

## *Variability in dispersal distances generates typical successional patterns: a simple simulation model*

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During colonization or after disturbance, plant communities frequently show a predictable succession of species, each with typical combinations of life-history traits (cf. Huston and Smith 1987). As outlined in the review by McCook (1994), attempts to explain this successional sequence of plant recruitment are generally based on assumed trade-offs in resource allocation (cf. Pickett and McDonnell 1989). For example, trade-offs between different traits relevant for competitive abilities (e.g., growth rate vs shade tolerance), between dispersal capabilities and competitive strength, or between seed production and longevity have all been suggested to result in a successional sequence of (re-)colonization of a habitat after disturbance (e.g. Mooney 1972, Liljelund et al. 1988, Smith and Huston 1989, Tilman 1990, Colasanti and Grime 1993, Berlow 1997; see also Kinzig et al. 1999).

More recently, it became clear that conclusions drawn from traditional ecological theory may be altered substantially if the spatial dimension of species interactions is considered explicitly. Regardless of the details of these models, spatially explicit simulations of ecological processes have nearly universally shown that spatial or spatio-temporal patterns in species distributions can emerge even from homogeneous starting conditions; limited dispersal is one of the key factors responsible for the development of such aggregated and patchy distributions (cf., Pacala 1986, Holmes et al. 1994, Molofsky 1994, Tilman 1994, Bascompte and Solé 1995, 1997, 1998, Jeltsch et al. 1999). In line with these ideas, we wish to draw attention to the fact that in heterogeneous landscapes differences in characteristic dispersal distances between species are a sufficient precondition for the emergence of a successional pattern. We will use a simple, spatially explicit simulation program to demonstrate the validity of this statement. We

will also show that the speed of the successional progress depends on scale and heterogeneity in the distribution of suitable habitat.

### The model

We performed computer simulations with an individual-based, spatially explicit patch model. In our simulations, different plant types are absolutely similar except for their dispersal strategy (see below). In particular there is no difference in their competitive strength. The plants “live” in a two-dimensional grid of  $n_x$  by  $n_y$  patches (Fig. 1). Simulations are performed in discrete time steps with a number ( $S$ ) of different types. After each individual has distributed the same number of seeds ( $n_{seed}$ ) according to a type-specific dispersal function, it will die with an age-independent probability ( $m$ ); this probability is identical for all types. If an adult

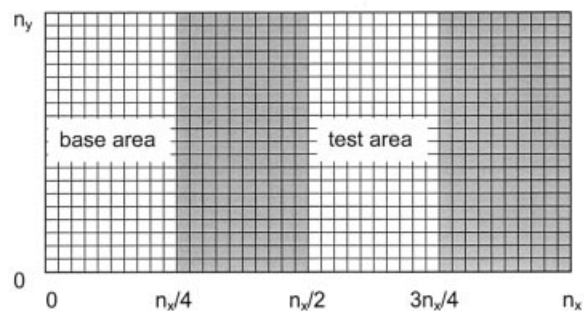


Fig. 1. The simulated landscape consists of a grid of  $n_x \times n_y$  patches. At the start of each simulation run only the “base area” is occupied by plants (except for the simulations presented in Fig. 6). Succession in the initially empty “test area” is subsequently observed.

Table 1. Parameter settings for the simulations presented in the figures.  $S = 9$ ,  $n_{seed} = 1$ ,  $n_x = 100$ , and  $d_s$  distributed from 0 to 8 for all simulations.

Scenario	Grid length ( $n_y$ )	Torus	Cell capacity (fraction)		Adult mortality ( $m$ )	Figures
			High $k_h$ ( $p_h$ )	Low $k_l$ ( $p_l$ )		
Homogenous torus	200	Yes	4 (0.5)	4 (0.5)	0.2	2A, 3A, 6
Homogenous island	200	No	4 (0.5)	4 (0.5)	0.2	2B, 3B
Heterogenous torus	200	Yes	6 (0.5)	2 (0.5)	0.2	2C, 3C, 4
Patchy torus	200	Yes	8 (0.5)	0 (0.5)	0.2	2D, 3D
Patchy torus	200	Yes	8 (variable)	0 (variable)	0.2	5A
Homogenous island	variable	No	4 (0.5)	4 (0.5)	0.2	5B
Torus	200	Yes	Variable (0.5)	Variable (0.5)	0.2	5C
Heterogenous torus	200	Yes	6 (0.5)	2 (0.5)	Variable	5D

plant dies, a successor is randomly chosen from the seeds that arrived in the patch during the same or eventually following time steps (“lottery model”). Self replacement is possible as mortality occurs after seed dispersal into the home patch. This procedure implies the following restrictions: (1) competitive similarity between all types at similar age, (2) asymmetric competition across age-classes, i.e., the selected plant cannot be replaced by seedlings from later arriving seeds, (3) no seed bank. For simplicity, we assume asexual reproduction.

