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# Estimating plant migration rates under habitat loss and fragmentation

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Changes in the global environment are modifying the geographical locations of habitats suitable for plant growth. The capacity of plants to migrate to sites of suitable environmental quality will strongly influence future distributions of plant diversity. However, it is not well understood how rates of plant migration are influenced by the habitat loss and habitat fragmentation that characterise contemporary landscapes. In this study we develop a model that can predict migration rates in both intact landscapes (potential migration rate) and in fragmented landscapes (realised migration rates). Migration rates in fragmented landscapes might be slower for many reasons. In this study we focus on two, non-exclusive reasons. First, the processes that move seeds may break down in fragmented landscapes causing seeds to be dispersed shorter distances. Second, in fragmented landscapes some proportion of seeds will not be deposited in habitats suitable for recruitment. We describe the breakdown of dispersal processes as a competing risk between the factors influencing dispersal in intact landscapes and the factors that may disrupt dispersal processes in fragmented landscapes. We show how the parameters that influence dispersal in fragmented landscapes can be estimated, and how these estimates can be used to forecast migration rates using an integrodifference equation (IDE). The forecasts of the IDE described the effects of reduced dispersal distances adequately. However, the IDE produced biased estimates of the effects of a reduction in plant habitat on migration rates. Model analyses showed that, although we can expect realised migration rates to be lower than potential migration rates, we can also expect the sensitivity of migration rate to habitat loss to vary. In addition, simulations showed that the qualitative nature of the responses of migration rate to habitat loss were variable – some model species responded non-linearly to habitat loss, others responded linearly. While our method provides guidelines for empirical data collection and model parameterisation, we recognise that obtaining these data will be challenging.

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Global environmental change is modifying the geographical locations of habitats suitable for plant growth (Hannah et al. 2002). While it is clear that the future distribution of plant diversity and corresponding changes in ecosystem functioning will be largely determined by the ability of plants to migrate to sites of suitable habitat (Pitelka et al. 1997, Kirilenko et al. 2000), our capacity to predict potential and realised migration rates, for a range of taxa, is still frighteningly rudimentary. Theories of migration (Skellam 1951, Weinberger 1982, Turchin 1998) recognise that the potential migration rate of a population is determined by the number of offspring that the population produces (fecundity) and the distance that these offspring

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move (dispersal); more recently it also acknowledges the quantitative importance of relatively infrequent long-distance dispersal events (Shigesada et al. 1995, Clark 1998, Clark et al. 1998). In practice, however, our empirical knowledge of potential migration rates remains poor. This is because the great majority of quantitative dispersal studies have concentrated on local dispersal (Howe and Smallwood 1982) and have explicitly ignored the rare ($<5\%$) long distance (an order of magnitude greater than the modal dispersal distance) dispersal events which drive migration. The complexity of processes that move seeds is high, for this reason empirically based methods are a favoured method for describing seed dispersal (Clark et al. 1999, Higgins and Richardson 1999, Bullock and Clarke 2000). The problem with empirical methods, is that they require data. In the context of predicting migration rates this is problematical because data on rare long-distance dispersal are, by definition, rare. Despite these problems, the acknowledged importance of long distance dispersal has recently motivated an explosion of activity that is capturing the required, but elusive data (Cain et al. 2000, Nathan and Muller-Landau 2000).

While we now have both theory and techniques for improving our estimates of potential migration rates, the same cannot be said for realised migration rates. Realised migration rates are migration rates as influenced by barriers to migration processes. In the context of plant migration under global change, habitat loss and fragmentation create barriers to migration processes (Pitelka et al. 1997). These barriers to migration processes may act to reduce dispersal distances or to reduce the proportion of dispersed seed that land in habitat suitable for recruitment. How to translate potential migration rates into realised migration rates is currently not well established. Most theoretical and empirical studies of movement in fragmented landscapes have focussed on animals and on local movement processes (Gardner et al. 1987, With and Crist 1995, 1996, McIntyre and Wiens 1999). As a consequence, these approaches seem poorly suited to addressing how plant migration, as driven by long distance dispersal processes, is influenced by barriers to dispersal (Higgins and Richardson 1999).

The aims of this paper are to (1) propose a function, the realised dispersal function, that can describe the effects of barriers on seed dispersal distances. (2) Show how the parameters of the realised dispersal function can be empirically estimated. (3) Use the realised dispersal function to forecast plant migration rates. (4) Use models to explore the effects of barriers to dispersal, habitat loss, dispersal syndrome and fecundity on potential and realised migration rates.

## Realised dispersal distance and plant migration rates

Predicting migration rates involves linking a function that describes the number of offspring that a plant population produces with a function that distributes these offspring (Skellam 1951, Weinberger 1982). In an integrodifference framework Weinberger (1982) showed that the asymptotic speed of migration can be generalised as,

$$c = \min_{s} \left\{ \frac{1}{s} \ln[\lambda M(s)] \right\} \tag{1}$$

where $\lambda$ is the finite rate of increase of the population and $M(s)$ is the moment generating function of the dispersal kernel. This result holds for populations that increase when small, that are negatively influenced by density, and that have dispersal kernels that are exponentially bounded (Neubert and Caswell 2000).

To use this result to investigate the consequences of barriers to dispersal process on migration rate we need to define a moment generating function that describes how dispersal processes may break down when there are barriers to dispersal. The definition of a moment generating function is,

$$M(s) = \int_{-\infty}^{\infty} e^{sx} f(x)\, dx \tag{2}$$

where $f(x)$ is the probability density function of the dispersal kernel. The processes that influence $f(x)$, the distances that seeds can move, are diverse. However, there are two qualitatively different kinds of processes that influence the distances that seeds move. First, there are those processes that operate in the absence of barriers to dispersal. For example, wind velocity and terminal velocity of the seed influences the distances that seeds are dispersed by wind; while net displacement rates of animals and retention times influence the distances that seeds are dispersed by animals. The second set of processes (which we call stopping processes) are processes that operate in the presence of barriers to dispersal. For example, the movement of a seed dispersing by wind from a grassland may be terminated when the seed encounters a forest edge, or the movement of a seed in the gut of an animal may be terminated when the animal encounters unfavourable habitat.

The realised distances that seeds move can therefore be thought of as a competing risk between a seed's movement, terminated by processes that act in the absence and presence of barriers to dispersal. The definition of a competing risk, $R(x)$, (for two risk generating factors) is,

$$R(x) = 1 - [1 - D(x)][1 - S(x)] \tag{3}$$

$R(x)$ is the cumulative density of realised dispersal distances and $D(x)$ and $S(x)$ are the respective cumulative density functions of dispersal and stopping distances. In the sections below we propose functions for $D(x)$ and $S(x)$.

