survival probability. The models explored to date have assumed either that the system is not subject to any external disturbance, or that disturbance operates at the finest scale (e.g. at the level of the individual or the patch) in a spatially random pattern (i.e. without correlation). In nature, most disturbances are physical processes correlated on multiple spatial and temporal scales. For example, disturbances may vary from the death of an individual organism (fine-scale,

random process), through regional disturbances that can take out local populations, up to the global events that affect entire species ranges. This patchiness of disturbance is known to affect a species' population dynamics (Kallimanis *et al.*, 2005) and therefore we expect it to affect the evolution of dispersal in general and of dispersal distance in particular. In the present study, we assess the effect of the spatial and temporal pattern of disturbance on the selection of an optimal dispersal strategy.

OUR MODEL

Experimental settings

To study the selection of an optimal dispersal strategy, we followed an approach similar to that of McPeek and Holt (1992). Using this approach, we allow many populations with different dispersal characteristics to exist simultaneously under the same environmental conditions. We focus in particular on the effects of the quantity and spatial arrangement of available habitat, and of the spatial pattern of the disturbance regime.

Habitat availability refers to the amount of suitable habitat as a percentage of the total landscape area. In this sense, different amounts of habitat availability could signify different amounts of habitat loss from a once continuous habitat. Habitat spatial arrangement investigates the effects of habitat fragmentation and ranges from totally random to highly aggregated. Disturbance leads to the death of the individual occupying the disturbed cell, and we investigate the effect of different spatial patterns of this disturbance.

At the beginning of each run, 80% of the suitable cells were randomly assigned as occupied. Each simulation was initially seeded with equal proportions of 50 populations that all had the same dispersal rate but different dispersal distances (see below).

Each simulation time step starts with a disturbance event to be followed by recolonization through dispersal. Every disturbed cell becomes vacant and immediately available for recolonization. When more than one propagule arrives at the same vacant suitable cell, only one establishes according to the competition rule, described below.

In each simulation run, the disturbance–dispersal cycle is repeated for 500 time steps (generations). Each simulation run is completed after 500 generations, or before if it goes extinct earlier. In the latter case, the generation when the simulation went extinct was recorded. At the end of the 500 generations, we recorded the size of each population (how many cells it occupies across the landscape). For each combination of habitat availability, landscape pattern and disturbance regime, we repeated the process 15 times.

Landscape generator

The experimental arena consists of a square lattice of 65,536 (256×256) cells. Each cell can be characterized as either suitable or not, as habitat or as matrix (i.e. we do not simulate any qualitative variation among suitable cells). The borders of the arena are periodic – that is, when an individual crosses the border at any point, it re-enters from the opposite side of the lattice. At each run, a percentage of the lattice cells were defined as suitable (habitat availability). This percentage varied between 10% and 100%. At each time step, a suitable cell may either be occupied or empty. Within each cell, only a single individual may establish and reproduce.

The landscape was generated using an iterative process appropriate for a grid-based arena, similar to the null model described by Gardner (1999). In the first iteration, the lattice was considered as one cell suitable for colonization. At each subsequent iteration (scale of resolution = i), each suitable cell was divided into four quarters and a random number between 0 and 1 was assigned to each. If this random value was less than p_i, a specified probability of occupation for iteration i, then the quarter was characterized as suitable. The operation was repeated, dividing each occupied quarter into four new quarters, for a total of eight iterations. The probabilities p_i were chosen so that their product was equal to a pre-specified proportion p of suitable habitat in the final landscape $p = \prod_{i=1}^{8} p_i$. For our simulations, we used two variants of this generator and a block landscape generator:

- The *random* landscape: $p = p_8$, $p_1 = p_2 \ldots = p_7 = 1$. This landscape is characterized by gaps only at the finest scale (that is, single cells).
- The *fractal* landscape: $p_1 = p_2 = \ldots = p_8$, $p = p_i^8$. In this case with constant occupation probability for all scales, the result is the percolation model described by Falconer (1990).
- The *block* landscape consisted of a single block of habitable cells, with gaps only at the coarsest scale.

