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Evolution of reduced dispersal mortality and 'fat-tailed' dispersal kernels in autocorrelated landscapes

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Models describing the evolution of dispersal strategies have mostly focused on the evolution of dispersal rates. Taking trees as a model for organisms with undirected, passive dispersal, we have developed an individual-based, spatially explicit simulation tool to investigate the evolution of the dispersal kernel, $P(r)$, and its resulting cumulative seed-density distribution, $D(r)$. Simulations were run on a variety of fractal landscapes differing in the fraction of suitable habitat and the spatial autocorrelation. Starting from a uniform $D(r)$, evolution led to an increase in the fraction of seeds staying in the home cell, a reduction of the dispersal mortality (arrival in unsuitable habitat), and the evolution of 'fat-tailed' $D(r)$ in autocorrelated landscapes and approximately uniform $D(r)$ in random landscapes. The evolutionary process was characterized by long periods of stasis with a few bouts of rapid change in the dispersal rate.

Keywords: individual-based model; dispersal distance; passive dispersal; spatial autocorrelation; seed-density distribution; dispersal kernel

1. INTRODUCTION

The explicit consideration of the spatial distribution of habitats and organisms in landscapes has substantially shifted our view of the principal mechanisms responsible for the coexistence of species, the maintenance of diversity and species distribution, and the dynamics of (meta)populations in fragmented landscapes (see Kareiva 1990; Hassell *et al.* 1991; Tilman & Wedin 1991; Durrett & Levin 1994; Hastings & Harrison 1994; Holmes *et al.* 1994; Bascompte & Solé 1995; De Roos & Sabelis 1995). In all of these approaches, dispersal is the principal 'transmitter' of interactions in space. Consequently, increasing attention has been directed towards the analysis of the evolution of dispersal strategies as well as their ecological consequences (Dieckmann *et al.* 1999).

The probability that a single dispersing organism will travel a certain distance before it settles is described by a probability density function $P(r)$, the dispersal kernel. As any dispersing organism has to arrive somewhere, the dispersal kernel must integrate to 1 across the range of possible dispersal distances. The resulting cumulative distribution of all individuals dispersed from the same starting point, for example the seeds dispersed by a single tree, is the distance density distribution. As we will take dispersal of seeds as an example, we will call this function the seed density distribution, $D(r)$, throughout the paper. In the case of radially symmetrical undirected dispersal, i.e. dispersing organisms select directions at random and do not respond to habitat quality when settling, $D(r)$ can be calculated from $P(r)$ as $D(r) = P(r)/2\pi r$.

By considering specific movement patterns of dispersing organisms (e.g. simple diffusion, correlated random walk) and their resulting dispersal kernels, it has become evident that the details of the kernel and the landscape structure will have important consequences for various ecological processes. In particular, whether the kernel is 'thin tailed' or 'fat tailed' will strongly affect the spread of the invading species (e.g. Van den Bosch *et al.* 1992; Kot *et al.* 1996; Lewis 1997; Cain *et al.* 1998; Clark 1998; Clark *et al.* 1998), the metapopulation dynamics (With & King 1999), the colonization of new sites (Portnoy & Willson 1993), and the formation of spatial patterns in the distribution of species (Holmes *et al.* 1994). Certainly, the details of the dispersal kernel should affect individual fitness and, consequently, be shaped by natural selection. Unfortunately, empirical data on long-distance dispersal are still hard to find (see Portnoy & Willson 1993).

The lack of empirical data is paralleled by a similar scarcity of models investigating the factors controlling the evolution of the dispersal kernel and the resulting $D(r)$, especially in spatially realistic, autocorrelated landscapes. Most models describing the evolution of dispersal strategies have focused on the evolution of optimal dispersal rates (e.g. Levins 1970; Hamilton & May 1977; Hastings 1983; Levin *et al.* 1984; Johnson & Gaines 1990; Gandon & Michalakis 1999; Parvinen 1999). As those organisms dispersing at all are usually added to a general pool of dispersers, which is uniformly distributed over the landscape, these models are spatially implicit. Only recently first steps have been taken towards a spatially explicit simulation of the evolution of the dispersal process itself (Leimar & Norberg 1997; Travis & Dytham 1998, 1999; With & King 1999). These grid- or patch-orientated simulations are spatially explicit inasmuch as dispersal is only allowed into neighbouring cells or patches, but they do not consider the evolution of the dispersal kernel. Ezoe (1998) investigated the trade-off between mean dispersal distance and seed size, assuming that large seeds are more competitive but disperse over shorter distances. Savill & Hogeweg (1998) modelled the evolution of maximum dispersal distance in a predator–prey system with uniform dispersal. However, none of these models has looked at the evolution of a complex dispersal kernel in various landscapes.

