

Determining pattern–process relationships in heterogeneous landscapes

6.1 Introduction

Landscapes are now being altered at unprecedented rates (Forman and Alexander 1998), resulting in the loss and fragmentation of critical habitats (Gardner *et al.* 1993), declines in species diversity (Quinn and Harrison 1988, Gu *et al.* 2002), shifts in disturbance regimes (He *et al.* 2002, Timoney 2003), and threats to the sustainability of many ecosystems (Grime 1998, Simberloff 1999). Because the ecological consequences of landscape change are difficult to measure, especially at broad spatial and temporal scales, the quantification of landscape pattern has often been used as an indicator of potential biotic effects (e.g., Iverson *et al.* 1997, Wickham *et al.* 2000). It is hardly surprising, therefore, that the development of methods to measure landscape pattern has become an important endeavor in landscape ecology (see O’Neill *et al.* 1999 for a recent review).

Numerous landscape metrics have been developed and applied over the last 15 years or so, but relatively few studies have been successful in using metrics to establish pattern–process relationships at landscape scales. The first landscape metrics paper (Krummel *et al.* 1987) attempted to do this by presenting the hypothesis that the shape of small forest patches should be affected by human activities while large patches should follow natural topographic boundaries. The analytical results showed that this was the case, but causal relationships were never experimentally confirmed. The prospect of this first study stimulated the rapid development of additional indices (see O’Neill *et al.* 1988, Haines-Young and Chopping 1996), with progress in this arena frequently reviewed (e.g., Gustafson and Parker 1992, Riitters *et al.* 1996, Hargis *et al.* 1998, Fauth *et al.* 2000, He *et al.* 2000, Tischendorf 2001) and computational methods codified (e.g., Gardner 1999, McGarigal *et al.* 2002). However,

the confirmation that pattern metrics reflect the changes in ecosystem processes as a result of landscape change has remained an elusive goal (but see Tischendorf 2001, Ludwig *et al.* 2002).

The absence of rigorous guidelines for the application of landscape metrics has raised additional concerns about their usefulness and validity (e.g., Fortin *et al.* 2003, Li and Wu 2004, Wu 2004). These concerns include that the use of multiple metrics to assess pattern change increases the probability of obtaining false positives (type I errors); that metrics with nonmonotonic relationships with pattern change are of limited usefulness and generality; and that the confidence levels associated with many metrics are difficult or impossible to estimate. In spite of these important issues, the results of landscape analyses using questionable measures of pattern are now driving costly programs to mitigate the effects of landscape change. Perhaps the most notable examples are the widespread use of corridors to link critical habitat areas in an effort to reduce extinction risks within fragmented landscapes (Anderson and Danielson 1997, Tewksbury *et al.* 2002).

In spite of the magnitude of efforts to increase the degree of habitat connectivity, the effectiveness of corridors as a species conservation tool remains controversial (Rosenberg *et al.* 1997, Beier and Noss 1998). The success of corridors is directly dependent on their use by target species to disperse to and populate otherwise unavailable patches of suitable habitat. Obtaining sufficient information on dispersal is notoriously difficult, resulting in a long history of using model simulations to define those features of the landscape which most impact the dispersal success (e.g., Murray 1967, Gustafson and Gardner 1996, Tischendorf *et al.* 1998).

The following analysis builds on past simulation methods to identify critical relationships between the landscape structure (corridor pattern) and ecosystem process (reestablishment of resident or invasion of exotic plant species), illustrating how pitfalls in analysis may be avoided. The subsequent results are both simple and robust, allowing a series of issues to be considered. Among these are the conditions under which corridors interact with the native biota to promote the reestablishment of endemics following disturbances or, alternatively, allow the invasion of exotics. The results of a factorial set of simulations are also used to offer recommendations for the general use of metrics to relate pattern and process within heterogeneous landscapes.

6.2 Methods

6.2.1 Model overview

The model used for simulating pattern–process within heterogeneous landscapes is CAPS, an individual based, spatially explicit model of plant

competition, establishment, and dispersal (Plotnick and Gardner 2002). Plants simulated by CAPS may differ in life history, relative fecundity, habitat preferences, properties of propagule spread, and ability to compete for space in which to germinate and become established. The landscape is described as a grid with each grid site defined by 1 of n different habitat types. Maps may be randomly generated within CAPS or imported from landscape data. Competitive success which results in establishment and reproduction is simulated via a seed lottery with success randomly determined from the abundance of propagules at that site and the suitability of the local habitat to support that species (see details below).

CAPS is written and compiled in Lahey Fortran 95 to be executed under the Linux operating system. Full details regarding model formulation may be found in Plotnick and Gardner (2002) and program source code and executables may be downloaded from <http://scout.al.umces.edu/~gardner>.

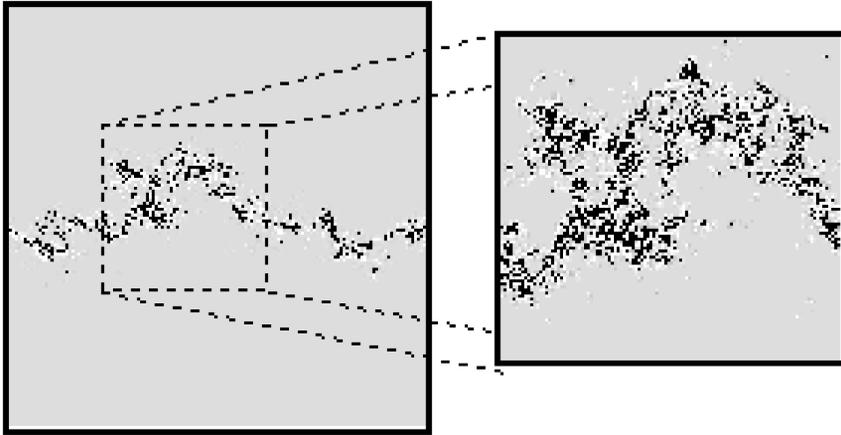
6.2.2 Corridor generation

Corridors were randomly generated in CAPS using a fractal algorithm (Gardner 1999) to produce landscapes with a central, narrow habitat corridor (Fig. 6.1). Two parameters control the character of these landscapes: H sets the spatial dependence (or “roughness”) of adjacent points (see Plotnick and Prestegard 1993 for a full description of the role of H in the generation of fractal maps), and p controls the amount of each habitat type. Resulting landscapes were composed of 512 rows and columns (262 144 lattice sites) with each site representing a 2 m \times 2 m habitat site (map size is 1024 by 1024 m or 104.9 ha). Differences in habitat types are considered as an abstract representation of the numerous biotic and abiotic factors (e.g., differences in soil type, moisture, elevation, light availability, etc.) that may negatively or positively affect the germination, survivorship, and reproduction of individual species.