Dispersal

Each individual is defined by two dispersal characteristics: dispersal rate and dispersal distance. In our simulations, the propagules inherit the dispersal characteristics of their parents.

Dispersal rate refers to the number of propagules dispersed by each individual at each generation. This rate is not associated with any cost for the parent, and therefore can be thought of as the population's intrinsic growth rate. In pilot simulations, we examined the selection of dispersal rate in our model and since dispersal rate is not associated with any cost for either parent or propagule, maximum dispersal rate was always selected for. Therefore, we only present results where all populations had the same dispersal rate. Three cases were examined with dispersal rate 2, 8 or 16 propagules per individual per generation. Dispersal rate was held constant – that is, demographic stochasticity in reproduction was ignored.

Each propagule ends up in a new cell, starting from its natal cell and randomly selecting an angle and a distance. Distance is a random value that comes from an exponential decay distribution. The probability for a propagule to choose a distance diminishes exponentially as distance increases. In the exponential decay distribution, there is no maximum value. Therefore, we define the dispersal distance of the individual as the distance (in number of cells) within which 90% of the propagules will end up. This distribution is widely used for the simulation of dispersal (e.g. Hanski, 1999; Travis and Dytham, 2002). In our model, dispersal is passive (e.g. anemochorous seed dispersal), and there is no mechanism for searching for suitable patches, so a propagule may bypass one or more suitable patches and continue to a different patch, even if it is unsuitable. The 50 dispersal types competing in our simulations had characteristic dispersal distances varying from 1 to 246 cells, in steps of 5 cells.

We did not explicitly simulate any dispersal-induced mortality. However, propagules faced two sources of mortality: not reaching an available patch, or competition with other propagules for establishment in a patch. Therefore, dispersal-induced mortality varied significantly and was dependent on both exogenous factors (landscape pattern, habitat availability) as well as on endogenous factors (population density for competition).

Disturbance

Disturbance may be characterized by many parameters. In this study, we were interested in three features of disturbance: its extent, and its spatial and temporal pattern.

For simplicity, we defined a single value for the disturbance extent. At each generation the same proportion of cells, 30% of the landscape, is disturbed. The landscape borders are periodic for these disturbance events, just as they are for dispersal.

We were especially interested in the pattern of the disturbance. We simulated four disturbance regimes. These regimes were based on the notion that in nature there are several processes that disturb the natural systems. These processes operate at different spatial scales and with different frequencies at each scale. More specifically, the disturbance regimes simulated are as follows:

1. *Random disturbance*. Disturbance operates at the finest scale of one cell, and has a random spatial pattern (homogeneous Poisson distribution).
2. *Fine-scale disturbance*. Disturbance is due to eight different processes that operate at eight scales [from the scale of 1 cell up to the scale of 16,384 (128×128) cells]. The number of cells that each process disturbs is inversely proportional to its spatial scale. More specifically, on average, the process that operates at the finest scale (1 cell) contributes 50% of the disturbed cells. The process that operates at the next scale (4 cells) contributes 25% and so on. The coarsest scale process contributes approximately 1% of the disturbed cells, and thus it occurs with a frequency of once every 83 generations.
3. *Fractal disturbance*. Disturbance is again due to eight different processes that operate at eight scales. Contrary to the previous regime, in this case each process contributes an equal number of disturbed cells on average (12.5% of the total extent). In this case, the coarsest scale process occurs with a frequency of once every 8 generations.
4. *Block disturbance*. Disturbance operates at a single scale, the coarsest. At each generation a large square gap is created.

Competition rules

Competition is especially important in our simulations. In this model, competition occurs for space and propagules can only establish in suitable vacant cells. When a propagule reaches a suitable but occupied cell, it disappears. This is appropriate for plant species and sessile animal species that compete only for establishment on new vacant patches, where the new seedling cannot competitively exclude an established mature individual. If more than one propagule ends up in the same cell, the one to be established is selected according to a competition rule.