## Dispersal distance

There are many candidate functions for $D(x)$. For predicting migration rates it is important to use a function that adequately describes both local and long-distance dispersal (Clark et al. 1999). We use a mixture of exponential distributions to describe dispersal distance data, although other functions could be used. Conceptually, the first component of the mixture distribution describes local dispersal and the second component describes the low frequency long-distance dispersal events. Mixture models are intuitively attractive because they assume that the distribution of dispersal distances is the sum of more than one process. A cumulative density function of dispersal distances $D(x)$ for a mixture of two exponential distributions is,

$$D(x) = 1 - p_1 e^{-u_1 x} - p_2 e^{-u_2 x} \tag{4}$$

where $p_1$ is the proportion of seeds which are locally dispersed and $1/u_1$ is the mean of local dispersal distance; the distance the remaining ($p_2 = 1 - p_1$) seeds move is described by $1/u_2$, the mean of long distance dispersal. We assume that dispersal is isotropic.

## Stopping distance

To define the stopping distance function, $S(x)$ we first need to clarify what barriers are. Barriers to dispersal are defined as landscape elements which can not be crossed by the dispersal agent. It is important to recognise that the environmental factors that influence habitat suitability for plants may be different from the environmental factors that influence the dispersal agent's movement. For example, home range boundaries may limit animal movement and hence may reduce the distances that animal vectors move seeds, even though these home range boundaries are invisible to the plants. On the other hand, a grassland-cropland transition may strongly influence plant demography, but have no effect on wind dispersal distances (because the wind vector is not influenced by the grassland-cropland boundary).

As was the case for dispersal distance functions, there are many candidate distributions that may adequately describe the distribution of stopping distances. We found the negative exponential suitable. When the stopping distances are negative exponential, the probability density function of stopping distances, $s(x)$ is,

$$S(x) = 1 - e^{-mx} \tag{5}$$

where $1/m$ is the mean stopping distance. In principle, dispersal agents that perceive most of the landscape as barrier would have short stopping distances, whereas dispersal agents that perceive most of the landscape as habitat would have longer stopping distances.

## Migration rate for a realised dispersal distribution

Substituting the above definitions of dispersal distance (eq. (4)) and stopping distance (eq. (5)) into the competing risk equation (eq. (3)) and differentiating $R(x)$ allows us to generate $r(x)$, the probability density function that describes realised dispersal distances. Using the definition of the moment generating function (eq. (2)) we can find $M(s)$, the moment generating function of $r(x)$,

$$M(s) = \frac{p_1(m + u_1)}{s - m - u_1} - \frac{p_2(m + u_2)}{s - m - u_2} \tag{6}$$

We substitute this moment generating function into eq. (1) and numerically solve for the migration rate $c$,

$$c = \min_{s} \left\{ \frac{1}{s} \left( \ln[\lambda] + \ln\left[ -\frac{p_1(m + u_1)}{s - m - u_1} - \frac{p_2(m + u_2)}{s - m - u_2} \right] \right) \right\} \tag{7}$$

## Estimating parameters of realised dispersal distance

We provide two examples of how the dispersal parameters in eq. (7) can estimated. The first example considers the dispersal of *Leucodendron rubrum* (Proteaceace) seeds by wind. The second example considers a weed (*Xanthium strumarium*, Asteraceae) that is dispersed by attachment to animal fur (we use the Iberian lynx, *Lynx pardinus* (Felidae), as a model animal vector for *Xanthium* dispersal). Each example describes how to estimate a distribution of dispersal and stopping distances, from which the distribution of realised dispersal distances and the migration rate can be calculated.

### Leucodendron tumbleseeds

Serotinous Proteaceae in fynbos (Mediterranean shrublands of South Africa) release seeds after fire. The seeds have small wings or plumes. Bond (1988) showed that although primary dispersal is not far, secondary dispersal along the soil surface can be substantial. Because seeds are released after fire, and because fires in fynbos remove most of the above ground biomass, these tumbleseeds can move potentially exceptional distances

(Bond 1988). Barriers, in the form of boulders or abrupt changes in topography limit these exceptional distances from materialising.

To estimate the parameters describing dispersal distance (eq. (4)), we use data from a seed release experiment (Keurink, pers. comm.). In this experiment seeds of *Leucodendron rubrum* (Proteaceae) were released on a large, obstacle free, flat beach under a range of wind conditions. Consequently, these data serve as an estimate of *L. rubrum*'s dispersal potential in the absence of barriers. We fit a mixture of exponential distributions (eq. (4)) to these data, estimating the mean potential dispersal distance as 63m ($p_1 = 0.34$, $u_1 = 1/2$ m $u_2 = 1/94$ m, $R^2 = 0.98$, Fig. 1B).

We have no empirical data on stopping distance for tumble dispersed seeds. However, by combining a map of barriers to tumble dispersal with the assumption that tumbling can occur only in the direction of the prevailing wind, we can generate a vector of stopping distances. We generate the barrier map by classifying a digital elevation model into flat areas and areas too steep (slope $>1$ degree) for tumble dispersal. Fig. 1A shows such a map based on a $5 \times 5$ km section of a digital elevation model of the Cape Peninsula (Higgins et al. 1999). We generate a vector of stopping distances from this barrier map by implementing a percolation algorithm that allows seeds to move only straight ahead on the map and by recording the distances that seeds move before being stopped by barriers. Fig. 1C shows the vector of stopping distances created by running the percolation algorithm on the barrier map (Fig. 1A). Using this vector, it is possible to fit eq. (5) to the data and thereby estimate the mean stopping distance as 59 m ($m = 1/59$, $R^2 = 0.87$, Fig. 1C).

Finally, we apply eq. (3) to the fitted models of dispersal distance (Fig. 1B) and stopping distance (Fig. 1C) to yield a mean realised dispersal distance of 24 m (Fig. 1D), which is substantially less that the mean of potential dispersal distances (63 m, Fig. 1B). Substituting these parameter estimates and a finite rate of increase ($\lambda$) of 2 in eq. (7) we estimate a realised migration rate of 83 m/yr. Ignoring barriers to dispersal the potential migration rate would be 216 m/yr.