6.2.3 Dispersal

CAPS allows a variety of probability distributions of propagule dispersal to be used in the dispersal kernel. The probability density functions (p.d.f.) for dispersal are uniquely specified for each species, and may be selected from either the uniform, normal, exponential, or Cauchy distributions (Fig. 6.2). The selected p.d.f. produces sets of values representing the probability, $d(i,r)$, of a viable seed released from a parental site, i , reaching a map site that is a distance r away. The p.d.f.s for the uniform, normal and exponential are more fully discussed in Plotnick and Gardner (2002), while the Cauchy distribution (Johnson and Kotz 1970) is a recent addition to the CAPS program. The

A



B

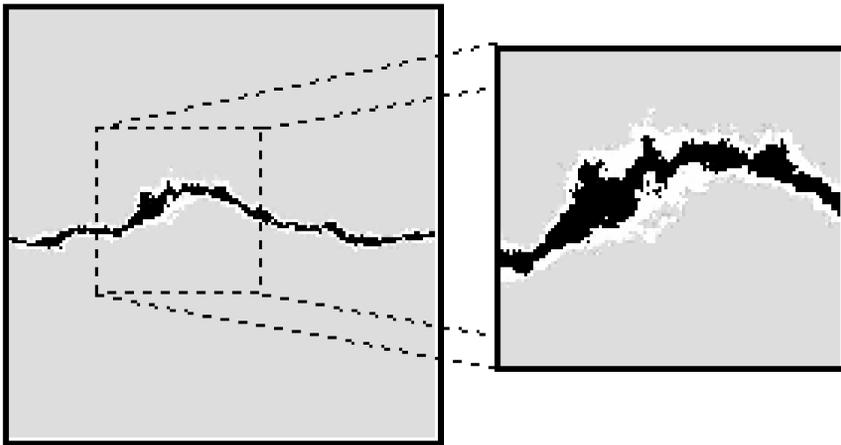


FIGURE 6.1

Example of two fractal maps (with expanded detail) used to generate random corridors. Both gridded maps have 256 rows and columns with p (the fraction of the map that is corridor) of 0.02. A: $H=0.3$; B: $H=0.7$ (see text for explanation of map generation procedure)

location parameter, θ , for the Cauchy was set to 0.0, allowing the Cauchy p.d.f. to be defined by the scale parameter, λ . Thus, the Cauchy p.d.f. = $1/\pi\lambda/(\lambda^2 + r^2)$, where r is the distance over which dispersal occurs.

Simulation efficiency was improved by setting finite limits on dispersal. For each distribution, a maximum dispersal distance, r' , was defined (see the evaluation of this constraint discussed below) limiting dispersal to the area

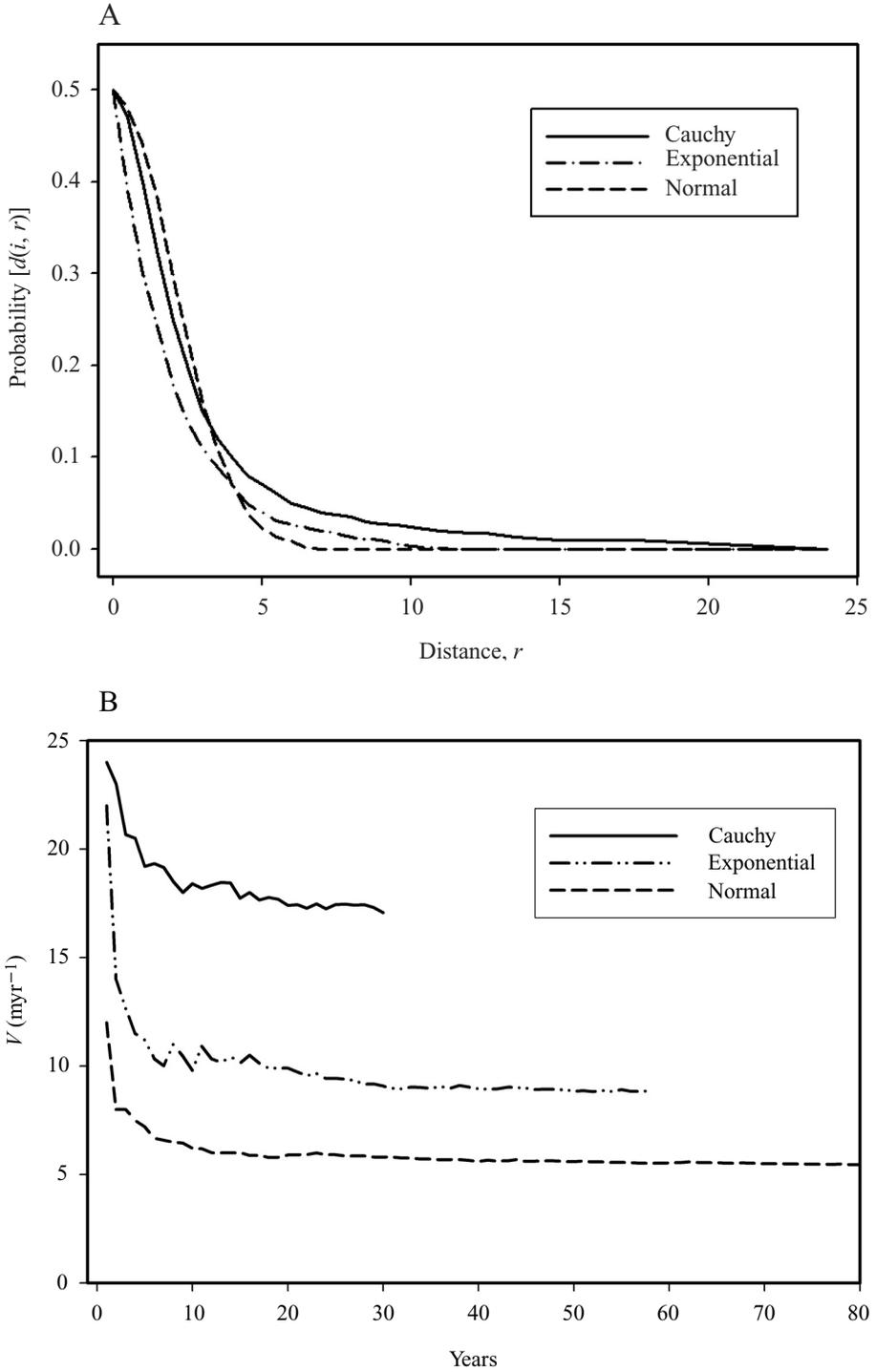


FIGURE 6.2
 Comparison of the probability of movement (A) and the rate of movement (B) for the normal, exponential, and Cauchy probability distributions

around the parental site defined by the radius r' . The total number of sites, S , over which dispersal may occur is determined by r' : $S = 5$, when $r' = 1$ (i.e., nearest neighbor dispersal), while $S = 441$ when $r' = 12$. All probabilities within the circle defined by the radius r' are summed and normalized so that the dispersal probabilities from a single site sums to 1.0. Our comparison of these discrete formulations with the equivalent continuous distributions used in a discrete time, spatially continuous integrodifference simulation of dispersal (Hart and Gardner 1997) has shown that the two methods are numerically equivalent provided that $d(i, r)$ is small when $r = r'$.

6.2.4 Competition

Competition for establishment, growth, and reproduction is simulated annually at each unoccupied site via a seed lottery (Lavorel *et al.* 1994, Plotnick and Gardner 2002). Sites are unoccupied if plant propagules have yet to reach that location, if the resident individual has died (this occurs yearly for annual plants), or if the habitat type is unsuitable for occupation (i.e., the optima, O_{ij} , for habitat j is 0.0 for all species, i). The seed lottery is performed as a two-step process:

1. The probability of viable seeds of species i landing on an unoccupied site of habitat type j is calculated and weighted by the suitability of that site for seed germination. This probability, T_{ij} , is estimated as:

$$T_{ij} = O_{ij} \left[\sum_1^z d(i, r) R_i \right]$$

where R_i is the relative fecundity of species i , z is the number of grid sites within the neighborhood defined by the radius r , and d is the dispersal kernel for species i . The suitability of each habitat type j for each species is described by the habitat optima matrix, O_{ij} : if $O_{ij} = 0.0$ then $T_{ij} = 0.0$ because species i cannot survive within habitat type j ; if $0.0 < O_{ij} < 1.0$ then the probability of success, T_{ij} , is scaled according to the relative inhospitality of habitat j ; if $O_{ij} \geq 1.0$ then the probability of successful establishment, T_{ij} , is proportionately increased for species i .

