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Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change

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Abstract

Climate change presents a potentially severe threat to biodiversity. Species will be required to disperse rapidly through fragmented landscapes in order to keep pace with the changing climate. An important challenge for conservation is therefore to manage landscapes so as to assist species in tracking the environmental conditions to which they are adapted. Here we develop a stochastic spatially explicit model to simulate plant dispersal across artificial fragmented landscapes. Based on certain assumptions as to the dispersal mechanism, we assess the impact that varying potential for rare long-distance dispersal (LDD) has on the ability to move over landscapes with differing spatial arrangements of suitable habitat (clumped versus fragmented). Simulations demonstrate how the relative importance of landscape structure in determining migration ability may decrease as the potential for LDD increases. Thus, if LDD is the principal mechanism by which rapid large-scale migrations are achieved, strategically planned networks of protected habitat may have a limited impact on rates of large-scale plant migrations. We relate our results to conventional principles for conservation planning and the geometric design of reserves, and demonstrate how reversal of these principles may maximise the potential for conservation under future climates. In particular, we caution against the justification of large-scale corridors on grounds of climate change since migration along corridors by standard dispersal mechanisms is unlikely to keep pace with projected change for many species. An improved understanding of the dispersal mechanisms by which species achieve rapid migrations, and the way that these processes are affected by patterns of landscape fragmentation, will be important to inform future conservation strategies.

Keywords: Long-distance dispersal; Climate change; Habitat fragmentation; Spatially explicit model; Systematic conservation planning

1. Introduction

Predicted rapid climate change over the next century (Houghton et al., 2001) poses a potentially severe threat to global biodiversity (Hannah et al., 2002; Midgley et al., 2003; Parmesan and Yohe, 2003; Thomas et al., 2004). Species are expected to respond to the changing climate by migrating to track the environmental conditions to which they are adapted (Collingham and Huntley, 2000), with required migration rates likely to exceed those observed during post-glacial times (Malcolm et al., 2002). The ability of species to track future climates will be tested not only by the rate of change, but also by the loss and fragmentation of habitats that is characteristic of modern landscapes (Sala et al., 2000).

Palaeoecological evidence suggests that species have responded to past climate changes with rates of migration in the order of magnitude of kilometres per year (Davis, 1981; Huntley and Birks, 1983), yet such rates cannot be explained by the observation that most seeds

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move very short distances, rarely more than a few tens of metres (Howe and Smallwood, 1982). There has thus been renewed interest in recent years in the potential role of rare long-distance dispersal (LDD) events as drivers of rapid plant migrations (e.g. Clark et al., 1998; Cain et al., 2000, 2003). Mechanisms by which seeds may be transported unusually large distances are diverse and include the transportation of seeds in updrafts, dispersal by birds in nest material and movement of seeds whilst attached to the fur of mammals (Ridley, 1930; van der Pijl, 1982; Higgins et al., 2003c). Although there remains uncertainty as to the importance of LDD for driving rapid migrations (Clark et al., 2003), evidence of LDD has been drawn both from the palaeoecological record (e.g. Kullman, 1998; Lyford et al., 2003) and from contemporary observations, particularly of island colonisation and alien plant spread (e.g. Pitelka et al., 1997; Whittaker et al., 1997; Clark, 1998; Higgins and Richardson, 1999; Cain et al., 2000; Horn et al., 2001; Gomez, 2003). Additionally, recent advances in mechanistic modelling of seed dispersal by wind have demonstrated the potential for uplifting and long-distance movement (Nathan et al., 2002; Tackenberg, 2003).

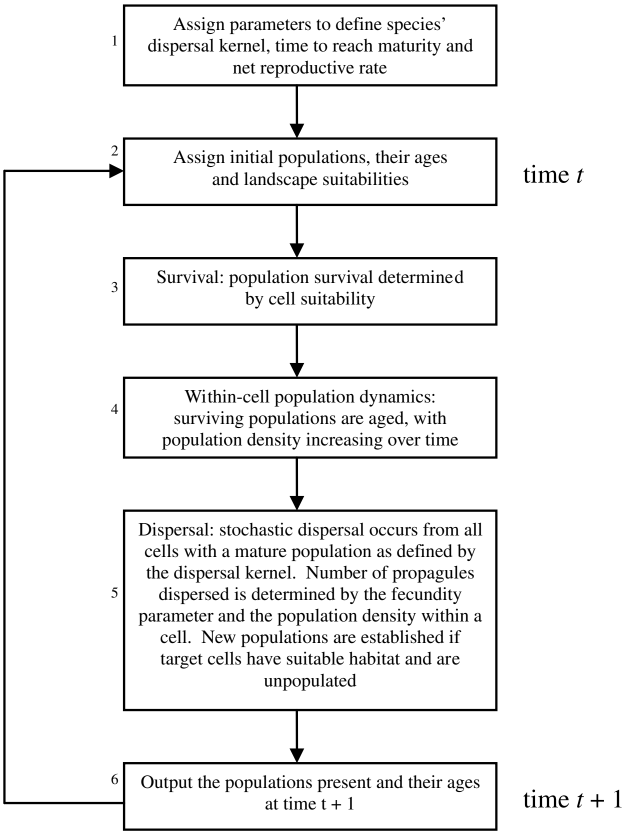
Studies that attempt to predict migration rates driven by LDD are severely limited by uncertainty as to the dispersal mechanism, difficulties of parameter estimation and, more fundamentally, inherent stochasticity (Clark et al., 2003). However, phenomenological modelling studies have greatly advanced our understanding of large-scale dispersal processes, demonstrating that low probability LDD events have the potential to significantly increase migration rates (e.g. Collingham et al., 1996; Kot et al., 1996; Higgins and Richardson, 1999; Clark et al., 2001). These insights provide a foundation for addressing the potential effects of habitat fragmentation on the ability of species to undertake large-scale migrations (Cain et al., 2003; Iverson et al., 2004). Here we address this question by, firstly, developing a simulation of species dispersal that incorporates a flexible dispersal kernel for modelling both long- and short-distance dispersal processes. We assume in our simulation that mechanisms for LDD are such that unsuitable patches of habitat can be crossed, and that dispersal occurs with random direction. Secondly, we simulate dispersal across artificial fragmented landscapes and assess the affects that different spatial arrangements of suitable habitat (clumped versus fragmented) have on the ability of species with varying potential for LDD to migrate. A number of previous studies have focused on the interaction between habitat fragmentation and migration rates (e.g. Schwartz, 1992; Malanson and Cairns, 1997; Ruckelshaus et al., 1997; Malanson and Cramer, 1999; Hiebeler, 2000; Richardson et al., 2000; Tischendorf and Fahrig, 2000; Fahrig, 2001; King and With, 2002; Söndgerath and Schröder, 2002). Such studies have greatly developed our understanding of the interplay between landscape fragmentation and dispersal ability, including identifying a general pattern of increasing migration rates with increasing degrees of habitat clumping (Ruckelshaus et al., 1997; King and With, 2002). We add to this body of knowledge by using a new model to demonstrate how increasing the probability of LDD results in a decreased influence of landscape structure on migration rate (cf. Schwartz, 1992) and discussing the implications of this in the context of climate change and systematic conservation planning. Our results are based on many thousands of realisations of artificial landscapes, unlike in previous studies that have utilised only a very limited sample of replicate maps (e.g. With and King, 1999; King and With, 2002; Higgins et al., 2003a).