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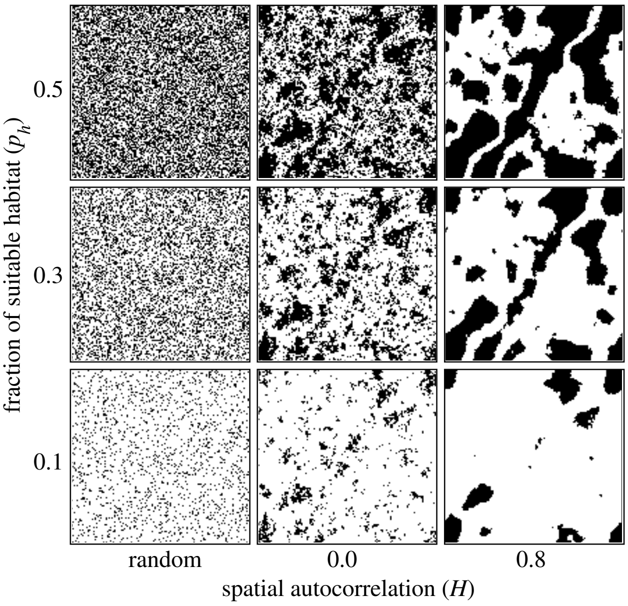

Figure 1. A series of three purely random landscapes in the left-hand column and a set of six artificial landscapes generated by Keitt's (2000) algorithm (two columns on the right). Autocorrelation increases from left to right with no autocorrelation in the left-hand column, low autocorrelation in the middle column (Hurst exponent $H=0.0$) and high autocorrelation in the right-hand column ($H=0.8$). The fraction of suitable habitat, p_{h}, increases from bottom (0.1) to top (0.5). To demonstrate the 'matching edges' in the periodic fractal landscapes, all six fractal landscapes presented here have been generated using the same random seed. It can be seen that habitat patches 'continue' across panels. In the simulations, different random seeds were used each time to create different landscapes.

To take first steps towards the investigation of this neglected problem, we used a spatially explicit simulation approach to investigate selection on $P(r)$, and thus $D(r)$, in landscapes with varying degrees of suitable habitat and spatial autocorrelation. Specifically, we simulated the dispersal of seeds and their subsequent establishment. The results of our simulations are thus most applicable to organisms with passive and undirected dispersal and where the dispersal of offspring is under the control of the parent. The principal goal of our approach was to estimate the effect of landscape structure on the evolution of adapted dispersal strategies. As we wanted to focus on the evolution of the optimal dispersal strategies *per se*, we did not consider most of the biologically reasonable costs and trade-offs (e.g. costs of production, constraints on dispersal function, trade-offs between competition and dispersal) that are likely to be associated with different dispersal strategies. We also did not include the consequences of habitat disturbance, which should have a strong effect on the readiness to disperse (see Venable & Brown 1993; Ronce & Olivieri 1997; Ronce *et al.* 2000; Hovestadt *et al.* 2000).

2. MODEL

To simulate the evolution of seed dispersal strategies, we used an event-driven (Grams 1992), individual-based model, with space modelled as a regular two-dimensional grid. If of suitable habitat, an individual cell is sufficient for the maintenance of a single adult tree only. In addition to its position, an individual is characterized by the time-step of its death and its individual dispersal kernel. Apart from these traits, all trees are considered to be similar. In our model, inheritance is strictly phenotypic and clonal. The simulation program consists of two modules, which are described in detail below: one for the generation of landscapes (§ 2(a)), and the other for the initialization and consecutive execution and actualization of the event list (§ 2(b)).