For all simulations, the probability distribution of dispersal distances ( $\phi$ ) follows a negative exponential function. Types differ in their specific mean dispersal distance ( $d_s$ ) only. The number of cells moved by a single seed of type  $s$  ( $s = 1 \dots S$ ) in  $x$ -( $\Delta x$ ) and  $y$ -direction ( $\Delta y$ ) are calculated according to the following algorithm:

$$\Delta x = \text{round}[d_s \phi \cos(\alpha)] \quad (1a)$$

$$\Delta y = \text{round}[d_s \phi \sin(\alpha)] \quad (1b)$$

with  $\phi = -\ln(U_1(0,1))$ , an exponentially distributed random number ( $E\{f\} = 1$ ),  $\alpha = 2\pi U_2(0,1)$ , a random number evenly distributed in the interval  $(0, 2\pi)$ , and  $U_2(0,1)$ , a random number evenly distributed in the interval  $(0,1)$ .

There are no energetic or allocation costs associated with a specific mean dispersal distance  $d_s$ , i.e., the cost of dispersing seeds over a long distance is similar to short distance dispersal.

A carrying capacity  $k_i$ , i.e., the maximum number of adult plants which could exist in the cell, was assigned to all cells of the grid (details below). To simulate the (re-)colonization of an empty stretch of land, three quarters ( $n_x/4 < x \leq n_x$ ) of the grid were cleared of all plants at the start of each simulation run (Fig. 1). In the remaining quarter ( $0 < x \leq n_x/4$ ; “base area”) each cell was filled with plants according to its capacity ( $k_i$ ). Dispersal types of individuals were randomly chosen (with equal probability) from a set of  $S = 9$  types with mean dispersal distances from 0 to 8 cells. For each

simulation run the frequencies of all types were recorded every five time steps in the test area ( $n_x/2 < x \leq 3n_x/4$ ). From these data we calculated mean dispersal distance and type diversity (Shannon Index). To evaluate variability in simulation runs, we performed five independent runs for each parameter setting.

To study consequences of differences in the geometry and heterogeneity of the landscape as well as the effect of adult survival on succession in the test area we performed various simulation runs of 10000 time steps each (Table 1). In the arrangement called “homogenous island” all cells in the grid had the same capacity ( $k_i = 4$ ). This world was finite and seeds crossing its boundary were lost. This scenario was selected to investigate the relevance of large scale heterogeneity. In the “torus scenarios” no seeds were lost at the edges. Instead, seeds dispersed over an edge re-entered the grid on the opposite side to eliminate the effect of large scale heterogeneity studied in the island scenarios. A capacity  $k_h$  was assigned to a fraction  $p_h$  of the cells (“high capacity cells”, randomly selected), the remainder of the cells (“low capacity cells”;  $p_l = 1 - p_h$ ) could support  $k_l = 8 - k_h$  adult plants. By varying  $k_h$  ( $k_h = 8, 7, 6, 5, 4$ ) we investigated the relevance of small-scale habitat heterogeneity. In the “heterogeneous torus” ( $k_h = 7, 6, 5$ )  $p_h$  was 0.5 in all simulations. For the “patchy torus” ( $k_h = 8$ ) we also varied the fraction  $p_h$  of high capacity cells to explore the effect of overall habitat suitability on the successional process. In the “homogeneous torus” with  $k_h = 4$  neither small- nor large-scale heterogeneity existed. Thus, the simulations on a “homogeneous torus” approximate dispersal in an infinite and homogeneous landscape.

Finally, we investigated the relevance of adult survival ( $m$ ) on the successional process for a specific landscape, i.e., a “heterogeneous torus” with  $k_h = 6$  and  $p_h = 0.5$ .