We relate our results to conventional principles for systematic conservation planning and the geometric design of natural reserves, so as to move towards identifying targets for conservation planning under climate change. Systematic approaches to conservation planning have been developed in recent years to guide the efficient allocation of areas for the protection of biodiversity (Margules and Pressey, 2000; Cowling and Pressey, 2003; Cowling et al., 2003). Conservation planning has been particularly influenced since the 1970s by principles of reserve design derived from island biogeography (MacArthur and Wilson, 1967; Diamond, 1975; Wilson and Willis, 1975) and metapopulation (Levins, 1969) theories. Accordingly, reserve-selection algorithms have recently been developed that incorporate consideration of spatial design and preferentially select areas following general design principles (Briers, 2002; Rouget et al., 2003; Cabeza et al., 2004). For example, clustered networks of well-connected reserves may be preferentially selected (Cabeza et al., 2004). However, the utility and validity of conventional design principles have been widely debated (e.g. Simberloff and Abele, 1976; Simberloff et al., 1992) and their potential effectiveness in the context of climate change has recently been questioned (Shafer, 2001; Araújo et al., 2004). Here we reassess conventional reserve design principles by focusing on the dispersal mechanisms by which species are expected to undertake rapid large-scale migrations in response to climate change.

2. Methods

2.1. Modelling approach

A model to simulate plant dispersal has been programmed and coupled with a grid-based Geographical Information System. The model operates in discrete time and space and aims to simulate stochastic dispersal at the landscape scale, with grid cell sizes in the order of magnitude of 100s to 1000s of metres. As such, the dispersal kernel is designed to be flexible and to incorporate rare LDD events, focusing on those few seeds that are expected to travel at least several hundred metres and thus drive migration at coarse spatial resolutions (Nathan et al., 2002). The model does not aim to simulate the fate of individual seeds, since this would be computationally impractical at the scale of analysis, but rather describes the dispersal of 'propagules', defined as the minimum number of individuals of a species capable of successfully colonising a new cell (Higgins et al., 2003b). Propagules arriving in unoccupied cells initiate population growth within those cells (i.e. they become occupied). The basic steps used in the model are set out in Fig. 1. Having assigned species' parameters and initialised the model with landscape suitabilities and initial populations, the model describes three basic steps: (1) survival; (2) within-cell population dynamics; (3) dispersal. The survival step is analogous to mortality since any population falling on an unsuitable cell fails to survive. Cell suitability is defined as binary suitable or unsuitable in the current study, and suitabilities are kept constant across time steps. Within-cell population dynamics are incorporated to determine the number of propagules released by a populated cell in each time step.



1 Assign parameters to define species' dispersal kernel, time to reach maturity and net reproductive rate

2 Assign initial populations, their ages and landscape suitabilities

3 Survival: population survival determined by cell suitability

4 Within-cell population dynamics: surviving populations are aged, with population density increasing over time

5 Dispersal: stochastic dispersal occurs from all cells with a mature population as defined by the dispersal kernel. Number of propagules dispersed is determined by the fecundity parameter and the population density within a cell. New populations are established if target cells have suitable habitat and are unpopulated

6 Output the populations present and their ages at time t + 1

Fig. 1. Flow diagram detailing the steps undertaken in the dispersal simulation.

2.2. The dispersal kernel

The dispersal kernel is based on a probability density function (p.d.f.) that describes seed arrival at distance x from a parent plant. The direction of each dispersal event is selected randomly. Following Clark et al. (1998, p. 16) we utilise a p.d.f. expressed in terms of two parameters, a 'distance parameter', α, and a 'shape parameter', c, to produce a kernel $k(x)$ where

$$k(x) = \frac{c}{2\alpha\Gamma(1/c)} \exp\left[-\left|\frac{x}{\alpha}\right|^{c}\right] \tag{1}$$

and $\Gamma(1/c)$ is the gamma function with argument $1/c$. It was considered more ecologically intuitive to work directly with the mean displacement, md, rather than the distance parameter α, so α was replaced in the implementation of Eq. (1) using

$$\alpha = \frac{md * \Gamma(1/c)}{\Gamma(2/c)} \tag{2}$$

derived from the calculation of md detailed by Clark et al. (1998, p. 16).