Two different competition rules were simulated. First, as a null model, we assumed that all propagules are equally efficient colonizers and one is selected at random for establishment. Alternatively, we assumed that the dispersal distance is inversely correlated with

competitive ability. Propagules that disperse longer distances tend to be smaller (so as to be lighter and better able to be carried long distances by wind), and therefore have smaller energy reserves, and are likely to be at a competitive disadvantage. If such propagules end up in the same cell with those from short-range dispersers, they are unlikely to be established.

We did not examine kin selection, so kinship did not influence the outcome of competition in our simulations.

RESULTS

Our simulation results show that the evolution of dispersal distance is highly dependent on both landscape characteristics and disturbance regime (Table 1). Figure 1 shows the distribution of dispersal distances in the populations persisting after 500 time steps for the null competition model in random and block landscapes under random and block disturbance regimes. As can be seen, the pattern of disturbance has a greater effect on the composition of the population than does landscape pattern. Under spatially random disturbance, short-range dispersers are favoured and dominate after 500 generations, especially with limited habitat availability. Also in the case of aggregated habitat, the range

Table 1. The distribution of dispersal distances persisting after 500 generations for different landscape patterns and disturbance regimes. The dispersal distances presented are the median [minimum/maximum] values for each combination. In all cases the dispersal rate is 16 individuals per cell per generation. (a) Null competition rule with all species having equal competitive abilities. (b) Competition rule in which short-distance dispersers have a competitive advantage over longer-distance dispersers

		Landscape pattern		
Disturbance type	Habitat availability	Random	Fractal	Block
(a)				
Random	Low	6 [6/6]	6 [1/11]	6 [6/11]
	High	23 [6/156]	16 [6/156]	23 [6/161]
Fine	Low	6 [6/11]	6 [6/11]	8 [6/11]
	High	51 [21/216]	51 [6/186]	52 [6/191]
Fractal	Low	16 [16/26]	16 [11/71]	21 [6/16]
	High	125 [31/226]	126 [26/211]	124 [6/186]
Block	Low	96 [76/111]	66 [31/171]	extinct
	High	191 [121/246]	191 [131/246]	191 [126/246]
(b)				
Random	Low	1 [1/6]	1 [1/1]	1 [1/1]
	High	1 [1/1]	1 [1/1]	1 [1/1]
Fine	Low	6 [6/6]	1 [1/1]	1 [1/1]
	High	1 [1/1]	1 [1/1]	1 [1/1]
Fractal	Low	6 [6/6]	6 [6/6]	extinct
	High	1 [1/86]	1 [1/26]	1 [1/36]
Block	Low	6 [6/41]	6 [6/21]	extinct
	High	6 [1/131]	1 [1/61]	1 [1/121]