## Results

Except for the high mortality scenarios (see below), the test area was rapidly colonized and the number of

individuals reached approximately 90% of the global carrying capacity in less than 50 time steps. Naturally, the completely philopatric type ( $d_s = 0$ ) never reached the test area and was rapidly displaced in the base area under all conditions. As our simulated landscapes usually had a total capacity of ca 80000 individuals we did not observe great variance between simulation experiments based on the same model parameters. Diversity of dispersal types (Fig. 2) and mean dispersal distance (Fig. 3) stayed in a rather narrow range in all five replicate simulations.

In the test area, we observed a clear successional pattern in most simulations (Fig. 4). It started with the initial dominance of the most dispersive type that reached the test area first and its successive replacement by types with lower and lower mean dispersal distances. Additionally, we could observe a unimodal pattern in the diversity of dispersal types over time. Due to the arrival of the less dispersive types in the test area diversity first increased after initial colonization. Later on, it decreased as the highly dispersive types were excluded by types of lower dispersal potential (Figs 2 and 3). However, the complete successional pattern did not occur in the homogeneous ( $k_h = k_l = 4$ ), and the slightly heterogeneous torus ( $k_h = 5$ ; Fig. 5C). In these scenarios, the types with high mean dispersal distances maintained their initial dominance in the test area over the course of the simulation. The dominance of the long-distance dispersers in the homogeneous torus is not only the consequence of a head-advantage in colonizing the test area. Simulations on a homogeneous torus filled from the beginning over its entire area clearly demonstrate a positive selective advantage for long-distance dispersal in a completely homogeneous landscape (Fig. 6).

With an increasing fraction ( $p_h$ ) of high capacity cells ( $k_h = 8$ ) on the patchy torus a slowing in the successional process could be observed. However, even in a landscape with 90% of the cells of high capacity, the type with a mean dispersal distance of  $d_s = 1$  finally prevailed (Fig. 5A).

Variation in large-scale heterogeneity, i.e., variation in the grid size of the homogeneous island had a substantial effect on the succession in mean dispersal distance over time (Fig. 5B). With increasing island size ( $n_y$ ) succession progressed slower and eventually a coexistence of several dispersal types became possible (see Discussion). Small-scale heterogeneity had a more pronounced effect on the speed and outcome of the successional process. Except for very moderate heterogeneity ( $k_h = 5$ ; see above), succession rather quickly proceeded towards complete dominance of the low dispersal types (Fig. 5C).

A surprisingly complex pattern emerged with respect to variation in adult mortality rates (Fig. 5D). Succession proceeded fastest at intermediate mortality rates ( $m = 0.2$  or  $0.3$ ) and slower with either very low ( $0.1$ ) or very high mortality rates. In fact, over the period of the simulations coexistence of several dispersal types was possible with high adult mortality. Equilibrium occupation of available positions (on average 20000 in the test area) decreased from nearly 100% at  $m = 0.1$  to ca 50% at  $m = 0.5$ .

## Discussion

The purpose of our model was to investigate the relevance of differences in dispersal strategy for the generation of a successional pattern on an originally

