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A general model for simulating the effects of landscape heterogeneity and disturbance on community patterns

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Abstract

An individual-based, spatially explicit stochastic lattice model, CAPS, was designed to examine multiple processes responsible for spatial patterns of abundance and diversity of sessile species in heterogeneous landscapes. Species simulated by CAPS differ in habitat preferences (niche width), dispersal of propagules, and relative fecundity. The spatial distribution of habitat types are represented as heterogeneous gridded landscapes. The outcome of competition and establishment processes in successive generations is determined locally via a seed lottery. A series of 200 year-long simulations was performed to investigate the effects of variation in species characteristics and competition, landscape heterogeneity, and disturbance on patterns of species abundances. The outcome of competition was most sensitive to differences in fecundity between species, the spatial distribution of suitable habitat and the initial distribution of species. Species with a narrow niche were confined to a single habitat type and remained at or near their initialization sites. Broader niches resulted in increasing niche overlap and competition but enhanced species mobility, allowing abundance levels to approach expected values determined by map resources. Even so, initial distributions still affected the spatial patterns of species distributions at year 200. Disturbance regimes were simulated by varying the frequency, extent and spatial pattern of disturbances. Disturbance events removed species from affected sites but did not otherwise alter habitat characteristics. Results showed that disturbances may lead to a reversal in competition and establishment, dependent on species-specific differences in fecundity and dispersal. Although intermediate levels of disturbance frequency and extent increased the probability of species coexistence, the spatial pattern of disturbance played an unexpectedly important role in the tradeoff between dispersal and fecundity. The ability to simulate multiple factors affecting patterns of persistence, abundance and spatial distribution of species provided by CAPS allows new insight into the temporal and spatial patterns of community development.

Keywords: Community dynamics; Spatial simulation; Cellular automata; Disturbance; Landscape; Heterogeneity; Lattice models

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1. Introduction

Assessing the causes of variation in the temporal and spatial distributions of competing species is a fascinating and complex subject. Because sessile organisms are fixed in time and space, one might expect changes in the patterns of these communities to be easily predicted. However, the characterization of spatial heterogeneity of landscape resources, differences in species characteristics affecting dispersal, establishment, and competition, and changes in disturbance regimes are rarely measured over satisfactory intervals of time and space. As a consequence, the combined effect of these factors in structuring terrestrial communities and maintaining biodiversity remains one of the more important and intriguing issues in ecology (papers in McKinney and Drake, 1998; Tilman and Kareiva, 1997).

The difficulty in measuring and predicting the simultaneous effects of multiple factors across a broad spectrum of ecosystems has sometimes produced conflicting and confusing results. For instance, disturbance mediated coexistence predicted by the intermediate disturbance hypothesis (Collins and Glenn, 1997; Connell, 1978; Denslow, 1985) has been the usual explanation for higher than expected levels of species diversity (Allmon et al., 1998). However, Hubbell et al. (1999) studied the effects of light-gap disturbances on tree diversity on Barro Colorado Island, Panama and found that recruitment limitation (the inability of competitors to disperse to an available site) rather than the spatial or temporal distribution of gap formation may be the principle determinant of local diversity patterns. Tilman (1999), in his commentary on Hubbell et al. (1999) suggested that diversity control by local recruitment limitation is a general characteristic of the ecology of sessile species, but also described several alternative mechanisms. One alternative is a tradeoff between dispersal and competitive ability (Tilman, 1997) while another is the suppression of competitive displacement; i.e. the reduced frequency of direct competitive interactions which allows weaker competitors to persist.