(a) *Generation of landscapes*

Before a simulation is started, an artificial landscape is generated with the pre-set parameters taken from the parameter database. For autocorrelated landscapes, parameters describe the fraction of cells to be assigned as suitable habitat (p_{h}) and the Hurst exponent (H) as a measure of habitat fractality. Several algorithms can be used to generate these types of landscapes (Mandelbrot 1982; Peitgen & Saupe 1988). We have chosen the one described by Keitt (2000), which allows the generation of periodic landscapes. This effect can be seen in figure 1 when looking across edges of panels with autocorrelated landscapes. We could thus close the simulation grid to a torus to avoid edge effects. Random landscapes are generated by randomly assigning habitat suitability to individual cells with a probability corresponding to the overall fraction, p_{h}, of suitable habitat. All simulations presented here were run on grids of 128 cells × 128 cells.

(b) *Event list*

After the landscape has been generated, trees are distributed into the suitable habitat cells. For the initialization of the event list, a survival time drawn from a uniform probability distribution ranging from 1 to 125 time-steps (years) is assigned to each tree. The initial event list is then prepared as a list of trees (cells) sorted according to their pre-assigned time of death. From then on the simulation procedure works through this sorted list always executing the next event in the list.

The death of a tree triggers four processes, which finally result in its replacement by a new tree and a new entry in the event list. These processes are first, collection of seeds from the surrounding trees according to their individual $D(r)$ (see § 2(c)); second, the establishment of a new tree; third, the assignment of the new tree's survival time and thus the moment when the cell will become open for colonization again; and eventually, fourth, the mutation of the new tree's dispersal kernel. From the seeds arriving in an empty cell, one seed is selected at random to become the new adult tree in this cell ('lottery model'). This procedure implies competitive similarity between all trees and all dispersal types. Replacement of established trees by arriving seeds is not possible, i.e. competition is completely asymmetrical across age classes. The individual survival time (i.e. lifetime) of the newly located tree is taken randomly from a normal probability function with a mean value of 100 ± 5 (s.d.); thus, mortality is age dependent. The simulation ends when the time of the next event in the event list exceeds the pre-set simulation time.

(c) *Implementation of seed dispersal*

Throughout all simulations presented here, each adult tree produced $S_p = 2^{24}$ (*ca.* 16.7×10^6) seeds at each time-step. Trees start to reproduce in the time-step following their recruitment. We assume that a dispersing seed cannot respond to its surroundings by actively searching for, or directing its movement towards, suitable habitat, i.e. seed dispersal is a purely statistical process. We also assume that habitat heterogeneity does not alter the statistical properties of the dispersal process, which may be the case in natural dispersal systems (e.g. movement patterns of seed-dispersing animals may depend on the type of habitat). Given that established trees cannot be replaced by arriving seeds, it is necessary to model the dispersal process only when a tree dies and its home cell becomes free for replacement ('target cell'). Thus, we implicitly account for the mortality of seeds due to arrival (including seeds staying in the natal cell) in suitable but occupied habitat. A target cell collects seeds from the neighbouring trees. The predicted number of seeds arriving in a target cell from a specific 'donor tree', i.e. $D(r) \times S_p$, depends on the distance, r, between cell midpoints, the donor tree's $P(r)$ (see § 2(d)) and the number of cells at distance r from the donor cell (simply dividing $P(r)$ by $2\pi r$ will result in minor inaccuracies in a grid-based simulation). The Euclidean distance between trees (cells) is not constrained to natural numbers and can fall between two distance classes. In this case, the expected number of arriving seeds is interpolated as the weighted average of seeds coming from the two neighbouring distance classes. The number of seeds arriving and the identity of the mother tree are stored until the seed-gathering process has been repeated for all trees lying within a pre-set maximum dispersal distance. The dying tree can disperse seeds prior to its death, thus generating the opportunity for its replacement by its own progeny. However, we did not allow for the accumulation of a seed bank.

When the seed-gathering routine is finished, a single seed from the accumulated pool is randomly selected to become the replacement tree. In theory, an empty cell could remain empty for several time-steps, but given the enormous seed production, the fraction of unoccupied habitat remained extremely small ($\ll 1\%$) at all times in all simulations.

To allow for maximum flexibility of the evolutionary process, we decided not to use a specific mathematical model for the dispersal kernel, $P(r)$ (e.g. negative exponential). This would automatically put constraints on the evolution of its specific form. Instead, we code $P(r)$ as a 'distance–probability histogram' with 30 distance classes ranging from 0 to 29. Due to limited computational power, we had to restrict the maximum dispersal distance to 29 (measured in cell widths). The '0 class', $P(0)$, represents the fraction of seeds remaining in their home cell and thus having the opportunity to replace their mother tree. No specific costs or trade-offs were associated with a specific dispersal strategy beyond the mortality inflicted on seeds due to dispersal into unsuitable or occupied habitat.