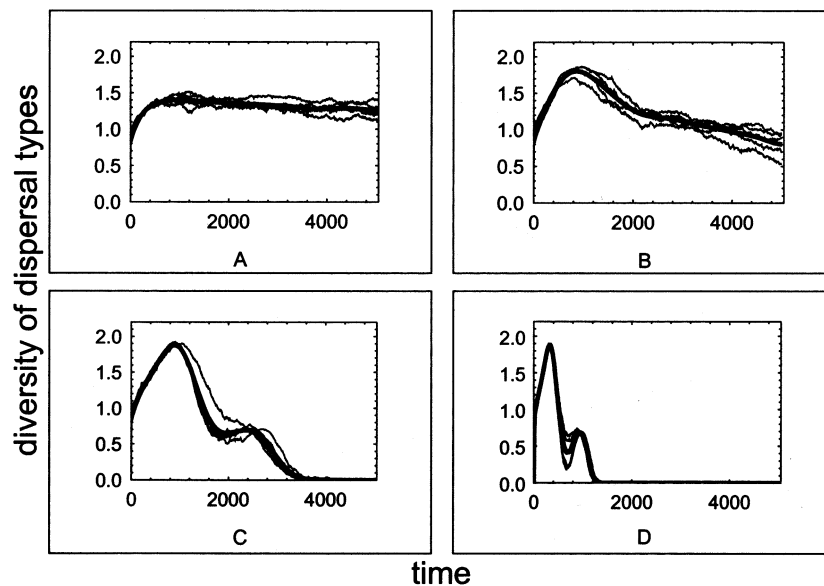
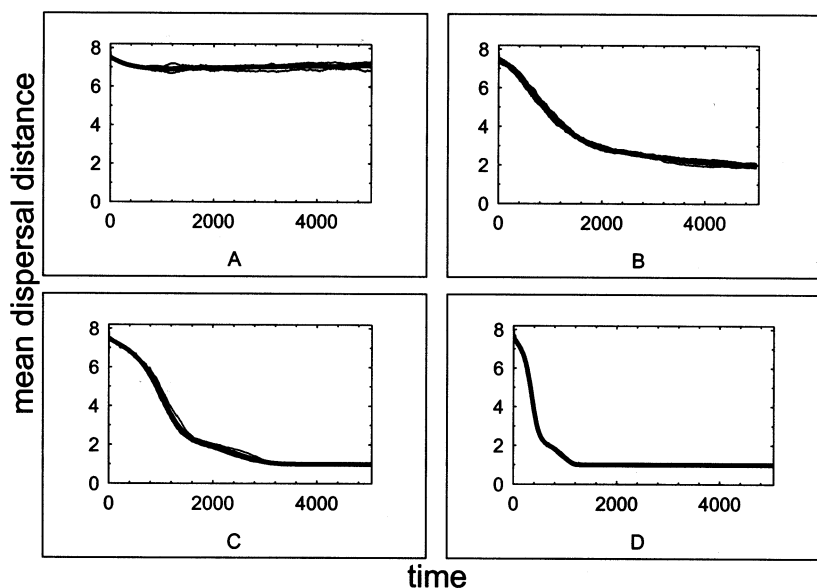


Fig. 2. Temporal development of the Shannon diversity index in the test area of worlds with different levels of spatial heterogeneity. Results for five independent simulation runs (thin lines) as well as mean results are presented for each parameter setting. (A) no heterogeneity: homogeneous torus, (B) large-scale heterogeneity: homogeneous island, (C) small-scale heterogeneity: heterogeneous torus, (D) small-scale heterogeneity: patchy torus. Details of the parameter setting can be taken from Table 1. For all simulation runs  $S = 9$ ;  $n_{seed} = 1.0$ .

Fig. 3. Change in mean dispersal distance (i.e., mean strategy type in the test area) in the test area over time in landscapes with different levels of spatial heterogeneity. Same parameter settings and simulations as in Fig. 2. Results for five independent simulation runs (thin lines) as well as mean results are presented for each parameter setting.



uninhabited piece of land. Our principal interest lay on the investigation of the succession sequence and not on long-term coexistence of species with different dispersal strategies in landscapes with regular occurrence of disturbances. The latter has been investigated already by several authors (e.g., Levins and Culver 1971, Horn and MacArthur 1972, Horvitz and Schemske 1986, Tilman 1993) and especially Lavorel et al. (1994) and Lavorel and Chesson (1995) with a simulation approach similar to ours. In our analyses we thus concentrated on the events in a single part of the landscape after an disturbance event.

The simulations have demonstrated that habitat heterogeneity – and a homogenous island is part of a heterogeneous world – will usually lead to a successional replacement of early-arriving long-distance dispersers by less mobile species even if species are similar in all other traits. At this point the qualitative agreement between our results and the shift towards lower dispersal rates in aging patches observed by Olivieri et al. (1995) should be noted, even though they considered the evolution of dispersal rates and not dispersal distance in their spatially implicit patch model. Long-distance dispersal reduces the chance to recruit offspring locally as a seed cannot be at two places at once. In addition, long-distance dispersers suffer higher dispersal mortality in a heterogeneous world as they distribute their seeds more homogeneously irrespective of habitat quality. In the extreme case (“patchy torus” and “homogeneous island”) dispersed seeds will partly end up in unsuitable habitat with a certain chance of failed recruitment. However, a related argument also applies in cases with less dramatic habitat heterogeneity. In this case, dispersal does not result in a loss of seeds in unsuitable patches, but dispersing individuals will be