Confusion may also exist because of the broad spectrum of models that have been developed to study competition of sessile organisms within spatially heterogeneous environments. A complete review of these models is beyond the scope of this paper, but selected examples provide a perspective on the potential importance of a variety of factors which may shape these communities. For instance, the effect of competition on the dynamics of native and alien plant invasions (Allen et al., 1996; Hart and Gardner, 1997; Higgins et al., 1996; Molofsky, 1994; Tilman, 1997); seed dispersal (He and Mladenoff, 1999; Lavorel et al., 1995; Malanson and Armstrong, 1996; Shmida and Ellner, 1984); environmental variability and disturbance dynamics (Caswell and Cohen, 1991, 1995; Klausmeier, 1998; Lavorel et al., 1994; Tilman et al., 1994); mutualism and trophic dynamics (Hacker and Gaines, 1997; Moen and Collins, 1996; Wootton, 1998); biogeochemistry and resource allocation (Bolker and Pacala, 1999; Tilman et al., 1997a; Wedin and Tilman, 1993) and, of course, community succession (Coffin and Urban, 1993; Pacala, 1987; Pastor et al., 1999; Weishampel and Urban, 1996) have been extensively studied.

The methods utilized to simulate these processes also vary across a broad range of model types and include Markov models (Barradas et al., 1996; Caswell and Cohen, 1995; Li, 1995); Lotka-Volterra (Cantrell et al., 1998; Holmes et al., 1994); the use of reaction-diffusion or integro-difference equations (Allen et al., 1996; Hart and Gardner, 1997; Higgins et al., 1996; Holmes et al., 1994); simulations of individual-based dynamics (Higgins et al., 1996; Molofsky, 1994; Wiegand et al., 1997); as well as spatially explicit gap models (He and Mladenoff, 1999; Weishampel and Urban, 1996). A comprehensive review of many of these models can be found in Czárán (1998).

One of the most useful approaches for simulating a diversity of processes affecting the spatial dynamics of plant communities are cellular automata models (Caswell and Cohen, 1991; Green, 1989; Silvertown et al., 1992; Molofsky, 1994; Balzter et al., 1998). Space is represented in cellular automata (CA) models as a lattice of cells with changes in the state of each cell determined by sets of neighborhood rules (Wolfram, 1984). Although each cell may exist in several different states (in our case the type of species present), the local conditions (i.e. the neighborhood rules) define the temporal and spatial patterns of change. CA models are especially useful for simulating community dynamics because the rules are flexible and easily modified, allowing the dynamics of a variety of different processes to be simulated (Hogeweg, 1988; Molofsky, 1994). Because the solutions are rapid and stable, the simulation of large, spatially extensive systems is also possible. Molofsky (1994), Higgins and Richardson, (1996), Czárán (1998) and Balzter et al. (1998) have provided extensive reviews of ecological applications of CA models. More recent uses of CA models include the simulation of forest dynamics (Lett et al., 1999; Alonso and Solé, 2000) and of plant competition processes (Grist, 1999).

This paper describes an individual-based, spatially explicit and variable stochastic lattice model, CAPS, that has been designed to examine a variety of processes affecting spatial patterns of abundance and diversity of sessile species in heterogeneous landscapes. Although models currently exist that examine components of this problem (Silvertown et al., 1992; Caswell and Etter, 1993; Colasanti and Grime, 1993; Tilman, 1997), CAPS has been developed to be a comprehensive model that considers changes in the spatial distribution of species through time as a consequence of degree of habitat heterogeneity, habitat disturbance, and competition among species differing in fecundity, dispersal ability, and habitat preference (niche breadth). Control of each factor is flexible, allowing users to vary the frequency and geometric distribution of habitats; the number of competing species; the fecundity and dispersal characteristics of each species; and create a wide range of disturbance regimes. CAPS also allows actual maps to be used in simulations to address specific ecological issues as well as theoretical questions concerning community development and persistence.

This paper begins by presenting the structure of CAPS and then describes the model parameters required to simulate differences in life history attributes of a variety of species, the nature of competition, variation in landscape heterogeneity, and the process of disturbance. A series of simulations were performed to illustrate the effect of these processes on patterns of species abundances. We then used CAPS to determine the relative impact of disturbances and landscape patterns on competition among species which differ in their life history attributes.