## Iberian *Lynx* as seed dispersal agents

Seeds of many species are dispersed by attachment to animals. For example, seeds of *Xanthium strumarium* have effective attachment devices, and they often attach to large and medium sized mammals in southwestern Spain, such as the Iberian lynx *Lynx pardinus* (Felidae). We use empirical data on the movement patterns of Iberian lynx as an example of how the movement of an animal dispersal vector may be influenced by habitat loss and fragmentation.

Since lynx clean themselves daily, the maximum seed attachment time is 24 hours. To estimate potential seed

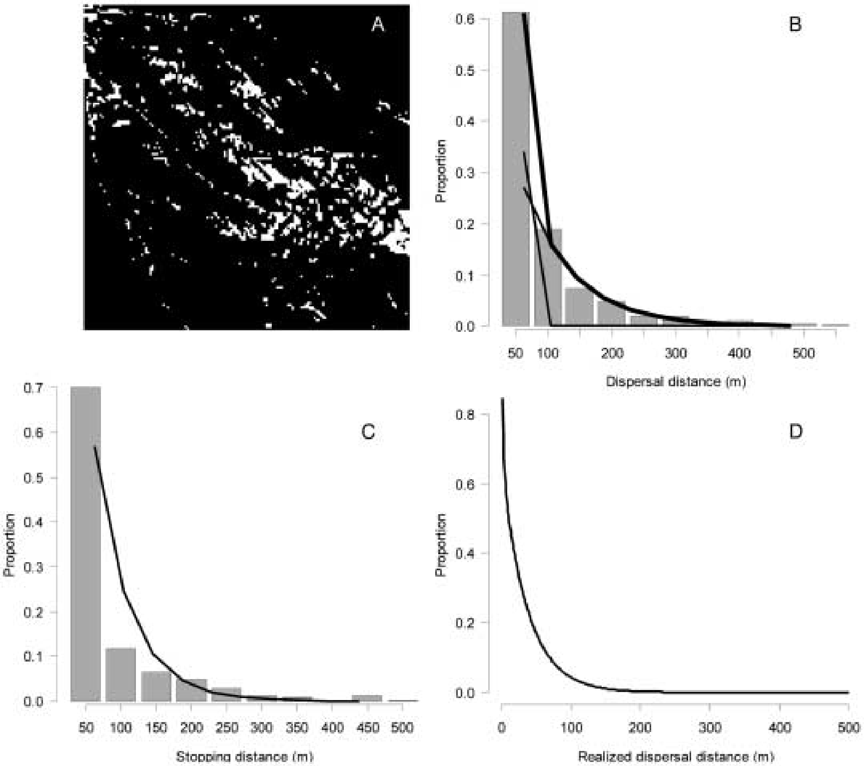

Fig. 1. Illustration of the process of estimating a realised dispersal function (eq. (3)) for *Leucodendron rubrum* (Proteaceae), a tumble dispersed shrub. Black areas in the map (A) represent parts of the landscape where tumble dispersal is not possible. The map is based on a digital elevation model of the Cape Peninsula, South Africa classified into areas with slopes $>1$ degree (black) and areas with slopes $\leq 1$ degree (white). Dispersal distance data from a seed release experiment were used to estimate the parameters of eq. (4). Light lines are the components of the mixture distribution, heavy lines are the mixture distribution (B). Stopping distances were generated by running a percolation algorithm on the landscape map, these data were then fitted to eq. (5) (C). Combining parameter estimates from eq. (4) and (5) using eq. (3) yields the realised dispersal distance (D).

dispersal data we use data on the net displacement of lynx in 24 hours. Data on the net displacement of lynx in preferred habitat comes from Revilla (pers. comm.), who collected hourly net displacement trajectories for 56 activity periods (up to 24 hours) of 29 individuals (Fig. 2B). If we assume that seeds attach at a constant rate, and are removed once every 24 hours, the attachment time should be distributed uniformly within 24 hours (Fig. 2C). We can then use this attachment time to sample a dispersal distance from the net displacement trajectories (Fig. 2B). Repeating this sampling process 10 000 times yields a distribution of dispersal distances, which we describe using eq. (4) (Fig. 2D). In this case, a single exponential distribution provided an adequate fit to the dispersal distance data (the resulting mean dispersal distance is 752m, $p_1 = 1$, $u_1 = 1/752$ m, $R^2 = 0.94$, Fig. 2D).

Based on the habitat preferences of the lynx, we can classify the landscape into three habitat types (preferred habitat, matrix habitat, barrier habitat, Fig. 2A, Palomares et al. 2000). Lynx move during their periods of activity (usually from dawn to dusk) through preferred habitat, formed by Mediterranean shrubland and other vegetation types with abundant cover. Occasionally, they also move through matrix habitat, formed by areas with no vegetation cover, which nevertheless is strongly avoided (especially during the daylight resting period). Barriers are areas that lynx never enter (e.g. large water bodies, urban areas). From radio-tracking studies of lynx at Doñana, we are able to generate a distribution of the interday distances (defined by the net distance between the resting points of two consecutive days, 760 observations) that lynx move in the fragmented landscape of Doñana. Fitting (5) to these interday stopping distance data yields an estimated mean stopping distance of 2390m ($m = 1/2390$, $R^2 = 0.99$, Fig. 2E).

Using eq. (3) we can combine the fitted models of stopping distance (Fig. 2B) and dispersal distance (Fig. 2E) to yield a mean realised dispersal distance of 572 m (Fig. 2F). In this case, the scale of stopping distance was much greater than the scale of dispersal distance. Substituting these parameter estimates and a finite rate of increase ($\lambda$) of 2 into eq. (7) we estimate a realised migration rate of 968 m/yr. Ignoring barriers to dispersal the potential migration rate would be 2186 m/yr.