(d) *Mutation of $P(r)$*

The simulations all start with a monomorphic population of trees. At initialization, all trees distribute their seeds uniformly across area (up to the maximum dispersal distance), i.e. $D(r)$ is constant. This implies a linearly increasing $P(r)$, which may be quite difficult to achieve with real seed-dispersal mechanisms. However, this is in agreement with spatially implicit models assuming uniform distribution of dispersing organisms in space (e.g. Levins 1970). A newly selected tree inherits the dispersal function from its mother tree. To allow for the creation of new dispersal strategies, this inherited function will eventually mutate with a probability of 0.01 to a new dispersal function.

The mutation procedure involves four steps. First, two distance classes of the probability histogram are selected at random; second, the seeds allocated to the two classes are pooled into a single seed reservoir; fourth, this single reservoir is then randomly split (uniform probability distribution) into two reservoirs; and fourth, the two newly created reservoirs are assigned at random to the two distance classes. Mutations can thus shift seeds from one distance class to another but the overall number of seeds distributed remains constant. We selected this mutation procedure for its flexibility and easy implementation. Without selection, the mutation procedure should shift $P(r)$ towards a random distribution at the individual level and a uniform $P(r)$ at the population level.

(e) *Data analysis*

Every 1000 time-steps, we recorded the mean fraction of seeds remaining in the home cell (distance class 0) for each simulation. At the same time, we also recorded the mean probability of arrival in unsuitable habitat ('dispersal mortality', m_d) as a specific risk for seeds leaving their natal cell (distance class > 0). At the end of each simulation, we estimated the evolved standardized mean $D(r)$, calculated from the $P(r)$ by averaging the fraction of seeds allocated to each distance class greater than 0 across all individuals divided by the number of cells falling into this distance class (*ca.* $2\pi r$). For data presentation and analyses, we averaged these results across the ten simulations for each parameter combination. To characterize the landscapes themselves, we calculated the mean probability, $p_f(r)$, of reaching suitable habitat starting from suitable habitat as a function of dispersal distance. We used Statistica 5.1 (StatSoft, Inc. 1999) to fit nonlinear functions to both the habitat distribution and the evolved $D(r)$.

3. RESULTS

In the simulations presented here, the fraction of suitable habitat, p_h, was fixed at three different levels (0.1, 0.3 and 0.5) and autocorrelation, H, was set to either random, $H = 0.0$ (low autocorrelation) or $H = 0.8$ (high autocorrelation). This gives a total of nine landscape-parameter combinations (figure 1). For each parameter combination, ten simulations were run on independently generated landscapes.

(a) *Seeds staying at home*

Compared to the initial conditions of a uniform $D(r)$, we observed a substantial increase in the proportion of seeds remaining in the natal cell in all simulations. In fact, this fraction increased from *ca.* 0.0004 to 0.08–0.22

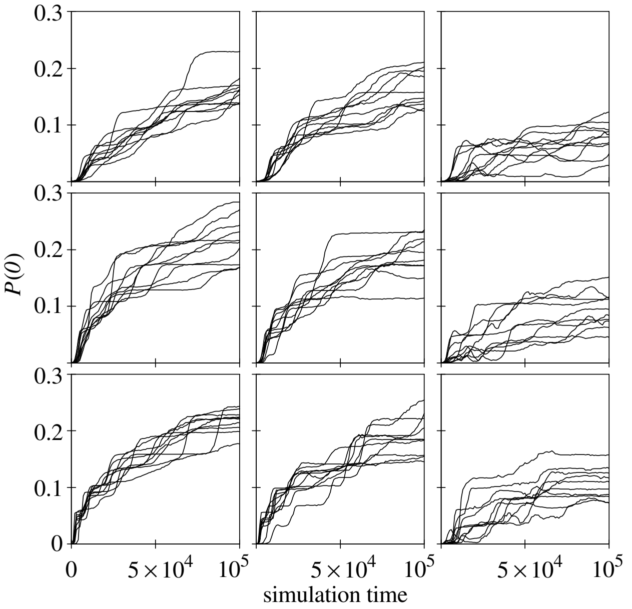

Figure 2. Evolution of the fraction of seeds staying in the home cell, $P(0)$, over the course of the simulations. On each graph, an individual line is given for each of the ten replicate simulations. Landscape parameters and panel arrangement as in figure 1.