2. Model design

CAPS is a rule-based approach to spatial modeling that integrates a variety of methods derived from both the physical and biological literature. It is both spatially explicit and spatially variable. The rules for species interactions are similar to those of traditional stochastic CA models (Hogeweg, 1988; Wolfram, 1984); rules for species dispersal and disturbance are based on percolation and kinetic growth models (Hermann, 1986; Plotnick and Gardner, 1993; Stauffer and Aharony, 1992); and the effects of species competition is simulated via a seed lottery (Chesson, 1981; Lavorel et al., 1994; Shmida and Ellner, 1984).

The process of simulation of species dynamics within CAPS involves: (1) creation or import of the habitat map; (2) definition of species habitat preferences; (3) defining species dispersal and fecundity parameters; (4) description of the disturbance scenario to be simulated; and (5) initialization of species distributions on the habitat map. Although a large number of parameters are used to control landscape features and species attributes, CAPS input requirements are easy to define and simple to modify. CAPS is written and compiled in Lahey Fortran 90 (Lahey Computer Systems, 1999), with the Interacter graphical software (Software Series, 1992) for display of time-dependent changes in species distributions. Simulation can be performed interactively under Windows 95 and 98, Windows NT, or MS-DOS. Multiple sets of simulations can also be performed using MS-DOS batch files.

3. Landscape structure

The landscape map is represented in CAPS as a 2-dimensional $m \times n$ square lattice. Each node of the lattice corresponds to a habitat site of sufficient size to support a single individual. Maps may be either generated or input as square or rectangular lattices with as many as 1024 rows and columns within the map, although fractal maps (see below) must be square with linear dimensions that are powers of 2.

Each node within the lattice can belong to 1 of 10 (or fewer) habitat types (h), with uninhabitable areas represented by setting nodes to 0. Habitat types represent an abstraction of the numerous biotic and abiotic factors (soil type, moisture, elevation, light availability, etc.) that affect survivorship and reproduction of individual species. This feature distinguishes CAPS from the multispecies spatial competition models of Tilman et al. (1997b) and Colasanti and Grime (1993) which used a single available resource type. Because habitat designations are arbitrary, an area showing a transition from $h = 1$ to 2 to 3 does not need to be considered as a cline. Likewise, a species may not be restricted to single or continuously numbered habitats, but may occupy discontinuously numbered habitat types.

The fraction of the map occupied by each habitat type, h, is equal to p_h, with the probability of uninhabitable sites (i.e. barren ground) equal to p_o. The values of p_h and p_o are set at the beginning of each simulation when the map is either input (as a space delimited ASCII file) or generated within CAPS. Values of p_h and p_o do not change during the course of a single simulation. A number of options exist for the creation of maps with differing distributions of habitat types, including:

3.1. Random maps

There are two options for the generation of random habitat maps. *Simple random maps* select the habitat type at each node independently on the basis of probabilities set by the vector p. The process of random selection results in a small degree of variation between maps in the actual number of sites set to each habitat type. A second method of map generation uses a process of random generation without replacement which forces the total number of sites of each habitat type to be exactly $p_h \times m \times n$. An example of a simple random map is shown in Fig. 1a.

3.2. Fractal maps

Fractal maps, as discussed by Palmer (1992) and illustrated in With et al. (1997), have spatial dependence intermediate between completely random and completely deterministic structures. CAPS generates spatially structured fractal maps using a modification of the midpoint displacement algorithm (MidPointFM2D, p. 101 of Saupe, 1988) to produce a 2-dimensional fractal Brownian landscape. The variance associated with the displacement of points, σ^2, and H, the parameter that specifies the dependence between adjacent points, are the only two parameters required by this algorithm. The process of successive displacement of points results in an expected difference between any two points a distance d apart equal to $E[X_1 - (X_1 - d)] \propto d^H$ (Plotnick and Prestegaard, 1993). When $H = 0.5$, the difference between any two points is proportional to the square of the distance d, and the correlation between any points separated by distance d is equal to $C(d) = 2^{2H-1}$ (Feder, 1988; Mandelbrot, 1983). Adjustment of the value of H between 0.0 and 1.0 results in maps that range from extremely fragmented to highly aggregated. The fractal dimension, D, of topographies generated by the midpoint displacement method is equal to $D = 3.0 - H$ (Saupe, 1988). The midpoint displacement algorithm produces a data structure of real numbers that are converted in CAPS to integer habitat types by subdividing the elevations into intervals proportional to p_h. Each map node is then assigned an integer habitat type based on this elevation interval. An option in CAPS allows the fractal maps to be 'tilted' by initially setting asymmetric values to the corners of the map, resulting in habitats distributed as gradients rather than randomly within the map. Examples of fractal habitat maps with five habitat types but different values of H are shown in Fig. 1b and c. Note that in the case of fractal maps, the sequence of habitat types may be considered to be a cline.