This p.d.f. includes the exponential ($c = 1$) and Gaussian ($c = 2$) density functions and can describe highly leptokurtic 'fat-tailed' functions ($c < 1$), which are appropriate for simulating low probability LDD events (Fig. 2). In order to define two-dimensional kernels with differing shapes, we calculated the probability of dispersing to each cell up to a maximum distance of 15 cells from the source by calculating the volume under the surface defined by rotating $k(x)$ about the origin. Self-seeding was not allowed in any kernel since propagules falling within the source cell contribute to local population growth, which was incorporated separately in the model (see Section 2.3). By cumulating probabilities across the kernel each dispersal event could be defined by a single random number drawn from a uniform distribution, enabling rapid computation as required in the current application (individual simulations took up to four days to run on an 800 MHz PC; see Section 2.5). We used $md = 1$ cell in each kernel to give three alternatively shaped kernels: fat-tailed ($c = 0.5$), mid-tailed ($c = 1.0$) and thin-tailed ($c = 2.0$). For comparison, we also applied a neighbourhood kernel in which each dispersal event is limited to reaching one of the four nearest-neighbour cells with equal probability. Fig. 3 demonstrates the different patterns of dispersal produced by the four kernels, ranging from the diffusive front-like advance of the neighbourhood kernel, to the highly fragmented pattern of colonisation described by the fat-tailed kernel.

2.3. Within-cell population dynamics

Within-cell population dynamics are often ignored by models that simulate dispersal (Hastings and Wolin,

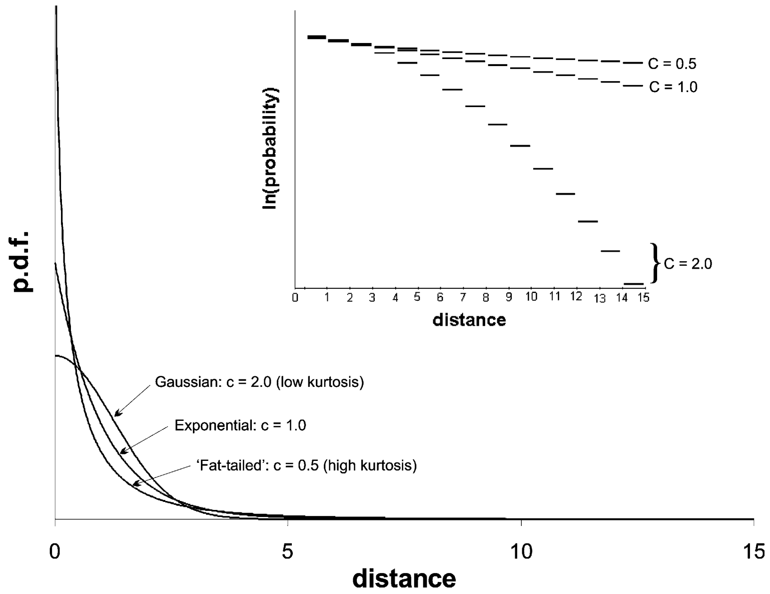


Fig. 2. Probability density functions (main axes) used in the dispersal simulation (after Clark et al., 1998). Plotting a cross section of probabilities from the kernel (at 90° to the source cell) on a log scale (inset) clarifies the differences between kernels at large distances from the source, showing the relatively high probability of LDD with the 'fat-tailed' kernel. Each function has the same mean and maximum dispersal distance, but a different amount of kurtosis.

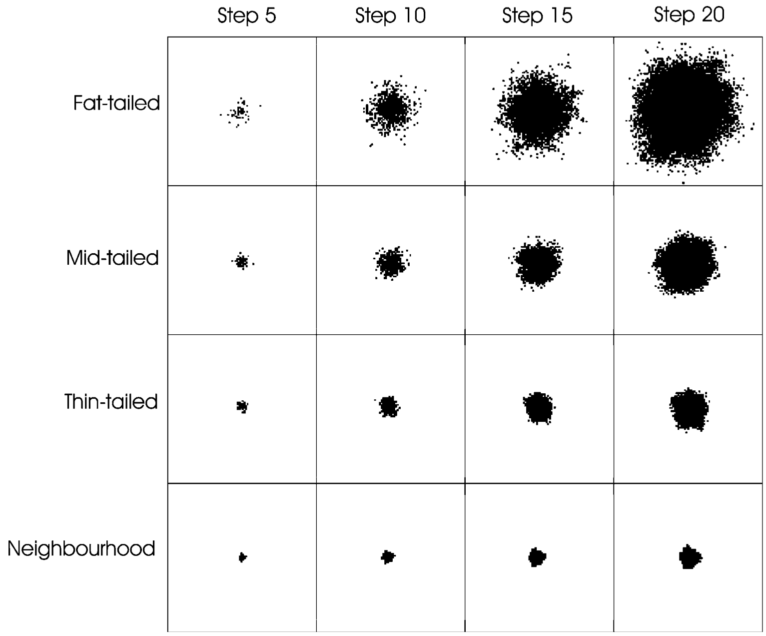


Fig. 3. Dispersal across a homogeneous landscape (100% suitable cells) using four alternative dispersal kernels: fat-tailed, mid-tailed, thin-tailed and neighbourhood. Dispersal was initiated from a single populated cell. Dispersal patterns are presented at $t = 5$, 10, 15 and 20. All other model parameters were kept constant.

1989) yet are expected to be crucial for the current application in accounting for short-distance dispersal events which lead to increased local (within-cell) population densities. We assume that the likelihood of a population releasing propagules increases with population size and that population size increases through time. A population density growth function is thus incorporated within each cell, such that older populations have a higher probability of releasing propagules. On arrival of a propagule in an unoccupied cell, a population is established and density begins to increase from an initialised value of 0.01. Multiple long-distance propagules arriving at a cell that is already occupied are ignored since local dispersal will be the dominant driver of within-cell population growth once a population has been established.