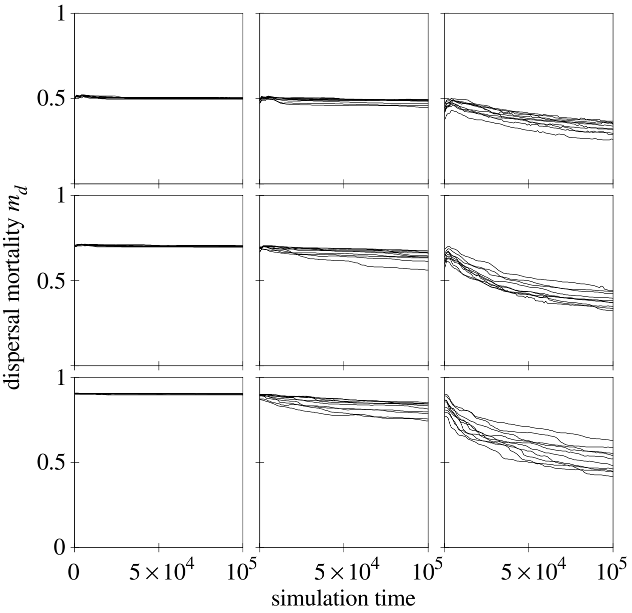

Figure 3. Evolution of mean dispersal mortality, m_d, over the course of the simulations. On each graph, an individual line is given for each of the ten replicate simulations. Only mortality due to arrival in an unsuitable habitat is considered, not the failure to establish in suitable habitat. Landscape parameters and panel arrangement as in figure 1.

depending on the simulation parameters (figure 2). The increase was lower in highly autocorrelated landscapes but little affected by the global fraction of suitable habitat. As can be seen in figure 2, a remarkable feature of most simulations is the occurrence of prolonged periods of evolutionary stasis with a few bouts of rapid change in the fraction of seeds allocated to the home cell. Especially for the random landscapes, the curves suggest that even after 100 000 time-steps evolution may not have reached a stable equilibrium in all simulations.

(b) *Mortality of dispersed seeds*

At the beginning of the simulations, dispersal mortality, m_d, was always related to the global fraction of unsuitable habitat as $m_d = 1 - p_h$. However, for autocorrelated landscapes, we observed a gradual decline in m_d over the course of the simulations, while it remained constant in random landscapes (figure 3). The reduction in m_d was especially obvious in highly autocorrelated landscapes with a low p_h (from 0.90 to 0.51).

(c) *Habitat distribution and evolution of $D(r)$*

In autocorrelated landscapes, we observed a strong deviation from the uniform $D(r)$, with a shift of dispersed seeds into the near-distance classes (figure 4, middle and right columns). This shift in seed dispersal is qualitatively matched by the distance-dependent probability $p_f(r)$ of finding suitable habitat starting from a randomly selected cell of suitable habitat itself. In fact, this probability follows very tightly ($r^2 > 0.98$ for all six landscapes with spatial autocorrelation) a negative-exponential distribution, $p_f(r) = p_h + h_1 \times \exp(-r/h_2)$, asymptotically approaching the global habitat fraction p_h with h_1 and h_2 as fitted constants. Regardless of overall habitat fraction, h_2 is *ca.* 3.2 in landscapes with low spatial autocorrelation and *ca.* 6.2 in landscapes with high spatial autocorrelation, indicating a prolonged reach of correlated habitat suitability in highly autocorrelated landscapes. In contrast, h_1 depends on both autocorrelation (positively) and the overall fraction of suitable habitat (negatively). The discrepancy between global habitat fraction and the 'local' probability of finding suitable habitat is thus strongest in landscapes with a low p_h and a high degree of autocorrelation. In landscapes with $p_h = 0.1$, the likelihood of finding suitable habitat in the near vicinity of a suitable-habitat cell is well above 0.5 in highly autocorrelated landscapes (0.86 in the first distance class, 0.77 in the second and 0.69 in the third). It is the adaptation of $D(r)$ to this predictable pattern of habitat distribution that is responsible for the reduced dispersal mortality in spatially autocorrelated landscapes.