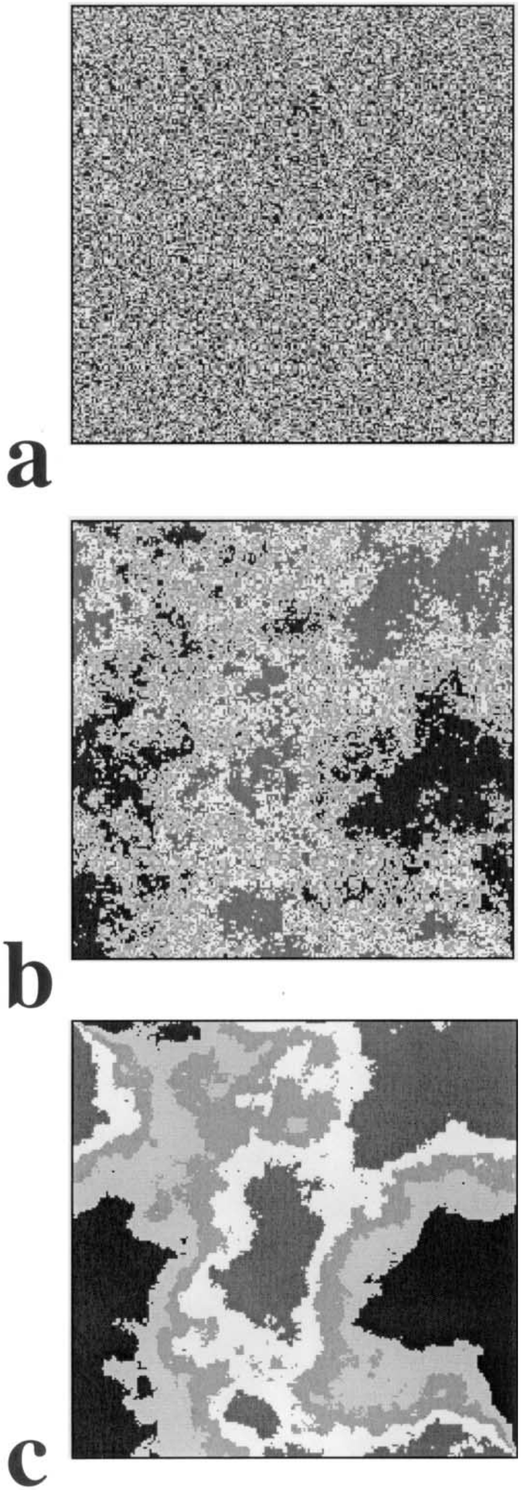

Fig. 1.

3.3. Imported maps

Maps can also be imported into CAPS as a space delimited ASCII file. The user must specify the number of rows and columns and the number of habitat types. This features allows maps produced by other programs, or digitized landscape data, to provide the required description of habitats for CAPS simulations. Because CAPS also allows generated maps to be output, a single map may be used for multiple sets of simulations within CAPS.