Population growth is modelled using a sigmoidal curve which describes growth as the population rises from low density and saturates at the highest number permitted by environmental resources. Such Sigmoidal growth curves assume that population density is only affected by intraspecific competition and take no account of interspecific competition, yet have been observed in many natural situations (e.g. Alliende and Harper, 1989). We describe population growth using the discrete equivalent of the logistic equation, after Begon et al. (1996, p. 238)

$$N_{t+1} = \frac{N_t R}{1 + \frac{(R-1)N_t}{K}}, \tag{3}$$

where N_t is the population size at time t, R is the net reproductive rate (difference between births and deaths), and K is the carrying capacity of the cell. Carrying capacity has been set at 1.0 in the current study to give a population size scaled between 0 and 1, which can be interpreted as a measure of the population density within a cell. Note that population growth is not initiated until the population in a cell has been established for a set period, defined by the number of time steps required for an individual plant to reach reproductive maturity.

The number of propagules released by a populated cell in each time step is then determined by combining the population density within the cell with a parameter value, F, which determines the number of propagules to be released from a populated cell if population density is equal to 1.0. The number of propagules released is calculated according to the following steps: (1) multiply F by the population density; (2) split the product into its integer and decimal components; (3) release the number of propagules defined by the integer, and release a further propagule with probability equal to the decimal component. This approach provides a simple parameterisation relating the population density within a cell to the number of propagules released by that cell in a given time step.

2.4. Monte Carlo method

Since we simulate dispersal as a non-deterministic process, incorporating low-probability dispersal events, the model was run using a Monte Carlo approach. Hereby, the dispersal process was run many times so as to build up a probability surface identifying those cells more/less likely to be populated under certain dispersal assumptions. The probability P_{xy} of cell xy being populated is calculated as

$$P^n_{xy} = \frac{\sum_{i=1}^{n} I^i_{xy}}{n}, \tag{4}$$

where I_{xy} is the presence/absence in cell xy and n is the number of Monte Carlo realisations.

The results obtained from Monte Carlo simulations are statistical in nature and must be regarded as the most accurate answer that can be obtained from a given investment of computer time (Kalos and Whitlock, 1986). In order to approximate the number of iterations required for the probability surface to stabilise we calculated the summed absolute change in P across all cells ($Sum\Delta$)

$$Sum\Delta^n = \sum_{xy} \left| P^n_{xy} - P^{n-1}_{xy} \right|. \tag{5}$$

By plotting $Sum\Delta$ against the number of Monte Carlo realisations completed, the number of iterations required for the probability surface to stabilise could be judged. Although different simulations required different numbers of Monte Carlo runs, tests across a range of parameterisations showed that 10,000 was sufficient in all cases and all simulations were thus run for this number.

2.5. Simulation design

A simulation experiment was designed whereby species with differing potentials for LDD were set to disperse through artificial landscapes with varying amounts of suitable habitat cells and different patterns in the distribution of these cells. Two-dimensional grids of 100 × 100 cells were used, with initial populations located on suitable habitat in the centre four cells of the grid at $t = 0$. Initialising the dispersal process from the centre of the grid minimised (and standardised) effects caused by propagules dispersing off the edge of the grid.

Artificial landscapes were generated with both random and fractal arrangements of suitable habitat. Fractal algorithms provide a method for controlling the relative abundance of suitable habitat and the degree of fragmentation, and have been used to produce patchy landscapes that bear a striking resemblance to real landscape patterns (With and King, 1997). Fractal landscapes were generated by the midpoint displacement method set out in With et al. (1997), which enables different realisations of statistically identical landscapes to be generated. The fractal dimension (D) of the landscapes is controlled by a roughness parameter H (where $D = 3 - H$) such that adjusting the value of H between 0.0 and 1.0 generates maps that range from extremely fragmented ($H = 0.0$) to highly aggregated ($H = 1.0$). Thus, by changing the percentage of suitable cells across the grid and the algorithm used to assign the spatial distribution of the habitat, we were able to quantify landscape structure as exemplified in Fig. 4.

Since fractal algorithms produce edge effects caused by the map boundary, landscapes were generated with