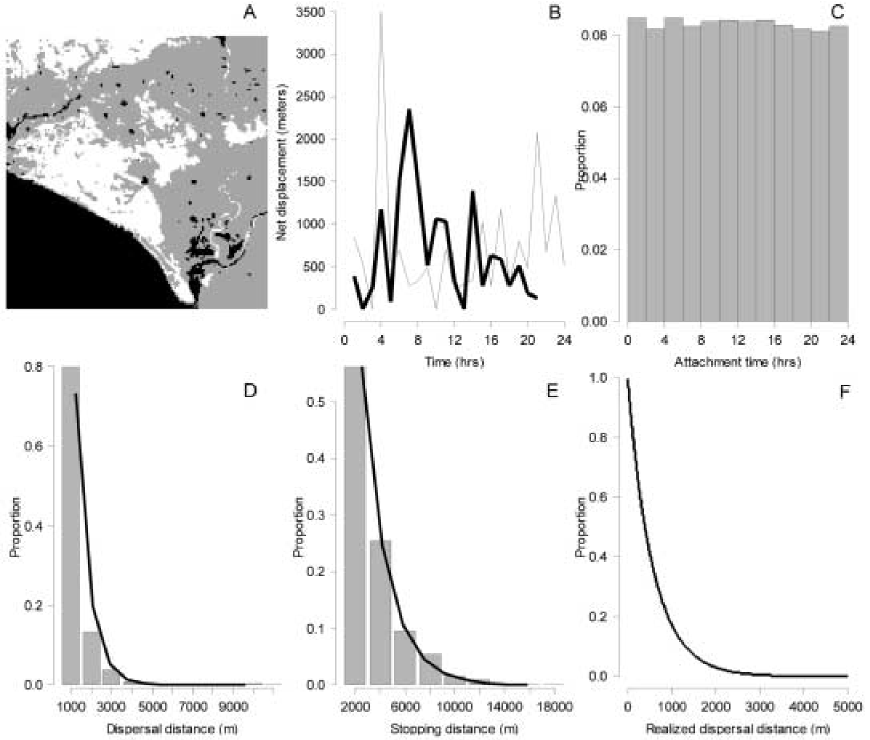

Fig. 2. Illustration of the process of estimating a realised dispersal function (eq. (3)) for *Xanthium strumarium* (Asteraceace), as dispersed by the Iberian lynx (*Lynx pardinus*). The map shows the lynx's perception of habitat in the Doñana National Park, Spain (A). Black areas are barriers to lynx movement, gray areas are matrix habitat and white areas are preferred lynx habitat (Palomares et al. 2000). Dispersal distance data were generated by assuming that the distribution of seed attachment time is uniform between 0 and 24 hours (C). These attachment times were then used to resample a dispersal distance from the net-displacement data (B – only 2 of 59 net displacement trajectories are shown). The net displacement data were derived from radio-tracking lynx in Doñana National Park in preferred habitat. The resulting potential seed dispersal distances were used to estimate the parameters of eq. (4) (D). Empirical data on lynx movement in Doñana National Park were used to estimate stopping distance parameters (eq. (5)) (E). Combining the parameter estimates from eq. (4) and (5) using eq. (3) yields the realised dispersal distance (F).

## Sensitivity of migration rate forecasts to barriers

Since the dispersal distance (eq. (4)) and stopping distance parameters (eq. (5)) are independent it is clear from eq. (7) that the ratio of realised to potential migration rates will range between 0 and 1. That is, some distributions of barriers will cause $m$ to be small and migration rates will consequently be very similar to the rates achieved without barriers. Other distributions of barriers will cause $m$ to be so large that a complete breakdown of dispersal processes occurs, with the consequence that migration rates will be close to zero.

## Sensitivity of migration rate forecasts to habitat loss

Equation (7) assumes that although barriers may limit the distances that seeds move, that all seeds find suitable habitat for recruitment. When habitat is unsuitable the rate of spread will be slower, because some proportion of the seeds will not be dispersed to suitable habitat. When habitat patches are randomly distributed, reducing $\lambda$ (eq. (7)) by the proportion of unsuitable habitat may generate reasonable estimates of migration rates. However when suitable habitat patches are aggregated this procedure may be biased since the probability that a seed lands in suitable habitat will be a function of distance. We use a spatially explicit simulation model to explore the extent of this bias and to explore the sensitivity of migration rates to habitat loss and habitat arrangement. In the sections below, we describe how we simulate the distribution of habitat in landscapes and the spread of plants across these landscapes.

### Model landscapes

The migration model is implemented in a two-dimensional, grid landscape. We simulate spread across rectangular landscape maps of 1024 × 1024 grid cells. Each grid cell is 5 × 5 m in size. The grid size of 5 × 5m is small enough to ensure that estimates of spread rates are not biased by cell size (Higgins et al. 1996).

We use neutral landscape models as a convenient means of generating theoretical distributions of habitat for systematically testing hypotheses about the effects of habitat loss and fragmentation on migration (With and King 1997). Neutral maps are used, not because they represent real habitat distributions, but because they provide a useful baseline for comparison with theoretical models (With and King 1997). Using neutral maps also allows us to explore the influence of multiple realisations of statistically similar patterns of habitat distribution on migration rates. In the simulations below we use two types of neutral landscape models: random (Gardner et al. 1987) and fractal (With 1994). All maps were generated and quantitatively described using the computer program RULE (Gardner 1999). For simplicity, we only consider two landscape states, (1) suitable habitat, in which plant growth is possible and (2) unsuitable habitat, in which plant growth is not possible.

Random maps were generated by randomly selecting habitat locations without replacement. Fractal algorithms allow the generation of maps with different levels of fragmentation and are particularly useful for representing landscapes where the distribution of habitat within a landscape is influenced directly or indirectly by topography and or geology. RULE (Gardner 1999) uses the midpoint displacement algorithm (Saupe 1988) to generate fractal maps. The parameter H, which varies from 0–1, describes the level of spatial auto-correlation in the map (the fractal dimension is 3-H). We generate maps using $H = 0.25$, this creates maps with intermediate levels of habitat aggregation (With et al. 1997). Habitat in the fractal landscapes are more aggregated and have longer correlation lengths than random maps with the same amount of habitat (Fig. 3).

### Spread model

The simulation model is designed to mimic eq. (7). We use an individual based approach, that is each cell in the simulation model is either occupied or unoccupied. We interpret $\lambda$ as the reproductive output per $m^2$. That is, we assume that a typical plant occupies an area of 1

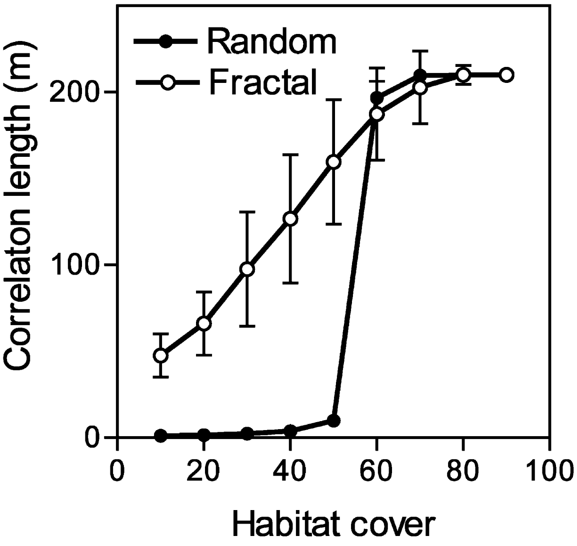

Fig. 3. Correlation lengths of 10 replicate, random and fractal, neutral maps with different levels of habitat loss generated with the program RULE (Gardner 1999). These maps were used for the migration simulations.

m$^2$. Since the model landscapes have a finite number of cells, the model includes density dependence. Each simulation year, for each cell, the model calculates the seed production of the cell and then distributes these seed using the realised dispersal kernel described above. Seeds can only recruit into the population if they land in suitable habitat. The model ignores seedbanks and age structure. A simulation is initiated with a strip of plants 50 cells (250 m) wide at one end of the 1024 × 1024 cell landscape (5.12 × 5.12 km). Each year the model records the distance of the furthermost plant from the site of initiation; at the end of the simulation the migration rate (m/yr) is estimated.