4. Species characteristics

Each map node can only be occupied by a single adult individual at any point in time. All species simulated within CAPS are sessile organisms, such as annual plants, which complete their life cycle within a single time step (i.e. 1 year). Up to 10 species, each with a unique set of characteristics, are defined on input. An example set of species characteristics is shown in Table 1. These characteristics include:

4.1. Habitat preference (niche breadth)

The habitat types, *h*, which can be potentially occupied by a given species, *j*, is specified on input within a matrix $\mathrm{iopt}_{j,h}$. Non-zero, positive values of $\mathrm{iopt}_{j,h}$ indicate that species *j* can occupy habitat type *h*. The number of habitat types that are greater than 0 within $\mathrm{iopt}_{j,h}$ is an indication of the niche breadth for that species; if the number of habitats with non-zero values of $\mathrm{iopt}_{j,h}$ is small then the species may be regarded as a specialist while the converse indicates a generalist. For example, species 1 in Table 1 is a specialist and can live only on sites of habitat type 2, while species 2

Fig. 1. Example of the three types of maps used in the simulations. All maps have five different habitat types with each type comprising 20% of the map area. (a) A simple random map. (b) A fractal map with $H = 0.2$. (c) A fractal map with $H = 0.8$.

Table 1
An example set of model parameters defining species characteristics within a landscape composed of three distinct habitat types

Parameter[a]	Species (j)		
	1	2	3
$\mathrm{iopt}_{j,1}$	0	1	0
$\mathrm{iopt}_{j,2}$	1	1	3
$\mathrm{iopt}_{j,3}$	0	1	1
fecund_j	3	1	1
DFT	exponential	exponential	exponential
$\bar{r}_j$	1	1	1
rmax_j	6	12	2
rain_j	0	0	0.1

[a] $\mathrm{iopt}_{j,h}$, the habitat optima for species j within habitat h; fecund_j, the relative fecundity of species j (values are habitat independent); DFT, dispersal function type (choices are uniform, normal, exponential, and inverse distance); $\bar{r}_j$, mean dispersal distance for species j; rmax_j, maximum dispersal distance for species j; rain_j, seed rain threshold for species j.

is a generalist able to live on all three habitat types.

Although the values of iopt must be positive, they are not restricted in magnitude; increasing values represent increasing degrees of habitat preference (i.e. likelihood of establishment). Table 1 shows that species 3 can live in habitats 2 and 3, but prefers habitat 2 because it is three times more likely to succeed in this habitat. Similarly, more than one species can occupy the same habitat type, indicating niche overlap. The species ratios of iopt values for each habitat type indicates relative competitive abilities of species within that habitat type. For example, species 1, 2 and 3 all compete for habitat type 2; species 1 and 2 are equal competitors, but species 3 has an advantage of establishment that is three times greater than either species 1 or 2.

There are few restrictions on the iopt matrix: the dimensions of the matrix are defined by the number of species and habitat types, but all habitat types need not be occupied. Although the values of iopt shown in Table 1 are integers, real numbers may be used to provide an infinite number of combinations of iopt values for any given number of species.

4.2. Relative fecundity

The production of propagules per individual of each species, j, at each time step is expressed in relative terms and stored as the parameter fecund_j. All members of each species are assumed to have the same fecundity. The example in Table 1 shows that the specialist species 1 produces three times as many propagules as each individual of species 2 and 3.

4.3. Dispersal

The dispersal algorithms of CAPS are designed to represent a wide range of biologically realistic dispersal strategies (Andersen, 1991; Lavorel et al., 1994). Probabilities of dispersal are species specific and may be selected from among four different functions used to generate probabilities of dispersal of propagules, $d(i, r)$, from a parental site to a site i a distance r away. These functions represent both continuous and discrete dispersal processes. Because the simulation of dispersal via continuous probability distributions is computationally expensive, a maximum dispersal distance, rmax_j, is specified for each species, j. Parent plants can distribute propagules to their own site and to neighboring sites within a radius rmax_j and the total number of sites S that can be reached is proportional to rmax_j^2. When $\mathrm{rmax}_j = 1$, propagules can only be dispersed to the four nearest neighbor nodes and S, the number of dispersal sites, equal five. When $\mathrm{rmax}_j = 12$, propagules can be dispersed over a neighborhood (S) of 441 sites.