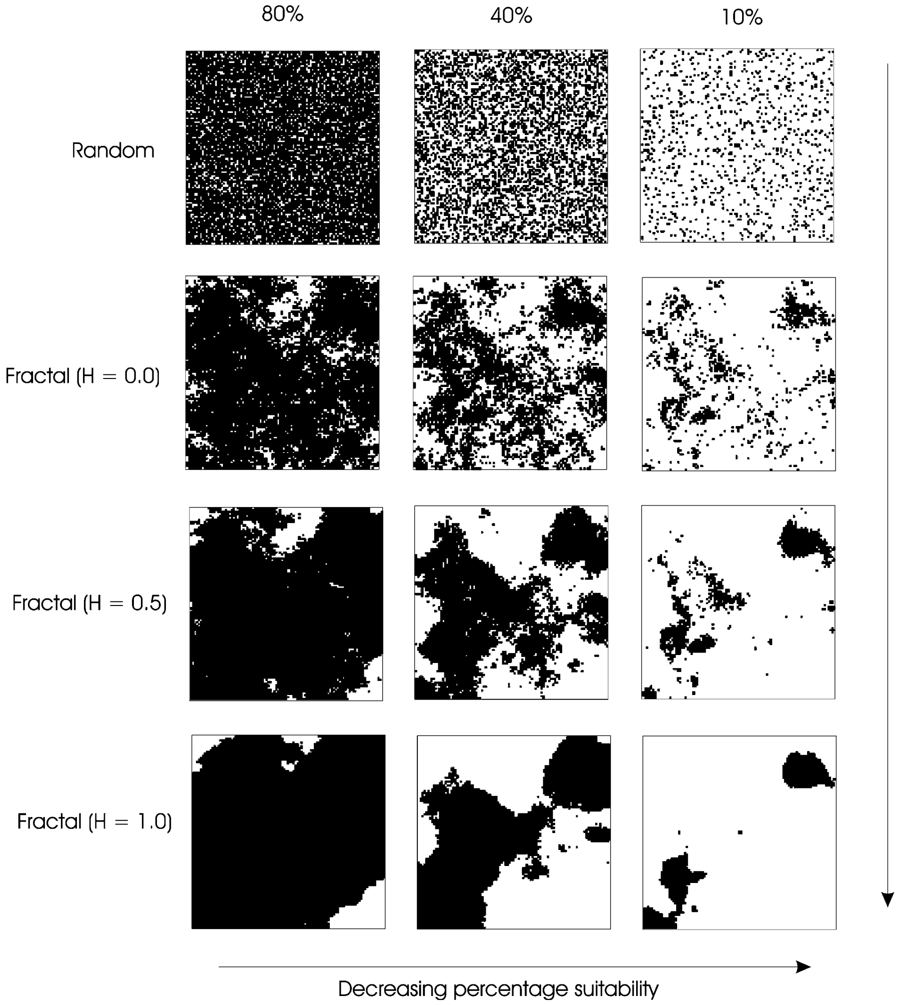


Fig. 4. Example artificial landscapes used in the simulation experiments. Landscapes have a percentage of suitable habitat cells (black) which are distributed either randomly or according to a fractal algorithm with adjustable degrees of fragmentation (*H*). Method after With et al. (1997) and With (2002).

129×129 cells and a central 100×100 grid was selected from the larger landscape so as to minimise this effect in the simulations. This approach was considered preferential to the ecologically unrealistic alternative of 'wrapping' map boundaries such that the habitat along opposite edges matches (With et al., 1997). Map boundaries were absorbent, with propagules that disperse outside the grid being lost. This approach was considered more realistic for plant dispersal than the alternative of reflective boundaries (With and King, 1999).

Three factors were adjusted between simulations: (1) the shape of the dispersal kernel: fat-tailed, mid-tailed, thin-tailed and neighbourhood kernels were applied; (2) the percentage of suitable habitat: simulations were run with 100%, 60%, 40%, 25%, 10%, 5%, 2.5% and 1% suitability (after Collingham and Huntley, 2000); (3) the degree of habitat fragmentation: random landscapes and fractal landscapes with $H = 0.0$, 0.5 and 1.0 were used. This resulted in 128 individual simulations (4 kernels $*$ 8 percentage suitabilities $*$ 4 degrees of fragmentation). All other model parameters were kept constant throughout the study: $md = 1$ cell, $maxd = 15$ cells, number of time steps (t) = 40, $R = 4.0$, $F = 4.0$, age to reach reproductive maturity = 1 time step.

Each simulation was run for 10,000 Monte Carlo realisations, with a new artificial landscape (of identical percentage suitability and degree of fragmentation) generated for each iteration. The use of many different realisations of each landscape parameterisation was to ensure that simulation results were generic to landscapes with given properties, and were not dependent on a very limited sample of replicate maps as in other studies (e.g. With and King, 1999; King and With, 2002; Higgins et al., 2003a).

In order to quantify the success in dispersing through a landscape we calculated the mean probability across all suitable cells, which we call the standardised probability (*SP*)

$$SP = \frac{\left(\sum_{x=1}^{N}\sum_{y=1}^{N} P_{xy}\right) - 4}{\frac{s}{100} * (N^2 - 4)}, \tag{6}$$

where N is the number of rows and columns in the grid, P_{xy} is the probability in cell xy, and s is the percentage suitability. Note that the central four cells, which were initialised as 'present', are subtracted within the calculation. An alternative measure of dispersal success is the migration rate (e.g. Collingham and Huntley, 2000; Higgins et al., 2003a). However, this relies on the identification of a migrating front, which is problematic when incorporating LDD because the wave front becomes highly fragmented (see Fig. 3) such that a limited number of distant cells may be reached even though few cells overall have been occupied. The SP is thus considered a more appropriate representation of dispersal success in the current context.

3. Results

Simulation results are plotted as SP against percentage suitable habitat for each landscape type (random and fractal) and for each dispersal kernel (Fig. 5). Increasing the probability of LDD is shown to greatly increase dispersal success across all landscape types and at all levels of suitability. Thus, use of a fat-tailed kernel gave the highest SPs, with values curtailed towards a probability of 1.0 at high percentage suitabilities (i.e. dispersal reached the edge of our experimental grid). As the probability of LDD decreased, through mid-tailed and thin-tailed kernels, SP values reduced significantly, with probabilities under a neighbourhood rule an order of magnitude lower (<0.1) than when incorporating rare long-distance events. It is thus apparent that dispersal success was more sensitive to the shape of the dispersal kernel than to changes in landscape structure.

Whilst landscape structure has less effect on dispersal success than does dispersal kernel formulation, landscape effects are shown to become relatively more significant as the probability of LDD is reduced (and SP decreases). For example, at 25% suitable habitat, changing landscape structure caused a maximum increase in SP from 0.35 to 0.41, a 17% change, when using a fat-tailed kernel. In contrast, when using a thin-tailed kernel, SP could be increased from 0.05 to 0.12, a 140% increase, by manipulating landscape structure. Mid-tailed, thin-tailed and neighbourhood