## Habitat loss simulations

Our first simulations test the robustness of the analytic models (eq. (7)) migration rate forecasts to the distribution of suitable habitat. The parameter ranges used for these simulations are presented in Table 1. In the first set of simulations, the entire landscape consists of suitable habitat. For this set of simulations the migration rates predicted by the analytic and simulation model agree (Fig. 4A). In the second set of simulations, the same demographic parameters listed in Table 1 are used; but habitat density ranges between 0.1 and 0.9 and habitat distribution is either a random or fractal (half the simulations use random landscapes, the other half use fractal landscapes; see Model landscapes above). Introducing habitat loss increased the variance in the relationship between simulated and numerical migration forecasts (Fig. 4B). It does not appear as if this relationship was better for random than for fractal patterns of habitat loss (Fig. 4B). Systematic bias was introduced at high levels of habitat loss, in these cases the reduction of $\lambda$ to simulate the reduced likelihood of a seed finding a suitable habitat often led to migration rates of zero being forecast by eq. (7).

To better understand how realised and potential plant migration rates are influenced by barriers, habitat loss, dispersal syndrome and fecundity we used a simulation experiment. The simulation experiment varies five key model parameters at two levels to create a factorial experimental design (Table 2). These levels were selected to represent a range consistent with our empirical experience. We run 9 replicates of each factor combination. Each replicate consists of simulations run on a set of landscape maps with 9 levels of habitat loss (0.1,0.2,0.3…0.9). We summarise the response of migration rate to habitat loss using linear parameters (described below), which we subsequently analyse using ANOVA.

The factor levels used for the stopping distance, $m$, require explanation (Table 2). The low-level of this

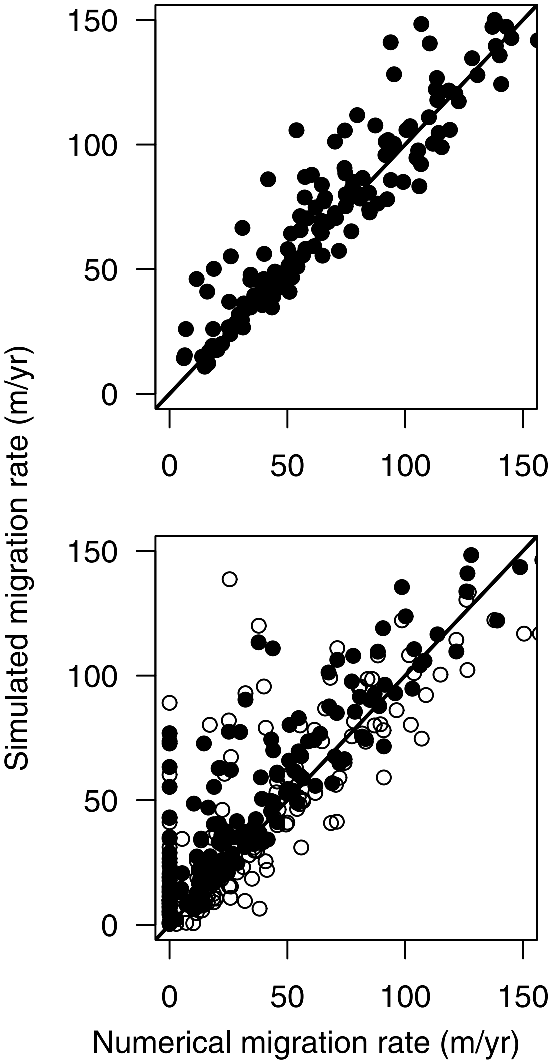

Fig. 4. Comparison of numerical and simulated estimates of migration rates based on parameter values drawn from Table 1. Top panel shows cases where all habitat was suitable for plant growth. Bottom panel shows cases where between 0.1 and 0.9 of the habitat was unsuitable – solid circles are for random distribution of suitable habitat and open circles are for a fractal distribution of suitable habitat.

Table 1. Parameter ranges used to compare the numerical (eq. (7)) and simulation models. For these simulations uniform random numbers between the lower and upper level were drawn for each parameter.

| Parameter | Low level | High level |
|---|---|---|
| Finite rate of increase ($\lambda$) | 1 | 10 |
| Proportion seeds dispersed long distances ($p_2$) | 0.01 | 0.05 |
| Mean of short distance dispersal ($1/u_1$, meters) | 1 | 5 |
| Mean of long distance dispersal ($1/u_2$, meters) | 5 | 100 |
| Mean stopping distance ($1/m$)* | 5 | 500 |

*Half the simulations assumed $m$ was 0, the other half used values drawn from the indicated range

Table 2. Factors and factor levels used in the $2^5$ fractional factorial design used in the simulation experiment. This design was repeated for 9 habitat levels of habitat loss (0.1,0.2,0.3...0.9) and the entire design was replicated 10 times.*

| Factor | Low level | High level |
|---|---|---|
| Finite rate of increase ($\lambda$) | 1 | 10 |
| Proportion seeds dispersed long distances ($p_2$) | 0.01 | 0.05 |
| Mean of long distance dispersal ($1/u_2$, meters) | 50 | 100 |
| Stopping distance ($m$) | Calculated$^+$ | 0 |
| Map type ($M$) | Random | Fractal |

*The mean of short distance dispersal was held constant ($1/u_1 = 5$m).
$^+$The stopping distance parameter ($m$) was calculated by running a percolation algorithm on the habitat map for each simulation.

factor simulates situations where sensitivity of dispersal processes to habitat loss is high. In these simulations it is assumed that habitat that is unsuitable for plants presents a barrier to the dispersal process. For each of these simulations we estimate $m$ by running a percolation algorithm on the landscape map, recording 10000 stopping distances, and then estimating $m$ (using eq. (5)). We use a percolation algorithm that assumes that movement is possible to any neighbouring cell, provided that cell is suitable habitat. Such algorithms are often used to represent animal movement – hence these simulations may be appropriate for estimating $m$ for animal dispersed plants. We implement the percolation algorithm following guidelines provided by Stauffer and Aharony (1992). The high level of factor $m$ simulates situations where the dispersal process is not sensitive to habitat loss – these simulations use $m = 0$. Such insensitivity to habitat loss may be typical for wind dispersed species in agricultural landscapes.