confronted with increased competition. Since cells with high capacity produce more offspring and consequently more emigrants than those with low capacity but receive only the same number of immigrants, a net flow of dispersing seeds from cells with high capacity to cells with low capacity will occur. Short-distance dispersers will leave a larger fraction of their seeds in patches of good quality, simply because the majority of seeds is produced in good patches (cf., Ellner and Shmida 1981, Hastings 1983). As this cost of dispersal increases with increasing degree of heterogeneity the speed of succession is markedly accelerated with increasing habitat heterogeneity.

Only completely philopatric species ( $d_s = 0$ ) are at a disadvantage under all conditions as they give up any chance to colonize additional patches and are not secure to keep their home patch against individuals with

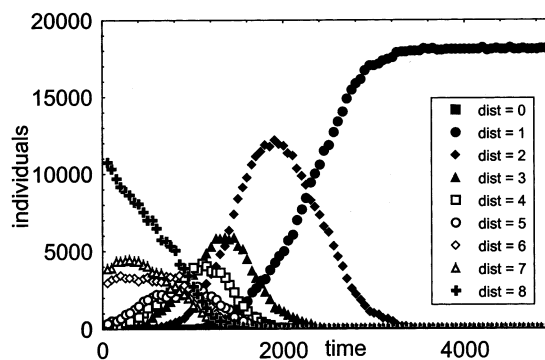


Fig. 4. Typical example for the succession of different dispersal types (characterized by their mean dispersal distance  $d_s$ ) in the test area. Result of a simulation run on a “heterogeneous torus” with  $S = 9$ ;  $p = 0.5$   $k_h = 6$ ;  $k_l = 2$ ;  $n_x = 200$ ;  $n_y = 100$ ;  $n_{seed} = 1$ ;  $m = 0.2$

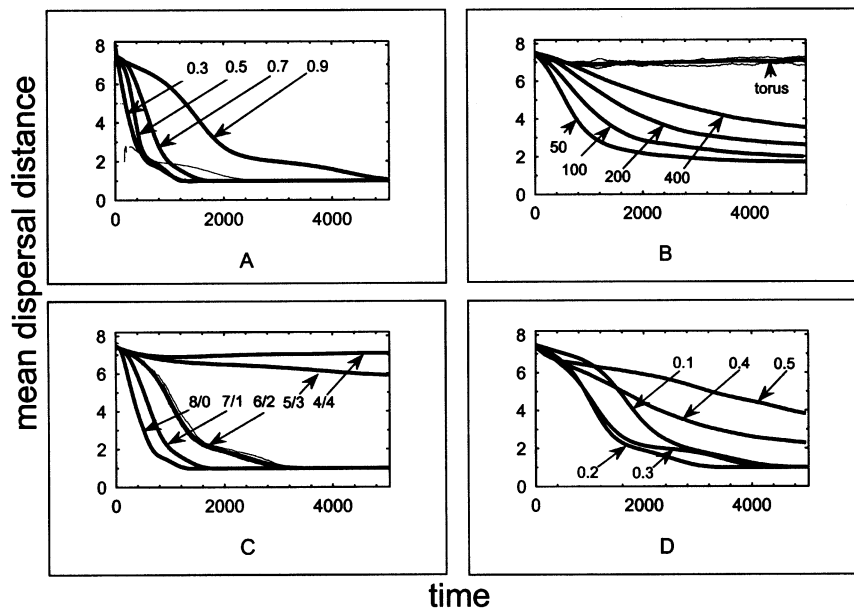


Fig. 5. Effect on succession of mean dispersal distance over time in the test area due to variation in (A) the fraction of high capacity cells ( $p_h$ ) on a patchy torus ( $k_h = 8$ ), (B) the grid dimension ( $n_x$ ) of a homogeneous island, (C) small-scale habitat heterogeneity ( $k_h/k_l$ ) on a torus, and (D) adult mortality ( $m$ ) on a heterogeneous torus ( $p_h = 0.5$ ,  $k_h = 6$ ). Further details on parameter setting can be taken from Table 1. For clarity, only the mean curves of the five simulation runs for each setting are shown.

other dispersal strategies (Hamilton and May 1977). It is interesting to note that a minimum of habitat heterogeneity is needed to select against high dispersal distances. As Hamilton and May (1977) have shown, selection will always favor uniform distribution of offspring in a homogeneous landscape as it results in the maximum reduction of kin competition. This will in general favor the types with the longest mean dispersal distance. This advantage is sufficient to compensate for the small costs of dispersal in slightly heterogeneous landscapes, as our simulations on a torus with  $k_h = 5$  have demonstrated.