2. Finally, the values of T_{ij} are normalized by the sum across all species present so that $\sum T_{ij}$ equals 1.0 for the site being considered. These distance and habitat weighted probabilities are then used in the seed lottery to randomly select the species that will establish at that site.

An average, nonspatial measure of competitive ability of each species within each habitat type may be estimated by: $\alpha_{ij} = O_{ij} R_j$, the product of the habitat optima and the relative fecundity. Calculation of α_{ij} ignores spatial effects

considered by T_{ij} by assuming that seeds of all species will reach all unoccupied sites. For competition between two species, the ratio of the α_{ij} s provides a mean-field estimation of expected success in seed lottery competition.

6.2.5 Simulating invasion

Simulations of species invasion along corridors were performed either with or without a resident species present. All species were annual plants, with simulated differences in species achieved by varying the relative fecundity, R , the p.d.f used for dispersal, and the range of habitats (niche width or habitat optima, O_{ij}) that may be occupied. Maps were initialized by placing the invader along the east and west edges of the map, while residents, if simulated, were placed on all other map sites. The rate of movement of invaders, v , was measured as the maximum distance moved, c , per time interval, t . Thus, $v = c / t$, where t is number of years simulated. The use of the maximum distance moved has two advantages: (1) extensive calculations of mean squared distances (see Turchin 1998) are unnecessary because the direction of movement is known, (2) c can be estimated for all distributions – even for fat-tailed distributions which may lack finite moments (Clark *et al.* 2001), and (3) this statistic allows asymptotic rates of spread to be unambiguously estimated (see Fig. 6.3 of Clark *et al.* 2001). The initial conditions of all simulations produce a concentration of invaders along the east and west edges of the map, biasing initial estimates of v . Therefore the most reliable averages for v were obtained over the interval $t = 30$ –35 years.

Four types of simulations were performed to evaluate model assumptions and determine the relative effects of landscape and biotic attributes on species invasions within habitat corridors. These simulations were: (1) an initial series to evaluate the performance of alternative dispersal kernels within lattice models, (2) a set of simulations with fixed species characteristics but variation in corridor width and degree of continuity, (3) a set of simulations of invasion with competition within homogeneous landscapes, and (4) a factorial set of simulations that systematically varied species characteristics, competition, and landscape structure to determine the relative importance of each set of factors in the invasion process. All simulations were run for 300 time steps (years), or until the invading species reached the center of the map. The initial landscape patterns and the final species distributions were analyzed with RULE (Gardner 1999).

6.2.5.1 Truncation effects for different dispersal kernels

The exponential distribution has frequently been used for modeling passive dispersal (Okubo and Levin 1989, Turchin 1998) and has been the foundation

upon which diffusive models are based (i.e., Skellam 1951, Okubo 1980). However, there are compelling arguments for using distributions whose extreme values do not decline exponentially with distance. These distributions, often termed “fat-tailed,” are distinguished by the formation of new colonies at the extreme limits of dispersal (Clark *et al.* 1999, Wallinga *et al.* 2002) and result in higher rates of population expansion than exponential or normal distributions. Although seed dispersal data are rarely sufficient to unambiguously identify differences in the tails of the distribution (Wallinga *et al.* 2002), it is important to evaluate the effect of different p.d.f.s (including truncation effects) on the simulation of dispersal in CAPS.

Alternative forms of the dispersal kernel were simulated within a landscape composed of a single habitat type ($p=1.0$), or with maps containing a linear corridor 4 m wide (2 grid sites) that connected the east and west edges of the map. The habitat optima and relative fecundity of the invading species were held constant at $O_{ij} = 2.0$, $R=2.0$ and resident species were not simulated. The dispersal kernels were either the Cauchy, normal, or exponential distributions with the controlling parameter of each set to 1.0 and the p.d.f.s truncated at either 12 or 24 m (total of six sets of simulations). Invaders were initialized on the edge of the map and the rate of movement, v , measured until the invader reached the center of the map.

6.2.5.2 Structured landscapes

A second set of simulations was performed to evaluate the effect of corridor structure (i.e., variation in corridor width or gaps) on the rate of dispersal of an invading species. Two types of structured maps were created: (1) maps with a single line of habitat from the east to the west edge of the map (i.e., parallel to the directions of invasion) with the width of the lines set at 1, 2 or 4 map sites (2–8 m), and (2) maps with multiple vertical lines of habitat from north to south (i.e., perpendicular to the direction of invasion) with distances between lines of 1, 2, or 4 map sites (2–8 m). Resident species were not simulated, the p.d.f. of the invader was set to the exponential distribution ($r' = 12 \text{ m}$, $z = 1$), and O_{ij} constant at 2.0. For each map type a value of R was set at 1.0, 2.0 or 4.0 for a total of 18 sets of simulations. The invading species was initialized on the map edges and the rate of invasion, v , was measured until the center of the map was colonized. An average rate of invasion was estimated from the values of v recorded at $t=30$ to 35.

6.2.5.3 Effect of competition

The effect of competition on invasion was evaluated with a series of simulations within a homogeneous landscape. The relative fecundity of residents and invaders was set at $R=2.0$, maps were of a single habitat type ($p=1.0$), and

invaders were initialized on the east and west edges of the maps. The rate of dispersal, v , was measured over a 300-year period, or until the invader reached the center of the map. The competitive abilities, α_{ij} , of each species was varied by altering only the habitat optima, O_{ij} , of the resident species to produce a series of simulations with the ratio of competitive abilities (resident/invader) ranging from 0.25 to 10.0.

6.2.5.4 *Landscape factorial*

The final set of simulations involved the examination of a wide range of landscape structures, life-history characteristics of the invading species, and competitive effects on the invasion process. The fractal map algorithm of RULE (Gardner 1999) was used to generate ten replicates of nine different landscape types (a total of 90 maps), with landscape types differing in the value of H (either 0.3, 0.5, or 0.7; Fig. 6.1) and the fraction of the map occupied by the corridor, p (either 0.005, 0.01, or 0.02). A buffer habitat surrounding the corridor was held constant at $p = 0.02$ for all simulations. The remaining portion of the map was a third habitat type that could be occupied by a resident species, but would not support the invader (i.e., $O_{13} = 0.0$). These maps were designed to represent a broad range of corridor types from highly diffuse to highly concentrated (Fig. 6.1).

The invading species was an annual plant with fixed dispersal characteristics (p.d.f. = exponential, $2 = 1.0$, $r' = 6.0$), but variable levels of relative fecundity ($R = 1.0, 2.0$, or 4.0). Because dispersal success is a function of the dispersal kernel and fecundity (Clark and Ji 1995, Higgins *et al.* 1996), varying just fecundity was sufficient for our purposes. But in reality, both the dispersal kernel and fecundity may be expected to vary. The niche width of invaders, defined by the values of O_{ij} for each of the three habitat types, was either narrow ($O_{ij} = 2.0$ for the corridor, but 0.0 elsewhere) or broad ($O_{ij} = 2.0$ for the corridor, 1.0 for the buffer, and 0.0 elsewhere). Invasion with competition was also simulated by initializing the map with a resident species with $R = 2$ and $O_{ij} = 0.0$ for the corridor, but $O_{ij} = 1.0$ elsewhere. The full factorial set of conditions resulted in a total of 810 simulations being performed.