However, the evolved $D(r)$ do not follow a negative-exponential distribution. To demonstrate this, we fitted negative-exponential and inverse-power functions to the evolved $D(r)$. As $P(r)$ has to integrate to 1 over the range of possible dispersal distances, we fitted the following two functions to the population mean $D(r)$ for each parameter setting, with the normalized negative exponential (equation (1)) and the normalized power function (equation (2)):

$$D(r) = \frac{d^2 r e^{dr}}{2r\pi(e^{29d} \times (29d - 1) - e^d \times (d - 1))}, \tag{1}$$

$$D(r) = \frac{(w + 1) \times r^w}{(29^{(w+1)} - 1) \times 2r\pi}, \tag{2}$$

where d and w are fitted constants. As can be seen in figure 5, the power function always shows a better fit to the evolved seed density distributions. In particular, this holds for long dispersal distances. $D(r)$ is even more fat tailed

Table 1. *Parameters (± s.e.m.) and variance estimates (r^2) of nonlinear-regression models fitted to evolved mean $D(r)$*

(Equation (1) (negative exponential) and equation (2) (power function) have been used for the two models, respectively. Data have not been transformed prior to fitting. Even though r^2-values are lower for the power model than for the negative-exponential model in some cases, figure 5 clearly shows that the negative-exponential model is principally flawed.)

	random landscape		$H=0.0$		$H=0.8$		
habitat fraction	parameter	r^2	parameter	r^2	parameter	r^2	model
$p=0.5$	-0.05 ± 0.008	0.47	-0.15 ± 0.013	0.60	-0.35 ± 0.015	0.87	d (negative exponential)
	$+0.59 \pm 0.051$	0.55	$+0.03 \pm 0.031$	0.47	-0.44 ± 0.036	0.85	w (power function)
$p=0.3$	-0.05 ± 0.006	0.59	-0.29 ± 0.019	0.73	-0.38 ± 0.012	0.92	d (negative exponential)
	$+0.59 \pm 0.029$	0.79	-0.37 ± 0.015	0.97	-0.50 ± 0.038	0.84	w (power function)
$p=0.1$	-0.04 ± 0.006	0.50	-0.33 ± 0.021	0.75	-0.41 ± 0.013	0.92	d (negative exponential)
	$+0.60 \pm 0.038$	0.75	-0.46 ± 0.011	0.98	-0.59 ± 0.014	0.98	w (power function)

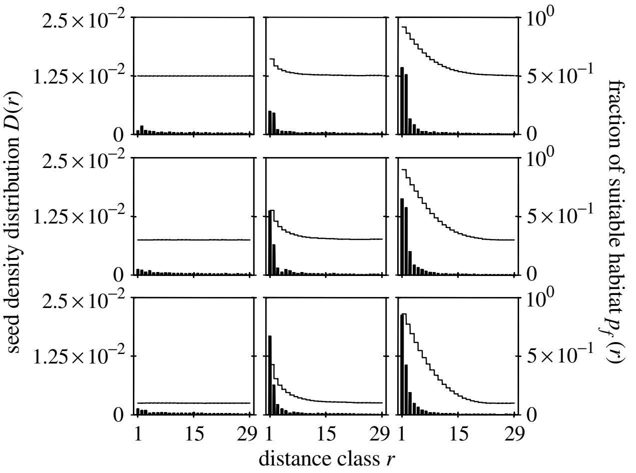

Figure 4. Evolved mean seed density distribution, $D(r)$, across distance classes 1–29 (bars) at the end of the ten independent simulations for the nine landscape-parameter combinations given in figure 1 (same arrangement of panels). All simulations started from a uniform $D(r)$. The lines represent the distance-dependent mean probability of reaching suitable habitat, $p_f(r)$, starting from a randomly selected cell of suitable habitat.