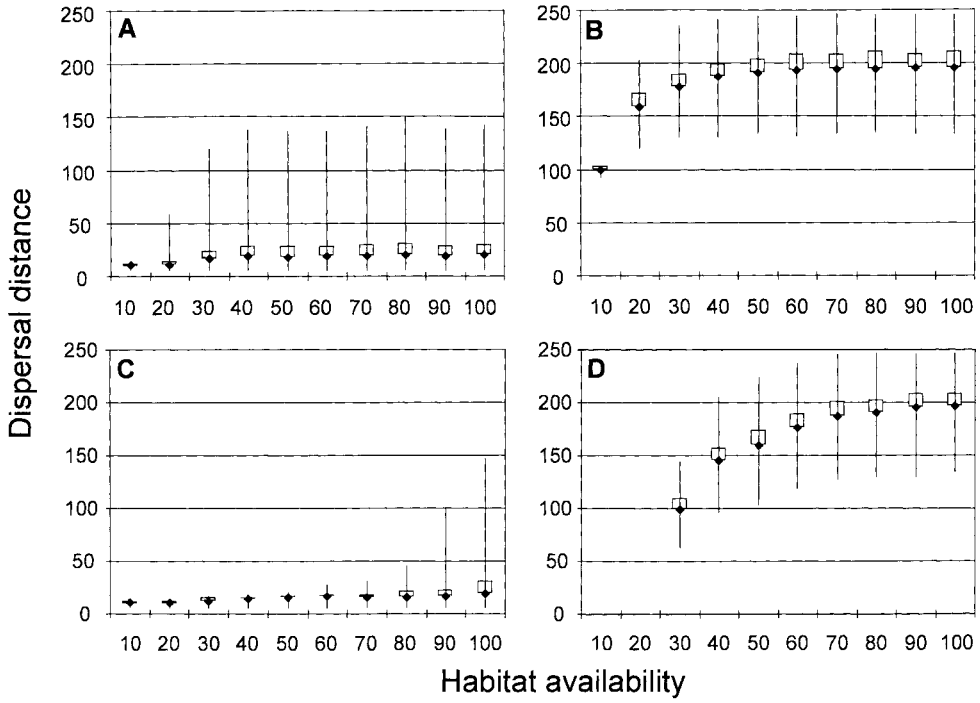

Fig. 1. Box and whiskers plots for the distribution of dispersal distances persisting after 500 generations, with dispersal rate equal to 16 individuals per cell per generation. The diamonds refer to the median value, the boxes cover the 2nd and 3rd quartiles, and the whiskers cover the minimum to maximum range. Runs on: (A) random landscape under random disturbance; (B) random landscape under block disturbance; (C) block landscape under random disturbance; and (D) block landscape under block disturbance.

of co-existing dispersal distances is decreased. Where populations face spatially aggregated disturbance regimes, however, short-range dispersers go extinct and longer-range dispersers are favoured.

We have also examined two intermediate disturbance regimes, with more classes of disturbance operating but with different frequencies. The results of these intermediate regimes are presented in Fig. 2 and lie between the extremes presented in Fig. 1. The populations persisting under fine-scale disturbance resemble more strongly the ones under random disturbance, whereas the populations persisting under fractal disturbance more closely resemble those under block disturbance. It would appear that the frequency of the coarsest-scale disturbance event plays a significant role in shaping the population persisting after 500 generations. If such events are very rare, the short-range dispersers dominate while the longer-range dispersers are driven to extinction.

Landscape effects can be divided into effects of habitat availability and of spatial pattern. Habitat availability has a more pronounced effect. Low habitat availability makes persistence harder and favours shorter-range dispersers and less polymorphism in dispersal distance (Figs. 1 and 2). As habitat availability increases, the contribution of short-range dispersers in the population decreases, while more classes of longer-range dispersers persist.