6.3 Results

6.3.1 Truncation effects for different dispersal kernels

The comparison of truncation effects for three p.d.f.s is shown in Table 6.1. Other species characteristics were held constant ($O_{ij} = 2.0$, $R = 2.0$) and dispersal was observed within maps composed of either a single habitat type (A) or a corridor of suitable habitat constrained to a 4 m-wide region (C4).

TABLE 6.1. Comparison of truncation effects for three probability distribution functions (p.d.f.). The probability, $d(i,r)$, and rate of dispersal, v , are shown when the p.d.f. tails were truncated at the maximum range, r' , of 12 or 24 m

| p.d.f | Map type ^a | $r' = 12$ | | $r' = 24$ | |
|-------------|-----------------------|-----------|------|-----------|-------|
| | | $d(i,r)$ | v | $d(i,r)$ | v |
| Normal | A | 0.22e-6 | 5.42 | 0.13e-27 | 5.47 |
| | C4 | 0.22e-6 | 4.08 | 0.13e-27 | 4.08 |
| Exponential | A | 0.39e-3 | 7.25 | 0.94e-6 | 8.87 |
| | C4 | 0.39e-3 | 4.59 | 0.94e-6 | 5.07 |
| Cauchy | A | 0.23e-2 | 8.94 | 0.44e-3 | 17.39 |
| | C4 | 0.23e-2 | 6.10 | 0.44e-3 | 8.77 |

^a All maps were 512 rows and columns with a single habitat type (A) or a 4 m corridor (C4) connecting the east and west edges of the map.

The effect of truncation of the p.d.f.s was most noticeable for the Cauchy distribution, causing a 50 percent reduction in the rate of invasion when r' was reduced from 24 to 12 m (Table 6.1). Even though the values of $d(i,r)$ at r' were always small, the fatter-tails of the Cauchy distribution (Fig. 6.2a) resulted in dispersal rates that were considerably larger than either the normal or exponential distributions (Table 6.1).

Truncation effects are barely noticeable for the normal distribution, but measurable for the exponential distributions in the solid (A) maps (Table 6.1). Reductions in the rate of dispersal due to the confines of the corridors were evident for all p.d.f.s, and considerably larger than those due to truncation of the p.d.f.s. The fatter-tails of the Cauchy distribution resulted in a larger number of propagules lost from the corridors, producing a 50 percent reduction in v when comparing results in the unconstrained maps (A) to those within the 4 m corridor when $r' = 24$ m (Table 6.1). The effect of the corridor on dispersal was small but also evident for the normal distribution. The lower probabilities in the tails of the normal distribution (Fig. 6.2a) resulted in no appreciable changes in v due to truncation effects (Table 6.1). The exponential case showed an intermediate corridor effect with v reduced from 8.9 myr^{-1} in the solid map to 5.1 myr^{-1} within corridors when $r' = 24$ m (Table 6.1). Because the following simulations considered the variation in a large number of species and landscape parameters, the dispersal kernel of the invading species was fixed to the exponential distribution ($\lambda = 1.0$, $r' = 12$ m) for all subsequent simulations.

TABLE 6.2. *The effect of corridor width and dispersal barriers on the rate of dispersal, v , for species differing in relative fecundity, R*

| Dispersal case | $R = 1.0$ | $R = 2.0$ | $R = 4.0$ |
|---------------------|-----------|-----------|-----------|
| Solid maps (A) | 7.21 | 7.31 | 8.25 |
| Corridor width: | | | |
| 2 m | 1.77 | 3.28 | 4.97 |
| 4 m | 3.36 | 5.17 | 6.24 |
| 8 m | 4.65 | 5.95 | 7.21 |
| Dispersal barriers: | | | |
| 2 m | 4.33 | 5.81 | 7.01 |
| 4 m | 3.24 | 4.69 | 6.02 |
| 8 m | 1.91 | 3.41 | 5.22 |

6.3.2 Effect of corridor width and gaps

Calculation of v within the solid map (A) provided an estimate of the maximum possible dispersal rate of 8.25 myr^{-1} when $R=4.0$ (Table 6.2). Differences due to variation in R were small, with an ~ 13 percent increase in v for a four-fold increase in R . When dispersal was constrained by narrow, 2 m corridors, with the highest level of fecundity ($R=4.0$), v was 40 percent slower than the solid (A) maps. Increasing corridor width resulted in proportionally fewer propagules dispersed into the nonhabitat areas surrounding the corridor and, therefore, an increase in v . The rate of invasion in an 8 m-wide corridor was only ~ 13 percent less than that of the A map when $R=4.0$ (Table 6.2).

Low fecundity and narrow corridors ($R = 1.0$, width = 2 m, Table 6.2) had a nonadditive effect on dispersal, with v increased ~ 62 percent from 2 to 4 m, and ~ 64 percent when R increased from 1.0 to 4.0. If these effects were independent and additive, then v would be greater than 9.0 myr^{-1} ; a rate greater than that observed for A maps (Table 6.2). This lack of additivity is probably due to the changing proportion of seeds falling into adjacent habitat as corridor width increases.

The results of the corridor gap simulations show that even the narrowest (2 m) gaps cause a decrease in dispersal rates (e.g., v reduced from 7.21 to 4.33 myr^{-1} when $R=1.0$, Table 6.2). The rate of invasion was very slow (1.91 myr^{-1}) when $R=1.0$ and the width of the barrier = 8 m. However, barrier effects were diminished as R increased (Table 6.2). The truncation of the dispersal kernel at 12 m determined the maximum barrier that could be crossed.

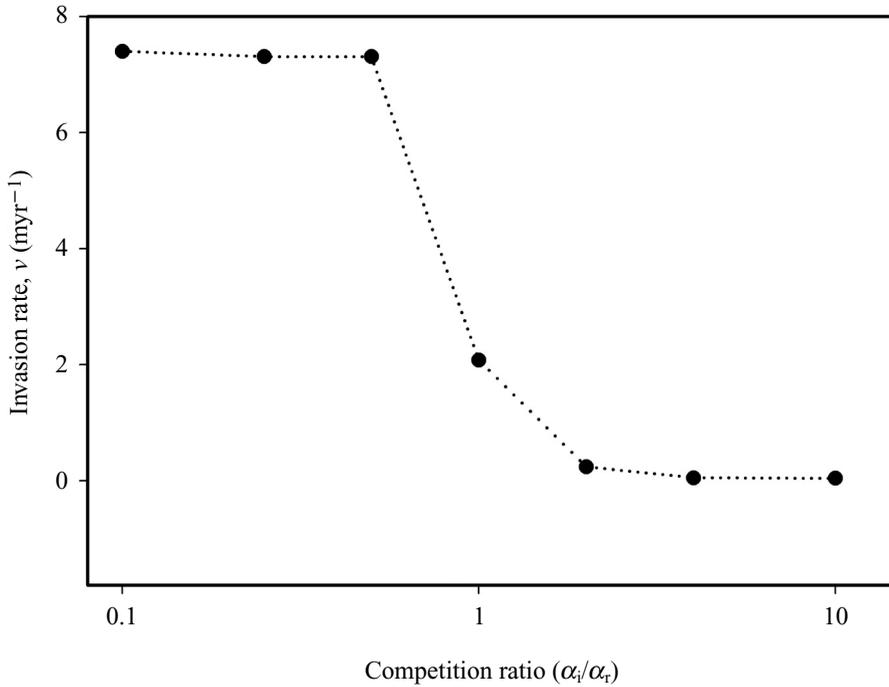


FIGURE 6.3
Changes in the invasion rate, v (myr^{-1}), as a result of increasing levels of competition from a resident species

6.3.3 Effect of competition on invasion

Systematic variation in the habitat optima of the resident species (O_r) allowed the competitive ability of the resident to be varied (e.g., α_i/α_r , Fig. 6.3). The rate of invasion, v , showed a threshold response to competition with a resident: v approached the maximum observed (7.31 myr^{-1} , Table 6.2) when the resident species was a relatively poor competitor ($\alpha_i/\alpha_r = 10.0$); but declined rapidly as the relative competitive ability of the resident increased (Fig. 6.3). When the two species were equal competitors ($\alpha_i/\alpha_r = 1.0$), v was reduced to $\sim 2.0 \text{ myr}^{-1}$; and when the resident species was the superior competitor ($\alpha_r/\alpha_i = 0.1$), v was barely measurable ($< 0.05 \text{ myr}^{-1}$, Fig. 6.3).