The long-term disadvantage of long-distance dispersal could be compensated for only in a world with temporal and spatial variation in patch quality (cf., Venable and Brown 1988, 1993). Under these conditions long-term coexistence of species with different dispersal strategies is possible (cf., Huston 1979, Lavelle and Chesson 1995) due to the balance between within- and between-patch selection (Olivieri et al. 1995). In agreement with these models and theories we observed sustained coexistence of species as soon as we added repeated occurrence of disturbances. As we excluded temporal heterogeneity as well as evolution or external immigration of new dispersal types in the simulations presented here, types with low mean dispersal distances finally displaced long-distance dispersers in most simulations, and the number of types continuously decreased. This result has also been confirmed by Lavelle et al. (1994) with a different simulation approach.

It should be noted that delayed germination, i.e., allocation of seeds to a seed bank may be another and usually alternative strategy to cope with habitat hetero-

geneity in space and time (Venable and Lawlor 1980, Cohen and Levin 1991). We actually expect to see a similar successional sequence after disturbance if we consider dispersal in time for principally the same reasons as those applying in our model. Species allocating a high fraction of seeds into the seed bank should be dominant colonizers after a disturbance event. However, as they trade immediate chances of recruitment for potential recruitment in the future, they should be replaced by species allocating a smaller fraction of seeds into the seed bank as long as the patch is not disturbed again (cf., Olivieri et al. 1995).

The sole exceptions to the general decline in diversity and prevalence of short-distance dispersal types were produced by simulations on large homogeneous islands. The habitat homogeneity of the islands should favor

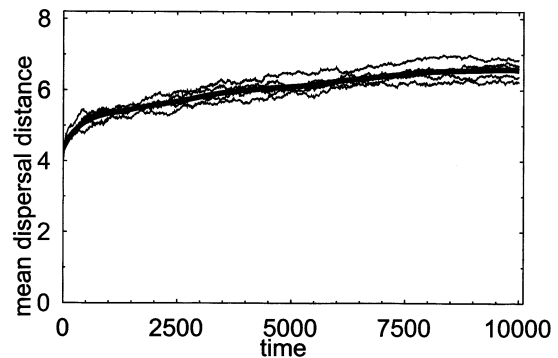


Fig. 6. Change in mean dispersal distance on a homogeneous torus filled from the beginning over the entire grid area by a random mixture of all dispersal types. Results for five independent simulation runs (thin lines) as well as the mean result are presented. Parameters as in Table 1.

long-distance dispersal types. However, while the capacity of the habitat cells were all similar in these simulations ( $k_i = 4$ ) a more subtle heterogeneity does in fact exist in the island scenarios: the cells vary in their distance to the island edge. This will lead to variable cost to benefit ratios depending on a plant's actual position. A long-distance disperser placed in the center of an island will lose less seeds into unsuitable habitat than a plant with a similar strategy placed at the edge of the island. This habitat heterogeneity may at least extend the period until high dispersal strategies are excluded from the landscape. Given this relationship we expect to see an effect not only of patch size but also of patch form (i.e., the perimeter to area ratio) on the selection against long-distance dispersers. Succession should thus proceed faster in elongated or irregularly shaped habitat patches compared to circular patches of the same size.