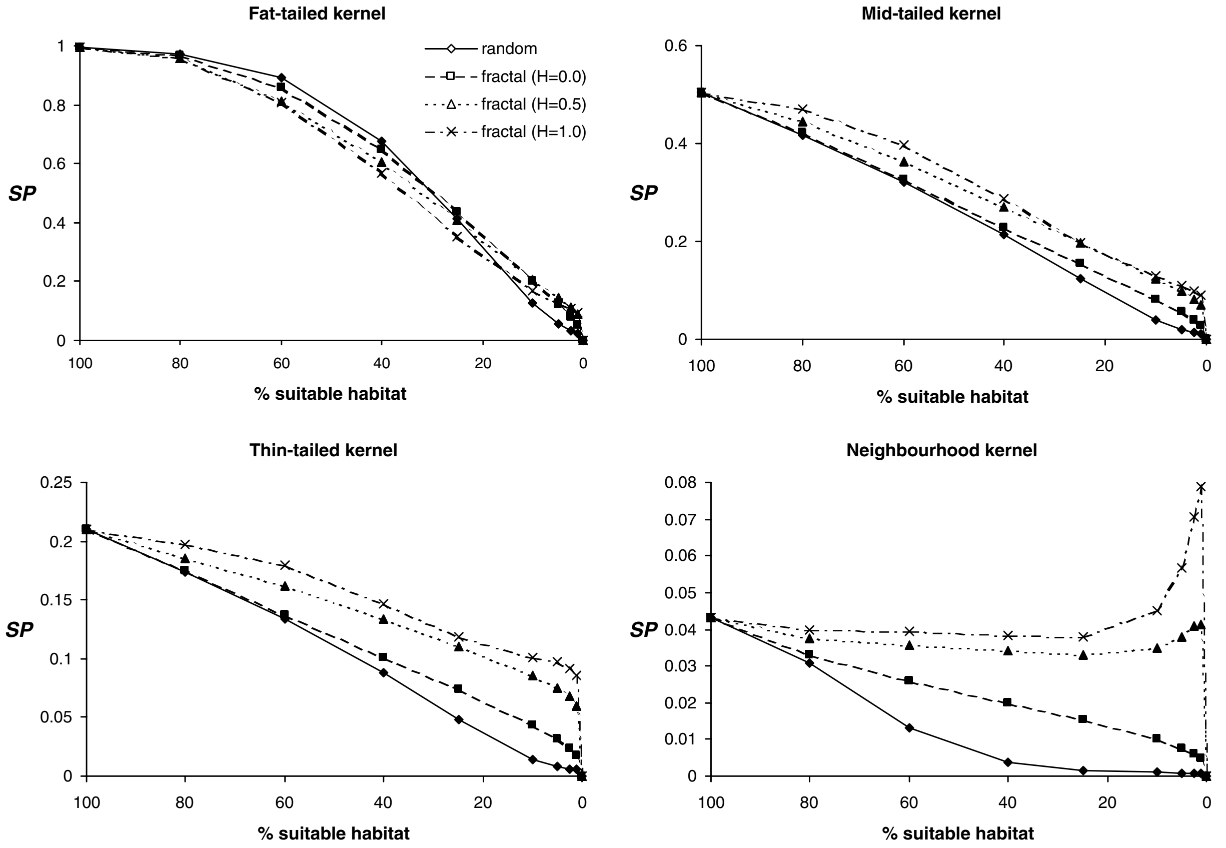


Fig. 5. Simulation results plotted as SP against the percentage of suitable habitat for each landscape type (random, fractal $H = 0.0$, $H = 0.5$, $H = 1.0$) and for each dispersal kernel (fat-tailed, mid-tailed, thin-tailed and neighbourhood).

kernels show a trend for less fragmented landscapes to result in higher probabilities of dispersal for a given amount of suitable habitat. This result is consistent with the logic that less fragmented landscapes have more connectivity and are therefore easier for species that do not disperse via LDD to migrate across. This general trend was not, however, apparent when using the fat-tailed dispersal kernel. In that case, changing the landscape structure towards more or less fragmented arrangements of suitable habitat had a less consistent and relatively less significant affect on dispersal ability.

The neighbourhood dispersal assumption yielded very low *SP*s under all landscape types, with the trend towards higher values under less fragmented landscapes apparent. Of note is a seemingly anomalous increase in *SP* at lower percentage suitabilities (<25%) in less fragmented landscapes ($H = 0.5$, 1.0). This result is attributable to the interplay between two factors in our simulation: Firstly, a theoretical maximum of approximately 33% of the grid could in fact be occupied in any model run since dispersal under the neighbourhood rule is inherently limited to a maximum distance of 40 cell lengths from the initialised cells (one cell length multiplied by 40 time steps). Thus, *SP* will be suppressed for percentage suitabilities above this threshold (since excess habitat could never be occupied). Secondly, the number of cells populated in a single Monte Carlo iteration will be higher in cases where the particular landscape realisation of that iteration positions a number of suitable cells contiguous with the four initialised cells. Such cases will lead to increased *SP* and are most likely to occur under less fragmented landscape structures ($H = 0.5$, 1.0). The anomalous increase in *SP* at low suitabilities is thus a result of the simulation design used. This was unavoidable whilst maintaining the generalities that could be achieved by using a new landscape realisation for each Monte Carlo iteration, and whilst enabling comparisons between dispersal kernels using the measure *SP*. This result is, however, of value in emphasising that the spatial structure of a landscape becomes increasingly important as the probability of LDD decreases. In the case whereby dispersal is limited to neighbouring cells, the particular arrangement of suitable habitat is shown to be of critical importance.

4. Discussion

The simulations presented have demonstrated that LDD has the potential to greatly increase the ability of species to migrate rapidly through fragmented landscapes. Species that are likely to disperse via rare long-distance events may thus be best equipped to survive current threats from climate change and habitat fragmentation. However, Iverson et al. (2004) have demonstrated that LDD may still not be sufficient to rescue migration. Furthermore, in cases where rapid large-scale migrations are driven by LDD the spatial arrangement of suitable habitat may be much less important for determining dispersal potential than simply the quantity of suitable habitat. Thus, landscape configurations of suitable habitat that are designed to facilitate the movement of species may have limited impact on rates of large-scale species migrations.