6.3.4 Fractal maps factorial

The corridors produced by the fractal map generator vary as a function of p (the fraction of the map occupied by the corridor) and H (the parameter controlling the spatial dependence or “roughness” of corridor habitat, Fig. 6.1).

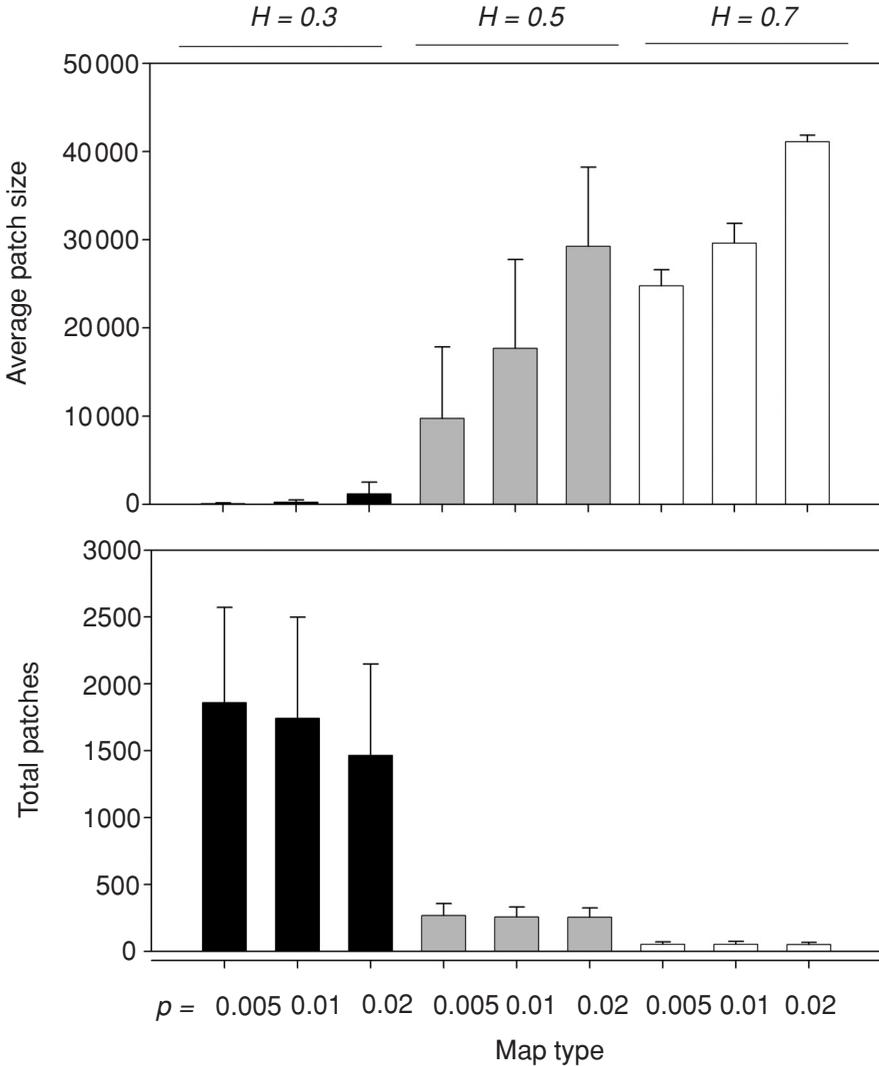


FIGURE 6.4 Changes in the mean number of habitat patches, $M(c)$, and average patch size, $S(c)$, within the randomly generated corridors as a function of p , the fraction of the map occupied by the corridor, and H , the spatial dependence of map habitat. Error bars represent one standard deviation above the mean.

The number and size of corridor patches were analyzed by RULE using the next-nearest neighbor criterion for patch identification (Gardner 1999). The results showed that p and H directly affected the average patch size within the corridors, $S(c)$, with the largest patches occurring when $p=0.02$ and $H=0.7$ (Fig. 6.4). The total number of patches, $M(c)$, was inversely related to patch size, with the greatest degree of fragmentation of corridor habitat occurring when $p=0.005$ and $H=0.3$ (Fig. 6.4).

TABLE 6.3. *The adjusted mean values estimated by SAS general linear model (Table 6.4)*

| Independent Variable ^a | Level | ν | S |
|-----------------------------------|---------|-------|------|
| H | 0.3 | 0.73 | ~0.0 |
| | 0.5 | 2.52 | 0.52 |
| | 0.7 | 4.08 | 1.14 |
| C | Without | 1.53 | 0.66 |
| | With | 0.92 | 0.44 |
| N | Wide | 3.32 | 0.89 |
| | Narrow | 1.67 | 0.21 |
| R | 1.0 | 1.42 | 0.46 |
| | 2.0 | 2.48 | 0.56 |
| | 4.0 | 3.44 | 0.63 |
| p | 0.005 | 1.44 | 0.32 |
| | 0.01 | 2.37 | 0.47 |
| | 0.02 | 3.53 | 0.87 |

^a H and p control the degree of map fragmentation and amount of habitat within the corridor, respectively; N defines the niche width (narrow or broad) of the invader; C indicates the presence or absence of competition; and R indicates the level of fecundity of the invader.

The adjusted mean rate of invasion, ν , and the average patch size occupied by the invading species (analyzed at year 300) are presented in Table 6.3. The greatest effect on ν was due to H, the parameter controlling map roughness (Fig. 6.1): ν ranged from a low of 0.73 myr^{-1} when $H=0.3$ to 4.08 myr^{-1} at $H=0.7$. Relative fecundity of the invader, R, and the proportion of the map that was corridor habitat, p, also had a positive effect on ν (Table 6.3); while the presence of a competitor reduced ν by ~40 percent and increasing niche width changed the average invasion rate by ~50 percent.

The average patch size, S, occupied by the invading species (analyzed in year 300) was correlated with the invasion rate ($r=0.765$). Patch sizes of the invader were largest when H, p, and R were highest, the species niche was widest, and competitors were absent (Table 6.3). Simple correlation coefficients – which measure linear relationships uncorrected for other covariates – showed weak overall trends with R and p, but a strong effect due to H ($r=0.65$).