From previous studies of movement in heterogeneous landscapes (Gardner et al. 1987, Lavorel et al. 1995, Wiens et al. 1997), we would expect that the response of migration rate to habitat loss can be summarised as a non-linear function of habitat cover ($P$),

$$v = -\frac{\alpha}{1 + \exp\left(\beta - \frac{P}{\varepsilon}\right)} \tag{8}$$

where $v$ is the migration rate (m/yr), $\alpha$ is the maximum migration rate, $\beta$ is the threshold level of habitat loss where migration rate switches, and $\varepsilon$ is the abruptness of change in migration rate. We use this function to summarise the results of each replicate of the factorial experiment. The parameters $\alpha$, $\beta$ and $\varepsilon$ are estimated using non-linear regression. Other response variables were also calculated for each replicate: the maximum migration rate, the minimum migration rate, and the ratio of minimum to maximum migration rate.

## Migration response surfaces

For all simulations estimates of $\beta$ (eq. (8)) fell below 10% habitat cover (Fig. 5). That is, the habitat loss after which migration rates rapidly fell was close to zero. Moreover, 73% of $\varepsilon$ estimates were greater than 10 suggesting that migration rate mostly changed slowly with habitat loss (eq. (5)). Overall, the parameter estimates for eq. (8) suggest that steep thresholds of landscape connectivity beyond which migration processes break down were uncommon in our results.

The different factor combinations used in the simulation experiment (Table 2) allowed us to identify qualitatively different responses of migration rate to habitat loss (eq. (5), Fig. 6). Fits of eq. (8) were used to subjectively assign each replicate simulation to one of these response types. In our simulations a sigmoidal response of migration rate to habitat loss occurred when $m > 0$

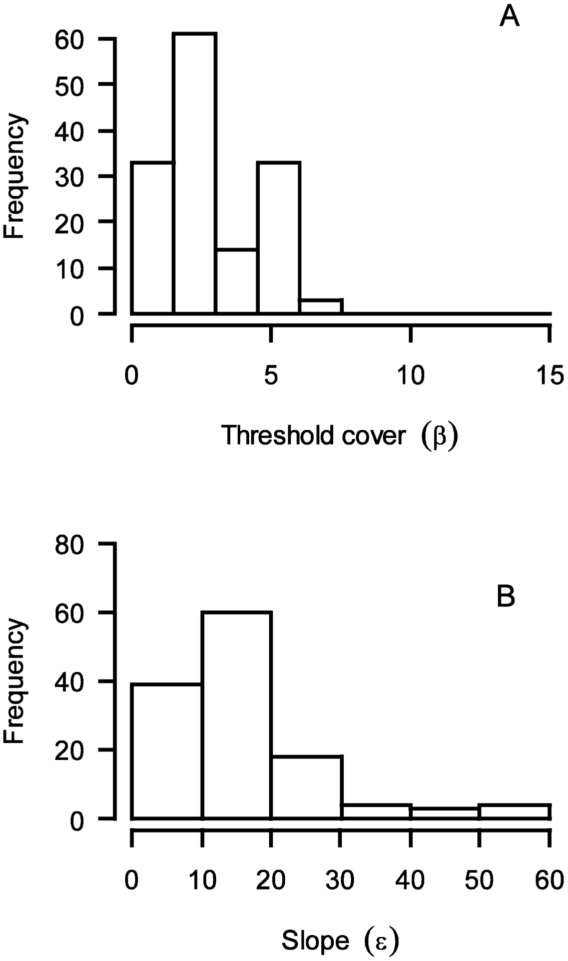

Fig. 5. Frequency distribution of parameter estimates of the threshold habitat cover at which migration rates drop rapidly ($\beta$) and the rate at which migration rates drop ($\varepsilon$). Parameter estimates are from non-linear regression fits to eq. (8). Data are from the simulations described in Table 2.

and landscapes were random. When $m > 0$ and landscapes were fractal the response was linear. A linear response suggests equal sensitivity to each incremental unit of habitat loss. Linear responses occur when dispersal processes still occur, albeit at a lower rate, as habitat is lost. The linear response also occurred when stopping distances were infinite ($m = 0$) and either the mean of long distance dispersal, the proportion of seeds dispersed long distances, or the scale of long distance dispersal was low. A third response type, the convex response, can be thought of as an incomplete sigmoidal, where the migration rate drops off at much lower levels of habitat cover than expected by percolation theory. Convex responses occurred when high fecundity, a large proportion of long distance dispersal, a large scale of dispersal, or infinite stopping distances ensured that migration rates were maintained under moderate levels of habitat loss and fell slowly at higher levels of habitat loss. Other simulations (not shown) that used different percolation algorithms to estimate stopping distances ($m$) revealed a greater diversity of response types.

## Migration sensitivity

The factorial design allows the estimation of the relative effects of different factors on the response variables. The maximum migration rate can be thought of as the potential migration rate, as this is the spread rate recorded in landscapes with limited habitat loss. The distribution of maximum migration rates generated by the factorial sensitivity analysis was approximately normally distributed: the median of maximal migration rate was 113 m/yr whereas the mean of maximum migration rate was 130 m/yr (Fig. 7A). Using ANOVA we estimate the effect of each factor on the response variables. The effect of a factor is the average change of the response variable when the factor is moved from a low to a high level. The effect is relative to the overall mean response for all factor combinations. Maximum migration rate, was primarily and positively influenced by $\lambda$, the mean of long distance dispersal ($1/u_2$) and the proportion of seeds dispersed long distances ($p$) (Fig. 7B). The effects of the other factors on maximum migration rate were unimportant. Interactions between the three important factors $\lambda$, $1/u_2$, and ($p$) were also important.

The minimum migration rate, the migration rate achieved when habitat density is lowest, was strongly left skewed (Fig. 7A). The median minimum migration rate was 14 m/yr and the mean minimum migration rate was 29 m/yr. All factors and most interactions contributed to the minimum migration rates (Fig. 7B). The only large negative interaction was that between map type ($M$) and the sensitivity of the dispersal vector to habitat loss ($T$). Although both insensitivity to barriers or fractal map types leads to higher minimum migration rates – the interaction suggests that these effects on minimum migration rate are not additive.