If *uniform* dispersal probabilities are selected then propagules of species j will have an equal probability of reaching any site within the neighborhood. Thus, the probability of reaching any one site within a radius r is:

$$d(j, r)_{uniform} = \frac{1}{S}.$$

For the *inverse distance function* (*IDF*), the probability is a function of the square root of the distance from the parental site:

$$d(j,r)_{\mathrm{sqd}} = \frac{r_i^{-2}}{\sum_{i=1}^{S} r_i^{-2}},$$

where $r_i = 0$ is arbitrarily set to one to allow self-seeding. In *exponential* dispersal the function is:

$$d(j,r)_{exp} = \frac{\lambda\, e^{-(1/\lambda)r_i}}{\sum_{i=1}^{S} \lambda\, e^{-(1/\lambda)r_i}},$$

where $\lambda = 1/\bar{r}$, and $\bar{r}$ is the mean dispersal distance. The fourth dispersal option is the *normal*:

$$d(j,r)_{nor} = \frac{e^{-z_i^2/2}}{\sum_{i=1}^{S} e^{-z_i^2/2}},$$

where z_r is the normalized value of r, with a user determined mean equal to $\bar{r}$ and S.D. $S_r = (r - \bar{r})/3$.

The values of $d(j,r)$, are calculated for each species and stored in a lookup table before actual simulations begin. Fig. 2a illustrates the four dispersal functions for $\mathrm{rmax}_j = 12$ and $\bar{r} = 1$. The probabilities decline asymptotically with distance for the normal, exponential, and inverse distance functions, so that the differences among them are clearly most important for small dispersal distances.

Fig. 2b illustrates the dispersal functions for the species in Table 1. This figure shows that for some functions, such as the exponential, small values of rmax result in a truncated distribution, so that the actual mean of the function mean may less than the value of $\bar{r}$ used to generate it. However, sufficiently large values have little effect on the distribution of dispersal distances (i.e. the functions for $\mathrm{rmax}_j = 6$ and $\mathrm{rmax}_j = 12$ when $\bar{r} = 1$ for the exponential distribution). As a result, it is rarely necessary to use large values of rmax_j.

CAPS also allows for long-range transport of propagules of species j beyond the distance set by rmax. If the parameter rain_j is > 0 for species j then at each generation CAPS determines the percentage of the map occupied by species j (v_j) and multiplies v_j by rain_j. The resulting factor is equal to the probability of sites receiving propagules from species j and is equivalent to the global dispersal parameter of Etter and Caswell (1995). For example, if species 3 in Table 1 occupied 50% of the map ($v_j = 0.5$), then the probability of each map site receiving propagules via seed rain would equal $v_j \times \mathrm{rain}_j = 0.5 \times 0.1 = 0.05$.

Dispersal characteristics of species in CAPS are not explicitly linked to their competitive ability as in the model of Tilman et al. (1997b), although this linkage may be simulated by proper selection of species dispersal, fecundity and habitat optima parameters.

5. Initialization

Several options exist for defining the initial distribution of species at the beginning of the simulation. Species may either be randomly initialized at the edges of the map to simulate invasions of unoccupied landscapes; placed on their optimal habitat sites throughout the entire map; or randomly located without regard to habitat type. When only two species are simulated, each may be initialized on alternate sides of the map.

6. Regrowth and competition

In the simulations reported here species represent annual plants, and all sites may potentially be occupied at the beginning of each time step (i.e. habitat values never equal 0). Actual occupation of each site is determined by niche characteristics of the species, their dispersal distances and initial distributions. The determination of the success of propagules of species j reaching each site is determined for each generation by: (1) finding all sites occupied by species j within distance rmax_j (map boundaries may be periodic, absorbing, or reflecting); (2) for each neighboring site, the value of $d(j,r)$ is obtained from the lookup table and all values summed; (3) the contribution from seed rain is added to the sum (seed rain is 0 if $\mathrm{rain}_j = 0.0$, otherwise equal to $\mathrm{rain}_j \times v_j$); and (4) the summed contribution of all sites of species j is multiplied by the relative fecundity fecund_j and the habitat optima, $\mathrm{iopt}_{h,j}$ for that species and site. This summation process results in the total relative number of propagules, rseed_j, of species j for a each map site. Thus:

$$\mathrm{rseed}_j = \left[\sum_{i=1}^{S} d(j, r) + \mathrm{rain}_j \times v_j \right] \times \mathrm{iopt}_{h,j} \times \mathrm{fecund}_j,$$

where S = number of sites within distance rmax_j occupied by species j: rseed_j will be 0 if $\mathrm{iopt}_{h,j} = 0$ or if no individuals of species j are within rmax_j of the given location and $\mathrm{rain}_j = 0$. Note that higher values of $\mathrm{iopt}_{j,h}$ yield higher values of rseed_j for a particular habitat type, whereas high values of fecund are equally advantageous for all habitat types that a species can occupy. To prevent exceptionally small values of rseed_j resulting in unlimited species expansion on sparsely occupied maps,

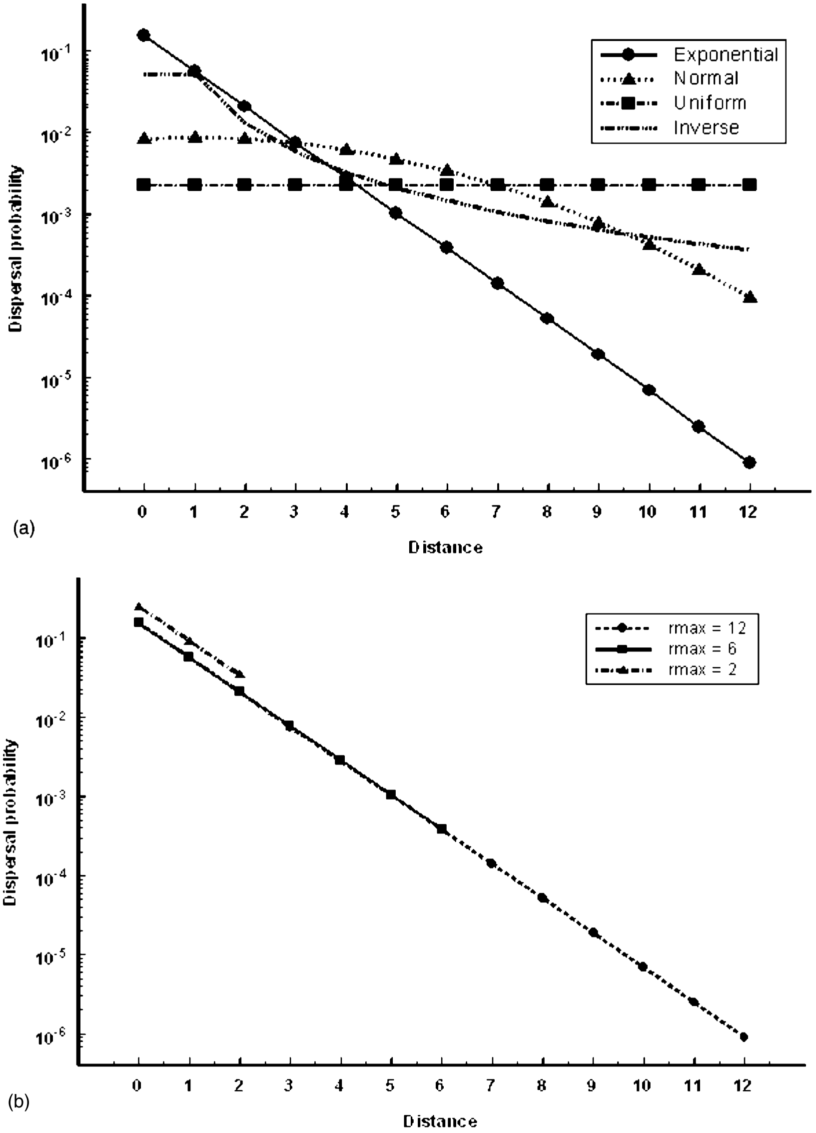

Fig. 2. Dispersal probabilities as a function of distance. (a) four alternative dispersal functions for the same maximum dispersal distance $\mathrm{rmax}_j = 12$; (b) The dispersal functions for the three species in Table 1. All dispersal functions are exponential, but differ in the maximum dispersal distance. Note that the functions for $\mathrm{rmax}_j = 6$ and $\mathrm{rmax}_j = 12$ are virtually identical; this is because the truncation of the tail of the distribution for $\mathrm{rmax}_j = 6$ is minor. In comparison, the truncation effect when $\mathrm{rmax}_j = 2$ is significant, producing a skewed distribution of dispersal probabilities.

values of $\text{rseed}_j < 1.0$ may be set to 0.0 with a probability $\propto 1/\text{rseed}_j$.