The analysis of variance of ν and S (Table 6.4) showed that landscape pattern, species characteristics, and the degree of competition accounted for a high degree of the total variation in these response variables ($R^2=84.3$ and 73.7 , respectively, Table 6.4). The variance terms for the ANOVA were estimated by

TABLE 6.4. *The relative sum of squares^a for the rate of movement (v) and the mean cluster size (S) of the invading plant at year 300 of the simulation*

| Source ^b | df | v | | S | |
|---------------------|----|------|------|------|------|
| | | I | III | I | III |
| H | 2 | 42.3 | 6.8 | 41.6 | 1.6 |
| p | 1 | 16.3 | 16.3 | 10.1 | 10.1 |
| Hp | 2 | 0.9 | 0.1 | 6.1 | 6.1 |
| N | 1 | 4.3 | 8.9 | 13.5 | 14.6 |
| C | 1 | 5.7 | 5.7 | 1.6 | 1.6 |
| R | 1 | 14.8 | 14.8 | 0.7 | 0.7 |
| R^2 | – | 84.3 | | 73.7 | |

^a The relative sum of squares are either the type I (uncorrected) or type III (the partial sum of squares) divided by the corrected total sum of squares and expressed as a percent. Values estimated by SAS (2001) generalized linear model procedure.

^b H and p control the degree of map fragmentation and amount of habitat within the corridor, respectively; N defines the niche width (narrow or broad) of the invader; C indicates the presence or absence of competition; and R indicates the level of fecundity (1.0 or 2.0) of the invader. R^2 is the total relative sum of squares for the general linear model. All effects are significant at $P < 0.0001$. See text for additional details regarding these simulations.

the SAS generalized linear model (SAS 2001), with the relative uncorrected (type I) sum of squares and relative partial sum of squares (type III) reported in Table 6.4. The difference between these two sums of squares is an indication of the colinearity found when analyzing complex phenomena. H accounts for 42.3 and 41.6 percent of the variance for v and S , respectively, when it is the first variable in the model (type I, Table 6.4), but drops to 6.8 and 1.6 percent (type III, Table 6.4) when corrected for all other effects. The relative importance of the independent variables on v , as measured by the partial sum of squares, was greatest for p and least for C (ranking: $p > R > N > H > C$, with all effects significant). Interactions between H and p were small but significant, while interactions among other variables were not statistically significant.

Similar results were obtained for S , except that the most important parameter affecting the mean cluster size was N , the niche width of the invader. A wider niche (i.e., the ability to germinate and establish in multiple habitat types) allows more habitat to be occupied and, therefore, larger final cluster sizes. The parameter affecting competition, C , map roughness, H , and fecundity of the invader, R , had the least important effect on S . Examination of the correlations among predicted variables showed that the average patch size and the total

TABLE 6.5. This ANOVA table shows the relationship between four landscape descriptors^a and the rate of invasion (v) and mean cluster size (S) of invading species after 300 years

| Source ^b | df | v | | S | |
|---------------------|----|------|------|------|------|
| | | I | III | I | III |
| H | 2 | 42.3 | 0.5 | 41.6 | 0.1 |
| p | 1 | 16.3 | 2.7 | 10.1 | 0.7 |
| $H p$ | 2 | 0.9 | <0.1 | 6.1 | 1.4 |
| $S(c)$ | 1 | 2.8 | 2.2 | 3.7 | 3.7 |
| $M(c)$ | 1 | 1.7 | 1.7 | <0.1 | <0.1 |
| R^2 | – | 63.9 | | 61.6 | |

^a The relative sum of squares are either the type I (uncorrected) or type III (the partial sum of squares) divided by the corrected total sum of squares and expressed as a percent. Values estimated by SAS (2001) generalized linear model procedure. All effects > 0.1 are significant at $p < 0.01$.

^b H and p control the degree of map fragmentation and amount of habitat within the corridor, respectively; $S(c)$ is the average patch size of available corridor habitat; $M(c)$ is the total number of habitat patches within the corridor estimated by RULE (Gardner 1999). R^2 is the total relative sum of squares for the general linear model. All effects are significant at $P < 0.0001$. See text for additional details regarding these simulations.

number of patches occupied by the invader were inversely related ($r = -0.732$) while the v and S were positively correlated ($r = 0.765$).

The role of landscape pattern on invasion was further examined by including other landscape metrics in the analysis of v and S (Table 6.5). Simple correlations showed that $S(c)$ (average patch size) was related to v ($r = 0.765$) and S ($r = 0.767$); while $M(c)$ (total number of patches) were inversely related to v ($r = -0.620$) but directly related to S ($r = 0.441$). The partial sum of squares accounts for the colinearity among landscape metrics, showing a drop among all responses to <4 percent. Although colinearity may always be expected among landscape metrics (Riitters *et al.* 1995), their presence makes the determination of cause–effect relationships problematic. For instance, if we drop H and p from the ANOVA then $S(c)$ and $M(c)$ alone explain 57.2 and 2.2 percent of the variance in v , respectively.

6.4 Conclusions and recommendations

Dispersal is a critical factor that may ensure population persistence at landscape scales even though local extinction events periodically occur (Hanski

and Gilpin 1991, Hanski and Simberloff 1997). The extensive changes in landscape pattern that are being experienced in many areas (Malhi *et al.* 2002, Lambin *et al.* 2003, Parmenter *et al.* 2003) often create a matrix that will not support the successful dispersal of many organisms (Goodwin and Fahrig 2002). Under these circumstances corridors of suitable habitat may provide a link through which dispersal may continue to occur (Gonzalez *et al.* 1998). Although there is general agreement that maintaining connectance between populations via dispersal is critical, the effectiveness of corridors must be evaluated for each species and each landscape configuration. The lack of empirical evidence verifying the effectiveness of corridors within many landscapes has raised doubts about their general effectiveness (van Dorp *et al.* 1997, Tikka *et al.* 2001, Tewksbury *et al.* 2002).

Theoretical studies are considerably easier to perform, and support the general conclusion that corridors may effectively link spatially distinct populations (Merriam *et al.* 1990, Danielson and Hubbard 2000). However, in many of these studies, corridors have been regarded as simple links between isolated areas of natural habitat. Reality is much more complex. Corridors are rarely continuous or uniform in size. In addition, the effectiveness of corridors will vary by the specific requirements of the dispersing organism. Consequently the natural history (here represented as fecundity and dispersal kernel) and the ecology (competition and niche width) of the organism need to be explicitly considered within the context of varying landscape pattern. The goal of these simulations is to provide a sufficient understanding of these processes, and their relationships to landscape heterogeneity, to allow landscape metrics to be used to predict the usefulness of corridors for species that may differ greatly in their dispersal ability and life-history attributes.

The simulations reported here illustrate the potential range of effectiveness of corridors for plant dispersal. The simulations are useful because they allow a broad spectrum of factors to be considered, because dispersal is difficult to experimentally manipulate, because the effects of landscape pattern are poorly understood, and because community structure (i.e., the presence of competing species) can dramatically affect invasion success. Exploring these multiple factors and their interactions provided an opportunity to understand corridors and, perhaps of greater importance, to illustrate the linkage of pattern and process within heterogeneous landscapes. Although the particulars of each species, community, and corridor may result in unique outcomes, the broad scope of these simulations provide unusual insight into the relationships and interactions among annual plants and the pattern of corridors through which they may disperse. Four results are of particular note:

1. Pattern and process are scale dependent. The distribution of propagules around the parent plant differs greatly between species, being dependent on the morphology of the seed, its mode of transportation, and the environmental conditions which favor seed establishment (Harper *et al.* 1970). These species-specific characteristics interact with the local pattern of the landscape to produce scale-dependent patterns of dispersal and establishment (Table 6.2, Fig. 6.4). The scale-dependent nature of pattern and process within heterogeneous landscapes is a well-recognized phenomenon (Gardner *et al.* 1992, Keitt *et al.* 1997) and a key issue in landscape ecology (Levin 1992, Wu and Hobbs 2002). As the widths of corridors decline, the edge-to-area ratios increase. The loss of seeds across habitat boundaries can dominate seed dispersal events (e.g., van Dorp *et al.* 1997), with losses increasing as the widths of corridors decline and dispersal distances increase. Breaks in corridors do not prevent dispersal when fecundity is high (Table 6.2) and the tails of the dispersal kernel are long (Fig. 6.3). It is possible that this scale-dependency may allow island stepping stones to be sufficient to link widely separated populations (Keitt *et al.* 1997, Hewitt and Kellman 2002).
2. Effect of fecundity. Higher fecundity results in greater dispersal with a consequent increase in competitive advantage (Clark and Ji 1995, Lavorel and Chesson 1995). These simulation confirm the importance of fecundity, R (Table 6.2), on the velocity of dispersal, v , but also show that R is less important than landscape pattern (H and p) for determining the final pattern of species distribution, S (Table 6.4). Therefore, the consideration of the interaction between pattern and process is necessary to predict invasion and distribution of species within heterogeneous landscapes (Plotnick and Gardner 2002).
3. Competition dramatically reduces dispersal. The rate of dispersal dramatically declines as competition increases (Fig. 6.3). A critical threshold exists near the point where the competing species have an equal probability of establishment (i.e., a competitive ratio of 1.0), with the rate of invasion approaching zero when the resident species is a better competitor. If the form of this function is constant (and that remains to be determined), then it may be possible to reconcile differences in empirical measurements made within recently disturbed regions (i.e., in the absence of resident species) with those made in an established community (i.e., the equilibrium case). The former represents a maximum realized invasion rate, while the latter reflects reductions due to competition. Differences between these two cases are also measures of the importance of disturbance in the invasion process.

4. The importance of pattern. It is hardly surprising that variation in landscape pattern is an important determinant of the speed and establishment of an invading plant. However, characterizing the attributes of pattern that affect a particular process remains a challenging problem (Bartlett 1978). Because we generated landscapes with two parameters, H and p , we have the luxury of being able to assess the impact of these parameters on the process of dispersal and establishment, v and S ($R^2 \sim 0.62$, Table 6.4). Patterns within actual landscapes are generated by complex environmental and historical events that are difficult to express with only a few parameters. Although the colinearity among landscape metrics (see the type III sum of squares, Table 6.5) makes it difficult to establish cause–effect relationships, only a few parameters are needed to adequately characterize pattern–process dependencies.

The analysis of dispersal of annual plants within corridors illustrates the larger issue of using metrics to identify pattern–process relationships in landscape ecology. The history of the development and use of landscape metrics is a recent one, evolving rapidly since O'Neill *et al.* (1988) presented a catalog of metrics. Simple metrics are certainly useful as a succinct description of spatial patterns, but pitfalls exist that hinder their use for determining pattern–process relationships. The well-known issue of colinearity (Riitters *et al.* 1995) noted above makes it difficult to define the most useful and robust set of pattern metrics. Without a clearly specified hypothesis the danger of a false positive (i.e., type II error) may be very large. A second pitfall is the existence of non-linear relationships, including critical thresholds, where small changes in pattern induce disproportionately large changes in the process being studied. For instance, the amount of edge within random landscapes is maximized when $p=0.5$ and is minimized when $p=0.0$ and 1.0 . Because actual landscapes show similar patterns (Gardner *et al.* 1992, Turner *et al.* 2001) metrics based on patch size and/or edge are descriptively useful but prescriptively dangerous. Many of these problems stem from the widespread use of gridded integer maps which make the use of classical spatial statistics for hypothesis testing much more difficult (Turner *et al.* 2001).

More rigor is needed in landscape ecology to avoid the propagation of error when pattern–process relationships are studied within heterogeneous landscapes. Foremost is the need for identification of algebraic relationships among similar landscape metrics. The existence of colinearity among metrics is a statistical indicator that metrics may be directly or indirectly developed from more fundamental variables, such as p . Secondly, indices must be extensively tested within random and real landscapes to assess their efficiency and usefulness for description and prediction. Metrics that are not monotonic, or show critical

thresholds of change, should be separated from those whose sensitivity to change is constant across the range of patterns to be investigated.

An equal burden should be placed on the description of the landscapes used within each study. The source of data from which landscape maps were developed, the grain and extent of the study area, and the land-cover classification rules (or reclassification) rules should be thoroughly explained. In addition, the software-dependent neighborhood rules (Gardner 1999) used to identify pattern should be documented. Although these suggestions are familiar, a complete specification of analysis methods is required before results among landscape studies may be compared. Only when these conditions are met can we expect to see significant progress in determining pattern–process relationships within heterogeneous landscapes.

Acknowledgments

This research was supported by NSF grants EAR-9506639 to Plotnick and NSF EAR-9506606 to R. H. Gardner. James Forester was supported by an NSF grant DEB-0078138 to M. G. Turner. Developments to RULE required to analyze corridor patterns were supported by funds provided by the National Park Service through Cooperative Agreement T-3097-02-001.

References

- Anderson, G. S. and B. J. Danielson. 1997. The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. *Landscape Ecology* **12**, 261–71.
- Bartlett, M. S. 1978. An introduction to the analysis of spatial patterns. *Advances in Applied Probability* **S10**, 1–13.
- Beier, P. and R. F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* **12**, 1241–52.
- Clark, J. S. and Y. Ji. 1995. Fecundity and dispersal in plant-populations: implications for structure and diversity. *American Naturalist* **146**, 72–111.
- Clark, J. S., M. Lewis and L. Horvath. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist* **157**, 537–54.
- Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* **80**, 1475–94.
- Danielson, B. J. and M. W. Hubbard. 2000. The influence of corridors on the movement behavior of individual *Peromyscus polionotus* in experimental landscapes. *Landscape Ecology* **15**, 323–31.
- Fauth, P. T., E. J. Gustafson and K. N. Rabenold. 2000. Using landscape metrics to model source habitat for Neotropical migrants in the midwestern US. *Landscape Ecology* **15**, 621–31.
- Forman, R. T. T. and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* **29**, 207–31.
- Fortin, M. J., B. Boots, F. Csillag, and T. K. Rimmel. 2003. On the role of spatial stochastic models in understanding landscape indices in ecology. *Oikos* **102**, 203–12.
- Gardner, R. H. (ed.). 1999. *RULE: Map Generation and a Spatial Analysis Program*. New York: Springer-Verlag.