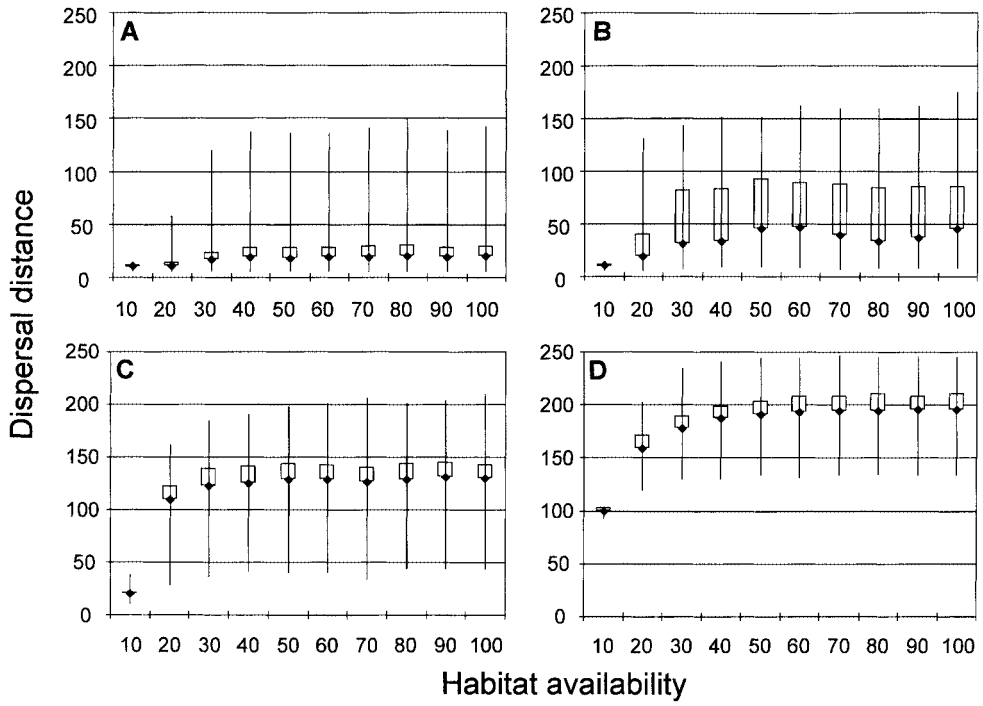

Fig. 2. Box and whiskers plots for the distribution of dispersal distances persisting after 500 generations, with dispersal rate equal to 16 individuals per cell per generation. The diamonds refer to the median value, the boxes cover the 2nd and 3rd quartiles, and the whiskers cover the minimum to maximum range. All panels refer to block landscape: (A) random disturbance; (B) fine-scale disturbance; (C) fractal disturbance; and (D) block disturbance.

Landscape pattern has a less strong effect, with spatial aggregation of habitat favouring the persistence of short-range dispersers.

We have repeated these analyses with different dispersal rates. Figure 3 presents the results for a dispersal rate of two propagules per individual per generation. More specifically, Fig. 3 displays the distribution of dispersal distances in the populations persisting after 500 time steps for random and block landscape under random and block disturbance regimes. As the dispersal rate decreases, the extinction probability for the entire population increases, and so habitat availability becomes more important for the persistence of the population. Furthermore, as dispersal rate decreases, the population size decreases and so does the polymorphism regarding dispersal distance. However, the trends in the selection of dispersal distance persist. Disturbance regime is still more influential than landscape pattern, and while aggregated disturbance favours intermediate- to long-range dispersers, aggregated landscapes favour short-range dispersers.

Finally, we also examined the effect of dispersal distance being inversely correlated with competitive ability (Table 1b). We found that our results are robust to the presence of competition related to dispersal. There are quantitative differences with the results presented above, but all the trends discussed are still present. Disturbance regime is more influential than landscape pattern and habitat availability is more important than habitat