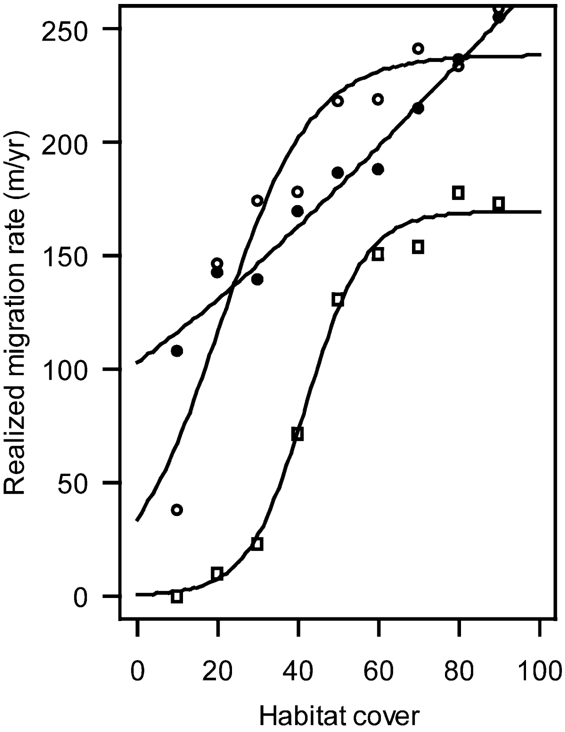

Fig. 6. Three qualitatively different responses of migration rate to habitat loss were identified. Examples of these different response types are shown. The responses were generated using simulations that were run following the experimental design described in Table 2. Equation (8) was used to derive the fitted curves. The three response types are sigmoid (squares), convex (open circles), and linear (closed circles).

The ratio of minimum to maximum migration rate is an indicator of the sensitivity of the migration response to habitat loss. If minimum migration rate is small relative to maximum migration rate, it implies higher sensitivity to habitat loss, conversely if minimum migration rate is large relative to maximum migration rate, it implies an insensitivity to habitat loss. The distribution of this ratio was left-skewed (Fig. 7A), that is most parameter combinations were highly sensitivity to habitat loss and very few parameter combinations were insensitive to habitat loss (the median and mean ratios were 0.16 and 0.2 respectively). Fractal rather than random map type ($M$) and insensitivity of the dispersal vector to habitat loss (high levels of factor $T$) were the most important factor in reducing the sensitivity of migration rate to habitat loss (Fig. 7B). As was the case for minimum migration rate, however the effects of these two factors were not additive (Fig. 7).

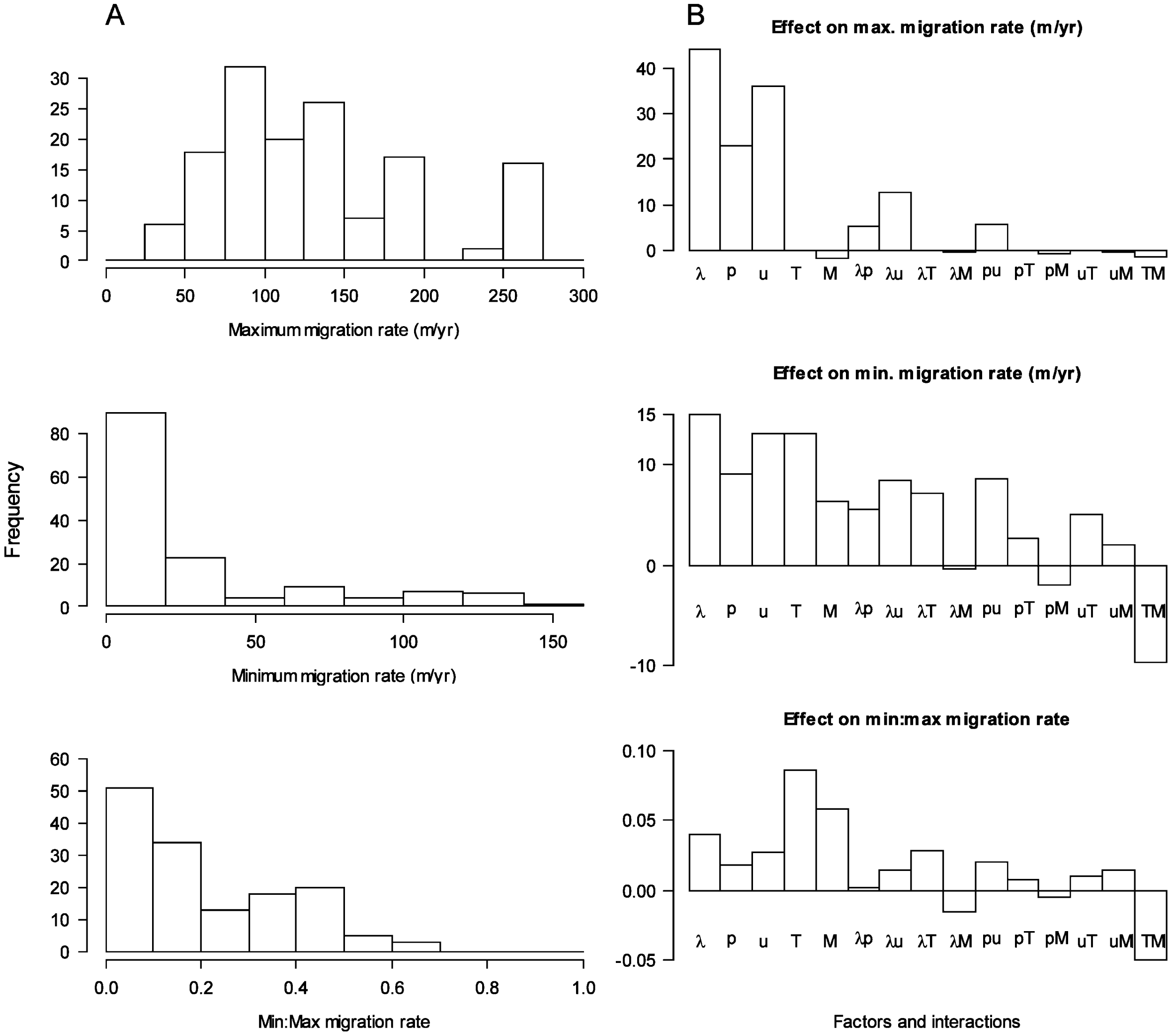

Fig. 7. A) Frequency distributions of responses for three response variables for the 1440 simulations that were run following the experimental design described in Table 2. These simulations were run on landscapes with 0.1 to 0.9 of the habitat remaining. Minimum (or realised) migration rates were recorded from landscapes with most habit loss, whereas maximum (or potential) migration rates were recorded from landscapes with little habitat loss. B) ANOVA was used to estimate the effects of the factors listed in Table 2 and primary interactions between these factors on the three response variables. The ANOVA was able to explain 99% of the variance in maximum migration rate, 62% of the variance in the minimum migration rate and 84% of the variance in the ratio of minimum to maximum migration rate.