For those species unlikely to disperse through LDD, rates of migration will be very much slower, making them more susceptible to rapidly changing distributions of suitable climate space. Additionally, our simulations suggest that species with poor dispersal abilities are relatively more affected by habitat fragmentation, with more fragmented arrangements of suitable habitat leading to decreased migration success. The findings of our study concur with those of previous modelling studies that have found that clumping of suitable habitat may mitigate the effects of habitat loss on dispersal success (e.g. Ruckelshaus et al., 1997; King and With, 2002). However, we have shown that the relative impact of landscape structure on dispersal success decreases as the probability of LDD increases. Thus, in cases where dispersal ability is limited, carefully planned landscape designs, such as corridors of contiguous suitable habitat, may be of potential conservation value, yet will only facilitate very slow migrations that are unlikely to keep pace with the changing climate. Our results are supported by empirical data collected by Honnay et al. (2002) who showed that, although colonisation success was higher in forests with higher connectivity, success was insufficient in both spatially segregated and connected forests to ensure large-scale colonisation via local dispersal mechanisms.

It is emphasised that it would be a misuse of the kind of model simulation used here to design conservation policy adhering to quantitative estimates produced by the modelling. The landscapes and dispersal kernels used are theoretical constructs that may not be directly applicable to natural systems (With and King, 1997). The simulations that have been presented are intended to focus our understanding of the problem and to guide the identification of general theoretical principles that can inform conservation policy. Many avenues for future research remain, including the need to test alternative measures of dispersal success (Tischendorf and Fahrig, 2000), to use continuous (rather than binary) representations of landscape suitabilities (Malanson, 2003), and to further elucidate the spatial scale over which different dispersal mechanisms operate. Perhaps most importantly, our ability to simulate LDD is greatly limited by the many possible mechanisms by which it may be achieved. Our model simulated dispersal via mechanisms with the ability to transport propagules over unsuitable habitat patches. Such mechanisms include seed capture in wind updrafts and dispersal by birds (either in the gut or attached to the feathers or feet), which are perhaps the most often cited examples of LDD mechanisms (e.g. Darwin, 1859; Ridley, 1930; Taylor, 1954; Horn et al., 2001; Nathan et al., 2002; Tackenberg, 2003). However, many other mechanisms for LDD may be more directly influenced by environmental factors that restrict movement through unsuitable habitats. For example, seeds may be attached to the fur or feet of non-flying fauna whose movements are restricted to suitable habitat patches (Higgins et al., 2003c). Seeds also often remain viable whilst floating in rain-wash, streams, rivers and ocean currents, or being transported on natural flotsam (Quammen, 1996; Higgins et al., 2003c). Long-distance movement is thus also likely to be more directional than the random process simulated in our model (Levine, 2003), with dispersal following predictable routes such as along water courses, bird migration routes, or 'wind highways' (Muñoz et al., 2004). Much more empirical research will be required to quantify the potential for dispersal via different mechanisms across a range of taxa and spatial scales before we can more confidently simulate and predict the impacts of LDD. Finally, we note that humans can provide a very effective vector for LDD, both through accidental and deliberate movement (Mack et al., 2000; Lidén et al., 2004). It may in fact be the case that translocation by humans is the only vector of LDD sufficiently predictable for consideration in conservation planning.

Although LDD events do undoubtedly occur, the importance of natural LDD for driving rapid migrations across a broad range of species remains contentious. Difficulties in tracking those few seeds that travel outside the normal dispersal range make empirical testing problematic, though a number of techniques, including genetic analysis, have been proposed for enabling the quantification of LDD (Nathan et al., 2003). An alternative mechanism to LDD for explaining rapid Quaternary migrations is that of refugia, whereby small isolated populations persisted in microclimates during periods when regional climate was unsuitable. It has been hypothesised that it was from these refugia that wider colonisation was initiated, through local dispersal, as the climate changed (McGlone et al., 1996; Stewart and Lister, 2001; Higgins et al., 2003b). The management implications arising from the LDD and refugia theories may be quite different, ranging from the possible need to translocate species with poor dispersal abilities, to the need to identify and manage isolated populations existing outside a species' core range.

5. Conservation targets for spatial landscape planning under climate change

Although social, economic and political imperatives usually modify scientific recommendations, theoretical principles can have an important role in influencing targets for conservation planning (Margules and Pressey, 2000). General principles to guide the ideal size, shape and distance between patches of suitable habitat (or 'reserves') were first proposed by Diamond (1975) and Wilson and Willis (1975). Elements of these principles have been widely incorporated into conservation policies, including those of the IUCN (The World Conservation Union), the World Wildlife Fund and the European Union's Habitat's Directive. Such principles are now recommended for use, along with guidelines derived from other branches of ecological and evolutionary theory (e.g. metapopulation dynamics; Hanski, 1999), in identifying targets for systematic conservation planning (Margules and Pressey, 2000). Geometric principles for the design of natural reserves have been widely debated and critiqued (May, 1975; Simberloff and Abele, 1976; Simberloff et al., 1992; Collingham and Huntley, 2000). Here, in light of improved understanding of how large-scale migrations are achieved, we highlight how the threat of climate change may be incorporated into this complex debate.