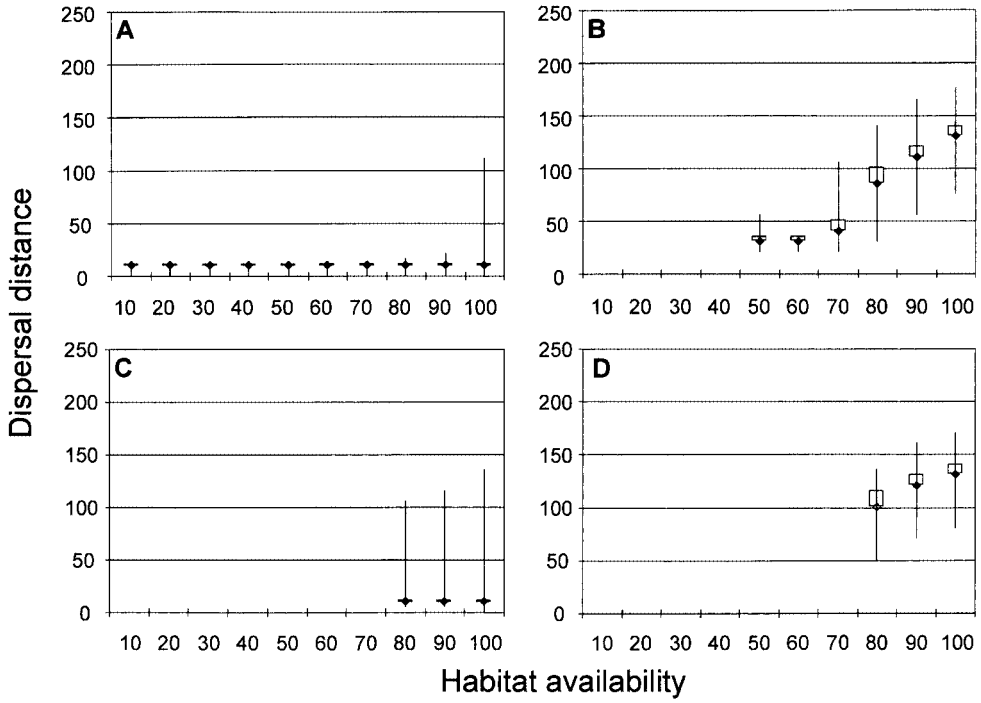

Fig. 3. Box and whiskers plots for the distribution of dispersal distances persisting after 500 generations, with dispersal rate equal to two individuals per cell per generation. The diamonds refer to the median value, the boxes cover the 2nd and 3rd quartiles, and the whiskers cover the minimum to maximum range. Runs on: (A) random landscape under random disturbance; (B) random landscape under block disturbance; (C) block landscape under random disturbance; and (D) block landscape under block disturbance.

configuration. Because of the advantage given to short-range dispersers under this competition rule, the median dispersal distance is greatly reduced here, relative to the results of the null competition model. Interestingly, the range of co-existing strategies also decreases, despite the fact that competition–colonization trade-offs are generally believed to increase the likelihood of co-existence among competitors (e.g. Tilman, 1994).

DISCUSSION

In this model, we studied the persistence of different populations in a spatially structured world – that is, under spatially explicit habitat distributions and disturbance regimes. These populations differ only in their dispersal characteristics (i.e. dispersal distance and/or dispersal rate) and in their competitive ability, if the latter is associated with dispersal characteristics. This approach showed that dispersal distance is indeed under selective pressure and that many variables may affect this selection but not to an equal extent. The most important of those studied here is the pattern of disturbance. Landscape characteristics affect the selection to a lesser degree.

The study of the evolution of dispersal in the past has focused on the selection of the optimal dispersal rate, while the selection of dispersal distance has been the subject of fewer

studies. Also, most previous studies simulated dispersal in a spatially implicit way, assuming that dispersers could colonize any patch irrespective of origin (pool of dispersers) or they could colonize only their nearest neighbours (stepping stone dispersal). In contrast, this study focuses explicitly on the evolution of dispersal distance.

In the main, this study examined the effect of disturbance on the selection of dispersal by means of an individual-based model. In our model, we ignored other well-known factors that are invoked in explaining the evolution of dispersal, such as kin selection and inbreeding depression. Rousset and Gandon (2002), for example, showed that kin selection favours longer dispersal distances, even if there is a distance-dependent cost of dispersal. Population dynamics are also not explicitly simulated in our individual-based models, even though they may help to explain the evolution of dispersal distance (Murrell *et al.*, 2002). In our model, we did not include explicitly any costs for dispersal. Pilot simulations have shown that including such costs alters the results quantitatively (different classes are categorized as short- or long-range dispersers) but not qualitatively. Finally, we did not include any mutation mechanism in the model. We have included a large range of dispersal distances, the longest of which hardly ever persisted and never dominated, so we do not believe that mutations would have changed the results significantly.

Landscape effects

The landscape characteristics examined here are habitat availability and habitat pattern. Landscape patterns examined ranged from totally random to highly aggregated. The major trend was that as the landscape became more aggregated, short-range dispersers were favoured and ultimately dominated. This trend was robust and has been reported also by Hovestadt *et al.* (2001). Even though our model is not directly comparable to their model (they studied the evolution of the dispersal kernel, and assumed that all populations had the same maximum dispersal distance of 30 cells), the two studies are in substantial agreement. In aggregated landscapes, a short-range disperser will have a higher probability of landing in a suitable cell and thus will have greater dispersal success and lower dispersal-induced mortality (With and King, 1999).