## Discussion

The rate of contemporary climate change is faster than the rates recorded at the end of the last glacial period, suggesting that many plants will have to migrate well in excess of 100 m/yr if they are to track changing climate. Our results, and those of previous studies, suggest that potential migration rates in excess of 100 m/yr could be expected for some plants (Clark 1998, Cain et al. 1998, Higgins and Richardson 1999). Our predictions of rapid migration were generated by using a dispersal function that allows for infrequent long-distance dispersal. Our function is a mixture of two exponential distributions, one for local and one for infrequent long-distance dispersal. Other functions can produce similar results (Clark 1998, Higgins and Richardson 1999). The distribution of potential migration rates we generate suggests that most plants are not capable of rapid migration. Since community assembly is strongly influenced by colonisation rates (Tilman 1997, Nathan and Muller-Landau 2000, Turnbull et al. 2000), we would expect that species capable of rapid migration will be over-represented in communities assembled during periods of rapid climate change.

The primary aim of this study was, however, not to demonstrate the potential for rapid migration, but to develop a method for predicting realised migration rates. Realised migration rates are migration rates as influenced by barriers to migration processes, particularly the habitat loss and fragmentation that characterise contemporary landscapes. We translate potential migration rates into realised migration rates by considering how habitat loss and fragmentation may reduce dispersal distances and reduce the likelihood of a dispersed seed landing in habitat. Reduced dispersal distances are simulated using a function that describes how the dispersal agent's movement is influenced by barriers. We demonstrated how the parameters of this realised dispersal function can be estimated for real situations. The realised dispersal function can be used to estimate a realised migration rate. The approach we adopt avoids the need to consider the explicit pathways of individual seed dispersal events. The consideration of individual dispersal events would be analytically intractable, excessively time consuming to simulate, and would require a detailed process level understanding of the movement of seeds in heterogeneous landscapes.

Simulations that used the realised density of dispersal distances showed that severe levels of habitat loss substantially reduced migration rates. Although a range of sensitivities to habitat loss are possible, our analyses suggested that insensitivity to habitat loss is a rare case. Plants that were insensitive to habitat loss had high fecundity, long distance dispersal, and were dispersed by dispersal agents that are not sensitive to habitat loss. Agricultural weeds may be typical of this category. Conversely species with little capacity for long distance dispersal, which are dispersed by agents that are sensitive to the barriers created by habitat loss are unlikely to migrate at all. Plant species dispersed by territorial, habitat specialist animals are typical of this category. However, as we do not have data on both the distance and stopping distance functions for a range of species, it follows that we have little basis for speculation on the sensitivity of migration rates to habitat loss across and within plant functional groups (Diaz and Cabido 1997).

While the model we present suggests that most plants have realised migration rates that are much slower than potential migration rates, migration rates do not change with habitat loss as rapidly as classical percolation theory would predict. Percolation theory predicts that there are thresholds above which movement is possible and below which movement is halted (Gardner et al. 1987). Our model relaxed the central assumptions of classical percolation theory, namely that dispersal is restricted to local neighbourhoods, that habitat is distributed randomly, and that landscapes are infinitely large. We used continuous functions to describe dispersal distances at scales greater than local neighbourhoods, considered both random and fractal distributions of habitat in finite landscapes. Our results showed that the threshold response of classical percolation theory is a special case, that is, the threshold response prediction is not robust to the relaxation of the fundamental assumptions of percolation theory. This finding has been reported by other authors (Plotnick and Gardner 1993, Lavorel et al. 1995, With et al. 1997, 1999, With and King 1999, Collingham and Huntley 2000, Monkkonen and Reunaen 2001). These studies have found that thresholds of landscape connectivity were at lower habitat density when habitat is aggregated and when movement neighbourhoods are larger; more recently a tendency towards linear responses of movement to habitat loss has also been reported (Higgins and Richardson 1999, With et al. 1999, this study). A linear response is to be expected when occasional long distance dispersal events or barrier crossing events are simulated; under these conditions reductions in habitat do not eliminate the possibility of dispersal, but merely reduces the probability of successful dispersal (Higgins and Richardson 1999). While it is recognised that landscape connectivity is defined by dispersal behaviour (Tischendorf and Fahrig 2000), classical percolation approaches aggregate dispersal behaviour using functions that emphasise the scale of dispersal (e.g. neighbourhood size). Our results suggest that in addition to the scale of dispersal, the shape of the dispersal function (e.g. fatness of the tail of the dispersal distribution) can qualitatively influence predictions of landscape connectivity.

## Conclusion

As repeatedly noted by other authors, predicting plant migration rates will require better data on dispersal distances, especially the rare long distance dispersal events that drive migration (Clark et al. 1998, Cain et al. 1998, 2000, Higgins and Richardson 1999, Bullock and Clarke 2000). Despite the optimism induced by recent advances in statistical techniques, data on long distance dispersal will remain elusive. This study shows that a better understanding of how dispersal agents interact with habitat loss and fragmentation is also needed. If the approach proposed in this paper is pursued, we would need better data on how dispersal agents move through landscapes, and we need to improve our ability to describe landscape heterogeneity from the perspective of the dispersal agent. Both requirements call for close collaboration between animal ecologists and plant ecologists.

This paper showed that many factors influence realised migration rates. However, these factors are themselves aggregates of underlying ecological processes. For instance, dispersal distance is the outcome of sometimes complex interactions between the seed, the dispersal agent and environmental conditions, and stopping distance is influenced by the dispersal agents ability to avoid and cross barriers. These underlying traits are quite different from those used to define classical dispersal syndromes (van der Pijl 1982) and additional to those used to define long distance dispersal syndromes (Bonn et al. 2000) suggesting that a broader concept of dispersal syndromes is needed for predicting which species will be limited by migration.

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