- Gardner, R.H., R.V. O'Neill, and M.G. Turner. 1993. Ecological implications of landscape fragmentation. Pages 208–226 in S.T.A. Pickett and M.J. McDonnell (eds.). *Humans as Components of Ecosystems: The Ecology of Subtle Human Effects and Populated Areas*. New York: Springer-Verlag.
- Gardner, R.H., M.G. Turner, R.V. O'Neill, and S. Lavorel. 1992. Simulation of the scale-dependent effects of landscape boundaries on species persistence and dispersal. Pages 76–89 in M.M. Holland, P.G. Risser, and R.J. Naiman (eds.). *The Role of Landscape Boundaries in the Management and Restoration of Changing Environments*. New York: Chapman and Hall.
- Gonzalez, A., J.H. Lawton, F.S. Gilbert, T.M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance and distribution in a microecosystem. *Science* **281**, 2045–7.
- Goodwin, B.J. and L. Fahrig. 2002. How does landscape structure influence landscape connectivity? *Oikos* **99**, 552–70.
- Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* **86**, 902–10.
- Gu, W.D., R. Heikkilä, and I. Hanski. 2002. Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. *Landscape Ecology* **17**, 699–710.
- Gustafson, E.J. and R.H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* **77**, 94–107.
- Gustafson, E.J. and G.R. Parker. 1992. Relationships between landcover proportion and indexes of landscape spatial pattern. *Landscape Ecology* **7**, 101–10.
- Haines-Young, R. and M. Chopping. 1996. Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. *Progress in Physical Geography* **20**, 418–45.
- Hanski, I. and M.E. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**, 3–16.
- Hanski, I. and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain and application to conservation. Pages 5–26 in I. Hanski and M.E. Gilpin (eds.). *Metapopulation Biology*. New York: Academic Press.
- Hargis, C.D., J.A. Bissonette, and J.L. David. 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology* **13**, 167–86.
- Harper, J.L., P.H. Lovell, and K.G. More. 1970. The shapes and sizes of seeds. *Annual Review of Ecology and Systematics* **1**, 327–56.
- Hart, D.R. and R.H. Gardner. 1997. A spatial model for the spread of invading organisms subject to competition. *Journal of Mathematical Biology* **35**, 935–48.
- He, H.S., B.E. DeZonia, and D.J. Mladenoff. 2000. An aggregation index (AI) to quantify spatial patterns of landscapes. *Landscape Ecology* **15**, 591–601.
- He, H.S., D.J. Mladenoff, and E.J. Gustafson. 2002. Study of landscape change under forest harvesting and climate warming-induced fire disturbance. *Forest Ecology and Management* **155**, 257–70.
- Hewitt, N. and M. Kellman. 2002. Tree seed dispersal among forest fragments: II. Dispersal abilities and biogeographical controls. *Journal of Biogeography* **29**, 351–63.
- Higgins, S.L., D.M. Richardson, and R.M. Cowling. 1996. Modeling invasive plant spread: the role of plant–environment interactions and model structure. *Ecology* **77**, 2043–54.
- Iverson, L.R., M.E. Dale, C.T. Scott, and A. Prasad. 1997. A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (USA). *Landscape Ecology* **12**, 331–48.
- Johnson, N.L. and S. Kotz. 1970. *Continuous Univariate Distributions*. New York: Houghton Mifflin Company.
- Keitt, T.H., D.L. Urban, and B.T. Milne. 1997. Detecting critical scales in fragmented landscapes. *Conservation Ecology* **1**, 4.

- Krummel, J. R., R. H. Gardner, G. Sugihara, R. V. O'Neill, and P. R. Coleman. 1987. Landscape patterns in a disturbed environment. *Oikos* **48**, 321–4.
- Lambin, E. F., H. J. Geist, and E. Lepers. 2003. Dynamics of land-use and land-cover change in tropical regions. *Annual Review of Environment and Resources* **28**, 205–41.
- Lavelle, S. and P. Chesson. 1995. How species with different regeneration niches coexist in patchy habitats with local disturbances. *Oikos* **74**, 103–14.
- Lavelle, S., R. V. O'Neill, and R. H. Gardner. 1994. Spatio-temporal dispersal strategies and annual plant species coexistence in a structured landscape. *Oikos* **71**, 75–88.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**, 1943–67.
- Li, H. B. and J. G. Wu. 2004. Use and misuse of landscape indices. *Landscape Ecology* **19**, 389–99.
- Ludwig, J. A., R. W. Eager, G. N. Bastin, V. H. Chewings, and A. C. Liedloff. 2002. A leakiness index for assessing landscape function using remote sensing. *Landscape Ecology* **17**, 157–71.
- Malhi, Y., P. Meir, and S. Brown. 2002. Forests, carbon and global climate. *Philosophical Transactions of the Royal Society of London Series A: Mathematical Physical and Engineering Sciences* **360**, 1567–91.
- McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. *FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps*. Amherst, MA: University of Massachusetts.
- Merriam, G., K. Henein, and K. Stuart-Smith. 1990. Landscape dynamic models. Pages 399–416 in M. G. Turner and R. H. Gardner (eds.). *Quantitative Methods in Landscape Ecology*. New York: Springer-Verlag.
- Murray, B. G. 1967. Dispersal in vertebrates. *Ecology* **48**, 975–8.
- O'Neill, R. V., J. Krummel, R. H. Gardner, et al. 1988. Indices of landscape pattern. *Landscape Ecology* **1**, 153–62.
- O'Neill, R. V., K. H. Riitters, J. D. Wickham, and K. B. Jones. 1999. Landscape pattern metrics and regional assessment. *Ecosystem Health* **5**, 225–33.
- Okubo, A. 1980. *Diffusion and Ecological Problems: Mathematical Models*. Berlin: Springer-Verlag.
- Okubo, A. and S. A. Levin. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* **70**, 329–38.
- Parmenter, A. W., A. Hansen, R. E. Kennedy, et al. 2003. Land use and land cover change in the Greater Yellowstone Ecosystem: 1975–1995. *Ecological Applications* **13**, 687–703.
- Plotnick, R. E. and R. H. Gardner. 2002. A general model for simulating the effects of landscape heterogeneity and disturbance on community patterns. *Ecological Modelling* **147**, 171–97.
- Plotnick, R. E. and K. L. Prestegard (eds.). 1993. *Fractal Analysis of Geologic Time Series*. Englewood Cliffs, NJ: Prentice Hall.
- Quinn, J. F. and S. P. Harrison. 1988. Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia* **75**, 132–40.
- Riitters, K. H., R. V. O'Neill, C. T. Hunsaker, et al. 1995. A factor analysis of landscape pattern and structure metrics. *Landscape Ecology* **10**, 23–39.
- Riitters, K. H., R. V. O'Neill, J. D. Wickham, and K. B. Jones. 1996. A note on contagion indices for landscape analysis. *Landscape Ecology* **11**, 197–202.
- Rosenberg, D. K., B. R. Noon, and E. C. Meslow. 1997. Biological corridors: form, function, and efficacy. *Bioscience* **47**, 677–87.
- SAS. 2001. *The SAS System for Windows*, Version 8.01. Cary, NC: SAS Institute Inc.
- Simberloff, D. 1999. The role of science in the preservation of forest biodiversity. *Forest Ecology and Management* **115**, 101–11.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**, 196–218.
- Tewksbury, J. J., D. J. Levey, N. M. Haddad, et al. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America* **99**, 12923–6.
- Tikka, P. M., H. Hogmander and P. S. Koski. 2001. Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology* **16**, 659–66.

- Timoney, K. P. 2003. The changing disturbance regime of the boreal forest of the Canadian Prairie Provinces. *Forestry Chronicle* **79**, 502–16.
- Tischendorf, L. 2001. Can landscape indices predict ecological processes consistently? *Landscape Ecology* **16**, 235–54.
- Tischendorf, L., U. Irmiler, and R. Hingst. 1998. A simulation experiment on the potential of hedgerows as movement corridors for forest carabids. *Ecological Modelling* **106**, 107–18.
- Turchin, P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sunderland: Sinauer.
- Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. *Landscape Ecology in Theory and Practice: Pattern and Process*. New York: Springer-Verlag.
- van Dorp, D., P. Schippers, and J. M. van Groenendael. 1997. Migration rates of grassland plants along corridors in fragmented landscapes assessed with a cellular automation model. *Landscape Ecology* **12**, 39–50.
- Wallinga, J., M. J. Kropff, and L. J. Rew. 2002. Patterns of spread of annual weeds. *Basic and Applied Ecology* **3**, 31–8.
- Wickham, J. D., R. V. O'Neill, and K. B. Jones. 2000. A geography of ecosystem vulnerability. *Landscape Ecology* **15**, 495–504.
- Wu, J. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecology* **19**, 125–38.
- Wu, J. and R. Hobbs. 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. *Landscape Ecology* **17**, 355–65.