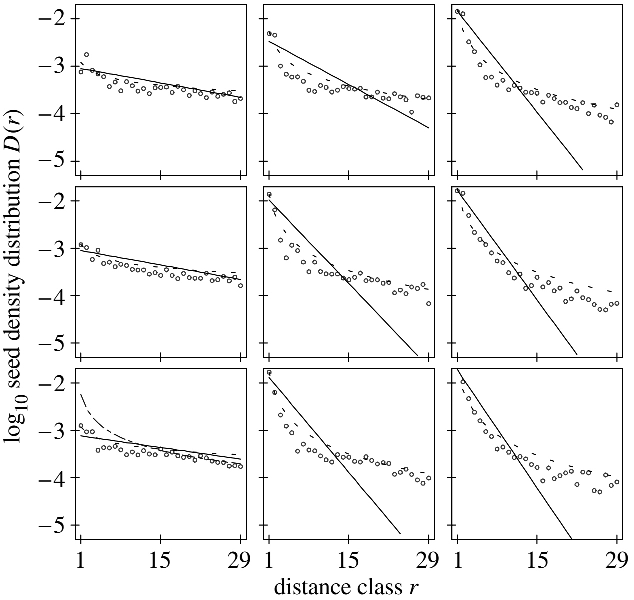

Figure 5. Evolved mean $D(r)$ (dots) and functions fitted to the data according to equations (1) and (2) (see § 3(c)). $D(r)$ has been transformed to a logarithmic scale to illustrate more clearly the differences between fitted negative-exponential (continuous line) and power functions (hatched line). As curves have been fitted to untransformed data, deviations from the fitted curves are not to scale. In the lower left graph, we have also plotted the $D(r)$ resulting from a uniform $P(r)$ (long-hatched line). This would be the resulting $D(r)$ due to the mutation algorithm with no selection. Parameter combinations and arrangement of panels as in figure 1.

than the simple inverse power function, as the exponent w is larger than -1 in all cases and larger than 0 in one case (table 1). In fact, even the power model principally fails for some parameter combinations ($H=0.0$ and $p_h=0.3$ or 0.5) as the evolved mean $P(r)$ rapidly decline in the first few distance classes but increase again with increasing distance. A power function cannot adequately describe such a relationship as it must always either increase or decrease monotonically.

In contrast to autocorrelated landscapes, we did not observe much change in dispersal mortality or $D(r)$ in random landscapes apart from a shift of seeds into the distance class $P(0)$ (figure 4, left column). As random landscapes are the spatially explicit analogue to spatially implicit landscapes with a fixed p_h, this should not be interpreted as a consequence of a lack of selection. It is due to the fact that, for those seeds dispersed at all, a uniform $D(r)$ is the optimal dispersal strategy (cf. Hamilton & May 1977). Thus, selection should result in a power model with the exponent $w=1$. However, the exponent is 0.6 and, thus, below the expected value. The slight shift is likely due to the mutation algorithm, which should result, on average, in a uniform $P(r)$, i.e. a power function with $w=0$.

4. DISCUSSION

In this paper we have presented, for the first time to our knowledge, Monte Carlo simulations of the evolution of dispersal distances for organisms with passive dispersal in spatially realistic landscapes. They clearly demonstrate the important effect of landscape characteristics on the evolution of dispersal strategies. To keep our model simple, we ignored many of the biologically reasonable constraints and trade-offs that are necessarily part of a complete evolutionary scenario. In spite of this simplicity, our simulations produced plausible and consistent results over a broad range of different landscape scenarios. Under all simulated conditions, fat-tailed dispersal functions evolved. Spatially autocorrelated landscapes allow for the evolution of adapted dispersal strategies with lower dispersal mortalities than predicted by spatially implicit models or for random landscapes. In this respect, our results match the observation that dispersal into neighbouring cells reduces dispersal mortality compared to random dispersal in autocorrelated landscapes (With & King 1999). However, seeds dispersed beyond the correlation distance of habitat suitability should be dispersed uniformly over the landscape. Thus, the frequently used negative-exponential distribution poorly matched the two parts of the evolved dispersal kernel. In random landscapes, dispersal mortality is completely insensitive to the selected dispersal kernel and thus will not affect selection of the dispersal kernel apart from selection on $P(0)$. Consequently, reduced dispersal rate, but uniform dispersal for the seeds dispersed, is expected.

Due to limited computational resources, we could not model dispersal over truly long distances. However, as the increased likelihood of finding suitable habitat levelled off before the maximum dispersal distance was reached, this should not be a major concern. It is unlikely that our principal results would have been different if we had allowed seed dispersal over much larger distances. We also did not investigate the consequences for simulation outcome of altered initial settings, e.g. all trees with seeds allocated to $P(0)$ or assuming much lower seed production. At the moment, we would expect only quantitatively different results in these cases. However, we cannot rule out the possibility of an adaptive landscape with several optima.