Two opposing effects must be accounted for to explain the unimodal pattern in the speed of succession as a consequence of variation in adult mortality (Fig. 5D). An increase in adult mortality rates from low to moderate values (e.g., 0.1 to 0.2) will accelerate succession because the turnover of individuals and replacement of long-distance dispersers is speeded up. However, this should not tempt us to assume that selection against long-distance dispersal is less intense at low adult mortality rates. A further increase in mortality rate is accompanied by a reduction in global cell occupancy and an increase in the probability of local patch extinction. Now dispersers profit from the chance to colonize suitable but temporally empty patches. High mortality thus introduces spatio-temporal variation in habitat occupancy inaugurating the advantage of long-distance dispersal mentioned in the previous paragraph. A principally similar relationship between demographic stochasticity and dispersal has also been suggested by Comins et al. (1980). However, Ronce et al. (2000) observed that dispersal rates decreased with adult mortality in their metapopulation model. Even though the modeling approach by Ronce and her colleagues differs in several aspects from ours, the reason for this discrepancy is probably due to the different factors creating spatio-temporal heterogeneity in the two models. As described above, in our model it is due to demographic stochasticity while in Ronce et al.'s model it is the result of externally driven patch-extinction only. Thus, in their model increasing adult mortality increases the chances of offspring to recruit in the home patch but does not alter the chance to find an empty patch elsewhere. Consequently, it increasingly pays to stay at home when adult survival declines.

Overall, the results of our simulations could be summarized as follows: (1) succession will proceed faster in landscapes with small-scale heterogeneity compared to large scale heterogeneity, (2) it will proceed faster when overall habitat suitability is low, (3) it will proceed

faster the more pronounced the habitat heterogeneity is, and (4) it will be fastest at intermediate levels of adult mortality.

Given the simplicity of our model the question arises why this successional mechanism – at least to our knowledge – has not been explicitly described before. A simple answer may be that the mechanism is detectable only in spatially explicit models. The majority of succession models proposed so far (e.g., Botkin et al. 1972, Huston and Smith 1987, Tilman 1990) are not spatially explicit, at least not with respect to seed dispersal (a notable exception is the spatial explicit version of the SORTIE model by Ribbens et al. 1994). Consequently, Pickett and McDonnell (1989): 243) distinctly excluded differences in seed dispersal as a mechanism that could serve as a generalizable core of a vegetation dynamic theory.

We do not want to suggest that successional changes are generally and exclusively based on the simple mechanism we have demonstrated in our model. The existence of allocation trade-offs considered in the models of Huston and Smith (1987) or Tilman (1988) are reasonable explanations for the emergence of real successional patterns and do not contradict the role of different dispersal distance for the emergence of a successional pattern. Equally, facilitation as well as different tolerance towards herbivory can lead to a succession of species (Connell and Slatyer 1977, Tilman 1990). However, the mechanism we have demonstrated in this paper appears to be a more parsimonious explanation for some aspects of successional pattern. For example, the model can explain why succession after small disturbances (either in extension or in intensity) frequently starts with rather late-successional species (cf., Connell and Slatyer 1977, Goldberg and Gross 1988; also Kotanen 1997) as rapid re-colonization of small patches is possible also for species with moderate to low dispersal capabilities. It is also in agreement with the observation that during the course of succession a shift in dispersal syndromes does usually occur (Brown 1992, Debussche et al. 1996, Wolff and Debussche 1999) or that perching trees may speed up succession as they facilitate the influx of bird dispersed species (Debussche et al. 1982, Duncan and Chapman 1999). Additionally, while our model makes the prediction that during the course of succession a gradual reduction in the abundance of early successional species should be observed, it is not based and would thus *not* predict a deterioration in the performance of individuals (e.g., growth, reproductive output) of these species during the course of succession.

One of the more interesting points raised by our simple model is the question whether the evolution of high dispersiveness (e.g., small seeds, wind dispersal) generally has preceded (as a preadaptation) or rather succeeded the evolution of other traits typically associated with early successional status or whether these

traits usually evolve in concert. In the first case, we should frequently find that early successional species evolved in lineages with efficient seed dispersal mechanisms. Appropriate comparative studies could eventually solve this question.

Finally, we want to draw attention to a further, more fundamental difference between our and most other models on the generation of succession. Compared to other models, succession in our model is not the result of a trade-off in the allocation of resource to two different trait categories, e.g., allocation of resources to growth or dispersal efficiency. Instead, succession is the result of the different expressions of a single trait. Which specific trait expression – in our case the value of the mean dispersal distance – is the best compromise between advantages and disadvantages depends on the actual environment of an organism only. In this respect, within-patch succession in dispersal rates observed under some conditions in the model by Olivieri et al. (1995) and Ronce and Olivieri (1997) shows a comparable behavior.

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