For reasons derived principally from the theory of island biogeography (MacArthur and Wilson, 1967) conventional biogeographic principles of reserve design state that: (1) reserves should be divided into as few disjunctive pieces as possible (since several small reserves will tend to support a lower number of species than a single large reserve of equal area, according to the species-area relationship; Fig. 6A); (2) when disjunctive reserves are unavoidable they should be clustered as close to each other as possible (so as to maximise immigration rates between reserves; Fig. 6B); (3) that reserves should be as nearly round in shape as is possible (so as to minimise dispersal distances within the reserve; Fig. 6C). However, when considering the potential effects of shifting climate space it is evident that reversal of the conventional design principles can maximise the area of reserve remaining within suitable climate in the future (Fig. 6A–C). This argument has two central precepts. Firstly, if the geographic scale is large then LDD may be the only mechanism by which species will be able to migrate rapidly enough to keep pace with the changing climate (Higgins and Richardson, 1999; Malcolm et al., 2002; Lyford et al., 2003; this study). If human mediated dispersal is the only mechanism by which LDD can occur with sufficient certainty for inclusion in planning, then the requirement for minimal inter-reserve distance can be relaxed (since artificial translocation will not be greatly affected by proximity). Secondly, if the direction of shifting climate space can be estimated from empirical evidence

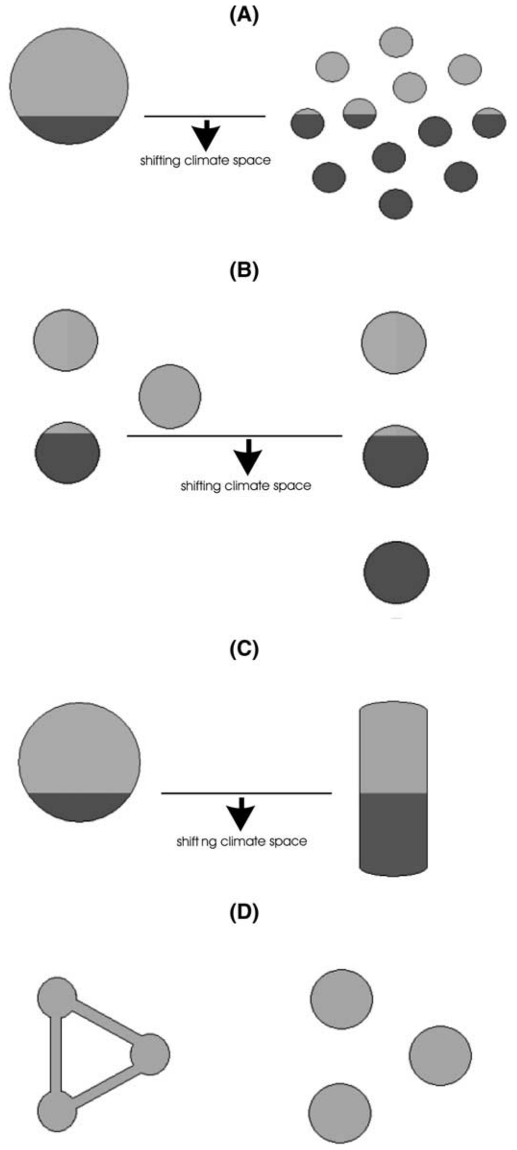


Fig. 6. Geometric principles for the design of natural reserves. Reserves are represented as islands in a homogeneous environment. In each case (A–D) both the left and right designs have the same total area and conventional principles state that the design on the left is preferable to that on the right. Light grey represents areas with current suitable climate, dark grey (A–C) represents areas with both current suitable climate and future suitable climate. The area of reserve remaining with suitable climate space in the future can be maximised by adopting several small reserves as opposed to a single large reserve (A), arranging disjunctive reserves linearly (B), or elongating reserve design (C) in anticipation of shifting suitable climate space. Connecting reserves with corridors of suitable habitat is expected to reduce extinctions by increasing dispersal between reserves (D). However, at large scales many species are not expected to keep pace with changing climate by migrating via normal dispersal mechanisms, potentially rendering corridors of little use.

(e.g. Walther et al., 2002) or using bioclimate envelope models (Pearson and Dawson, 2003), then relaxing the proximity requirement and arranging suitable habitat in the direction of change can maximise the climatic suitability of reserves into the future.

Conventional reserve design principles also suggest that if a reserve must be divided, then connecting fragments with corridors of suitable habitat will reduce extinctions by increasing dispersal between reserves (Fig. 6D). This principle has led to the suggestion that reserves should be connected by large-scale (continental) corridors running parallel to climatic gradients that would allow species to migrate in response to climate change (Graham, 1988; Hunter et al., 1988; Noss, 2001). Whilst corridors may have value in facilitating the migration of some animals, we have shown here that such landscape designs may have limited impact on the LDD mechanisms by which plants achieve rapid large-scale migrations. Whilst in some instances LDD of plants may be aided by corridors (e.g. seeds attached to the fur of migrating mammals), in many cases (notably seed dispersal in wind updrafts and, perhaps most significantly, translocation by humans) corridors are unlikely to facilitate LDD. We emphasise that arguments for and against movement corridors are complex (e.g. Simberloff et al., 1992; Earn et al., 2000) and our discussion aims to add to the debate, whilst not providing any definitive answers. Most importantly, we caution against the justification of large-scale corridors on grounds of climate change when migration along corridors by standard dispersal mechanisms is unlikely to keep pace with projected change for many species. Artificial translocation (of both plants and animals) may provide a more effective and efficient solution.

We conclude that climate change presents an important challenge to conventional conservation planning principles and reassessment of these may be important for the conservation of natural systems into the century ahead (Shafer, 2001). Different species will require different management approaches, depending on their climatic tolerances and dispersal abilities. For example, artificial translocation may be a more efficient policy than the creation of large-scale migration corridors for the conservation of many mammals, whilst wind-dispersed plants may be best conserved in disjunctive reserves aligned in the direction of projected climate change. We make the conceptual link here with bioclimate envelope models, which may prove useful in identifying sites suitable for the location of future protected habitats (Pearson and Dawson, 2003, 2004; Williams et al., 2004; Araújo et al., 2004). Conservation strategies that integrate knowledge of shifting climate space with an improved understanding of the dispersal mechanisms by which species achieve rapid large-scale migrations will be required in the coming century.

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