Of more fundamental concern may be the mutation algorithm we have used. While its principal advantage lies in its flexibility and the avoidance of predefined types of dispersal function, it has some disadvantages. In the absence of selection, the mutation algorithm would result in a uniform $P(r)$ at the population level, i.e. a power function with an exponent equal to 0. When fitted to a power function, the exponent, w, of $D(r)$ evolved towards values from -0.6 to $+0.6$, indicating the effect of selection and the flexibility of the mutation algorithm. More importantly, the evolved $D(r)$ did not fit the power model well under some conditions (see below). Thus, like any mutation algorithm, the one we used will produce certain biases but does not seem to principally constrain the evolution of $D(r)$ to a power model. Without selection, our mutation algorithm would allocate on average only 1/30 of the seeds to the natal cell, i.e. it would result in a dispersal rate of 0.97. We assume that this is one of the reasons for the evolution of dispersal rates (*ca.* 0.78–0.83) higher than predicted (0.53–0.67) by the Hamilton–May model (1977) for random landscapes. Another reason for this discrepancy may be that, starting from a dispersal rate above 0.99, the evolutionary change in dispersal rate had not reached a stationary state in the course of 10^5 simulation steps (cf. figure 2). This proposition is in agreement with the observed 'punctuated equilibrium', which indicates the extremely low likelihood of the successful establishment of a mutant with a higher $P(0)$. The predictions of the Hamilton–May model cannot be applied directly to autocorrelated landscapes as the costs of dispersal are lower than assumed by the model as long as the seeds are dispersed locally.

In some autocorrelated landscapes, the $P(r)$ increased with distance after a sharp decline across the near-distance classes. The evolved dispersal kernel thus appeared to be even more 'fat tailed' than the power functions we fitted to the data. Principally, neither a power nor a linear function can adequately describe $P(r)$ if we allow unlimited dispersal distance: the integrals over both functions are not bound to 1 for unlimited dispersal distances. In practice, we may solve this problem either by assuming a certain maximum dispersal distance (as we did in our simulations), or by using dispersal kernels made up of two (or more) different functions, e.g. several exponential functions with different parameters (see Higgins & Richardson 1999; Bullock & Clarke 2000). The evolution of such mixed dispersal kernels may come about by the action of different dispersal vectors (e.g. seed shadow created by different frugivorous animals) or by the creation of seeds with different dispersal morphologies (e.g. seeds with different wing loads in wind-dispersed species). Certainly, our simulations suggest that the dispersal kernels used in models should be selected for biological reasons and not just for mathematical convenience. Even though we do not know to what degree the evolution of fat-tailed dispersal kernels can be achieved, our conclusions are in agreement with evidence that the range expansion of plant species was too fast to be explained by dispersal kernels that are not fat tailed. (Kot *et al.* 1996; Cain *et al.* 1998; Clark 1998; Clark *et al.* 1998).

We wish to draw attention to the fact that the recognition of discrete patches in the landscape would not alter any of our conclusions. As long as we do not assume an effect of habitat heterogeneity on the dispersal process *per se*, it does not matter to an organism with passive dispersal whether it has to cross patch borders during dispersal or not. At least for organisms with passive dispersal, the distance-dependent probability of reaching suitable habitat may thus be an adequate description of landscape properties. It is a simple and more appropriate measure of the relevant habitat characteristics affecting the evolution of the dispersal kernel than those used in the typical patch-matrix (Hanski 1997) or mosaic-landscape models (Wiens 1995).

In the way we have built up our simulation, the evolutionary process can be considered to be a process of learning by evolutionary experience. Individuals using more 'sensitive' strategies, i.e. strategies that take into account the predictable distribution of habitat in spatially autocorrelated landscapes, are able to reduce the dispersal mortality of their offspring, thus transforming the cost-to-benefit ratio of dispersal compared to strategies with uniform dispersal. However, our simulations are only a first step towards a fuller understanding of the many ecological factors eventually affecting the evolution of optimal dispersal distances. For example, additional simulations are required to evaluate the role of variations in seed production and initial conditions, of the combined evolution of several traits, e.g. seed production and dispersal kernel, of habitat disturbance, and of various biological trade-offs and constraints. Of special interest may be the evaluation of emerging spatial patterns and their consequences for the coexistence of distinct dispersal strategies.

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