More importantly, habitat availability *per se* affects the selection of optimal dispersal distance, even more than landscape pattern. As habitat availability decreases (i.e. as habitat is lost), the percentage of short-range dispersers in the population increases, and dominance switches from long-range dispersers to shorter-range dispersers. This applies to all types of landscape pattern and disturbance regimes. Dytham (2003) reported that as habitat becomes sparser it pays to remain more sedentary because locating a suitable patch far away is difficult, and return to the natal cell is more likely. This may be related to the fact that bird species that inhabit small oceanic islands lose some of their dispersal ability compared with their mainland relatives – for example, the evolution of flightlessness in Pacific island rails (Slikas *et al.*, 2002). Similar trends have been recorded for plant species (Cody and Overton, 1996).

Disturbance effects

Maynard Smith (1982) described how, in evolution, an increase in disturbance favours increased dispersal rates. However, less attention has been focused on the effect of the spatial pattern of disturbance on the evolution of dispersal. The results of a previous study

showed that the disturbance regime has a direct effect on the probability of extinction (Kallimanis *et al.*, 2005). Here we have shown that disturbance pattern is very significant for the selection of optimal dispersal distance as well.

When disturbance is fine-scale, small gaps are created in the mist of occupied cells. Since all dispersal strategies disperse the same number of propagules, short-range dispersers show higher propagule density in the vacated cells than long-range dispersers. In the case where competition is not associated with dispersal characteristics, the propagule types with higher densities will have a greater probability of establishment, and thus will have an indirect competitive advantage. If competitive ability is inversely correlated with dispersal distance, the effect is even more pronounced.

When disturbance is spatially autocorrelated, as it is bound to be in nature, then the gaps created may be very large. It has previously been shown that under those conditions, short-range dispersers face a higher extinction risk (Kallimanis *et al.*, 2005). Short-range dispersers need several generations to recolonize the large gaps created by aggregated disturbance, and in the meantime a single disturbance event may drive them extinct. In the extreme case, a single disturbance event might take out the entire population. Long-range dispersers, on the other hand, are able to recolonize these large gaps quickly and thus face lower extinction risk. Simultaneously, the competition mechanism described earlier prohibits very long-range dispersers from dominating, and thus the optimum dispersal distance selected for is an intermediate one. Here it should be pointed out that known mechanisms selecting against long-range dispersers (like open boundaries in the landscape that lead to increased loss of long-range propagules) were excluded from our model and cannot be invoked to explain our results.

The temporal pattern of disturbance has an effect almost as important as the spatial pattern. In our model under the high-frequency block disturbance regime at every generation, only coarse-scale disturbance events took place. Empirical studies have shown that such events in nature occur more rarely than fine-scale disturbances. There are even cases where the frequency of the disturbance incident is inversely proportional to its extent [e.g. meteor impacts (Schroeder, 1991)]. We investigated such patterns in our model. As coarse-scale disturbance events become rarer, short-range dispersers have a higher probability of recolonizing the gaps created, and in the process they drive out long-range dispersers that colonized the gaps faster. This process resembles a successional change of species, from pioneer species (long-range dispersers) with better recolonization ability and lower competitive efficiency to more 'climax' species (short-range dispersers), similar to the one described by Hovestadt *et al.* (2000). Furthermore, as coarse-scale incidents become rarer, their impact on the selection outcome becomes weaker. In the extreme case (low-frequency block disturbance), where a coarse-scale incident occurs every 83 generations, long-range dispersers disappear and short-range dispersers dominate. Thus the impact of spatially autocorrelated disturbance becomes undetectable.

The study of dispersal evolution is a crucial aspect of understanding life histories. With the recent growth in interest in spatial aspects of ecology, the central role played by immigration and emigration in population dynamics and evolution is becoming increasingly clear. This study, together with other recent advances in modelling dispersal evolution, may help to explain the diversity of dispersal strategies in nature, and the potential impacts of an increasingly fragmented natural world.

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