The calculation of rseed_j is repeated for each species in the simulation, so that each site has an array of rseed_j values corresponding to species present within the vicinity of that site. Because fecund_j represents relative fecundity, values of rseed_j are also relative and not equivalent to the total number of propagules falling on an individual site.

In CAPS the best competitor is not guaranteed successful recruitment at a site (Tilman et al., 1997b). Instead, successful competition for occupancy of the site for the next time step is determined by a seed lottery (Chesson and Warner, 1981; Lavorel et al., 1994; Shmida and Ellner, 1984), with the probability of species winning the lottery proportional to their relative values of rseed. The combination of three factors—high local abundance, high values of iopt giving a competitive advantage for that habitat type, and high species fecundity—all lead to larger values of rseed and a higher probability of success in the lottery occurring at the end of each time step. However, the interaction of these factors with each other, with different dispersal characteristics, and different disturbance regimes makes the prediction of the local changes in site occupancy uncertain. For example, in the simplest case, one parental individual from each species can compete for an empty site. Fig. 3 illustrates the relative contributions to total rseed ($\Sigma\,\text{rseed}_j$) of equidistant single individuals of the species in Table 1, located at different distances from a site of habitat type 2. At distances $r \leq 2$, the greatest potential contribution comes from species 3 which has the smallest dispersal range, making $d(3, r)$ relatively large, and the greatest preference, ($\text{iopt}_{3,2}$), for habitat type 2. At distances $2 < r \leq 6$, beyond the dispersal range of species 3, individuals of species 1 have an advantage, due almost entirely to their greater fecundity; the values of $d(1, r)$ and $d(2, r)$ being essentially equal (Fig. 2b). Only individuals of species 2 can contribute from distances greater than $r = 6$. On densely occupied maps with multiple parental individuals, this seemingly simple picture breaks down. For instance, the low dispersal ability of species 3 allows only nine parental sites to contribute to rseed. In contrast, species 2 can potentially draw from a neighborhood of 441 sites allowing a much larger area to contribute propagules to the competition lottery.

Although the outcome of the competition lottery at individual sites is random, the vast number of locations within most maps make overall competitive success, in uniform habitats lacking disturbances, predictable from inspection of iopt, fecund, and the total amount of habitat available within the dispersal range of that species. However, as will be seen from the simulations reported here, the outcome of competition is also dependent on the spatial distribution of suitable habitat and the process used to initialize the species map.

7. Disturbance

Numerous possibilities are encompassed by the concept of disturbance (Pickett and White, 1985; White and Jentsch, 2001). Disturbances in CAPS are simulated by the death of adult individuals prior to reproduction and dispersal and are non-species specific. Disturbances thus remove individuals from sites and do not alter the habitat. This is in contrast to the disturbance algorithm of Tilman et al. (1997b), which produces permanent destruction of habitat sites.

The disturbance algorithm was designed to provide a systematic comparison of disturbance regimes that differ in extent (area disturbed) and/or timing (disturbance frequency). Such comparisons are usually difficult because changes in disturbance frequency often result in changes in the total area disturbed during the simulation (total extent). Two parameters are used in CAPS to allow the frequency of disturbance to be varied either independently of total extent or systematically correlated with the extent disturbed. These parameters are: e_y, the average fraction of the map disturbed per year and f_y, the average frequency of disturbance. A broad range of frequency distributions of disturbance sizes and timing may be specified, including: (1) disturbances of fixed extent and length spaced equally in time; (2) periodic episodes of disturbances with extent of disturbance varying as a sinusoidal func-

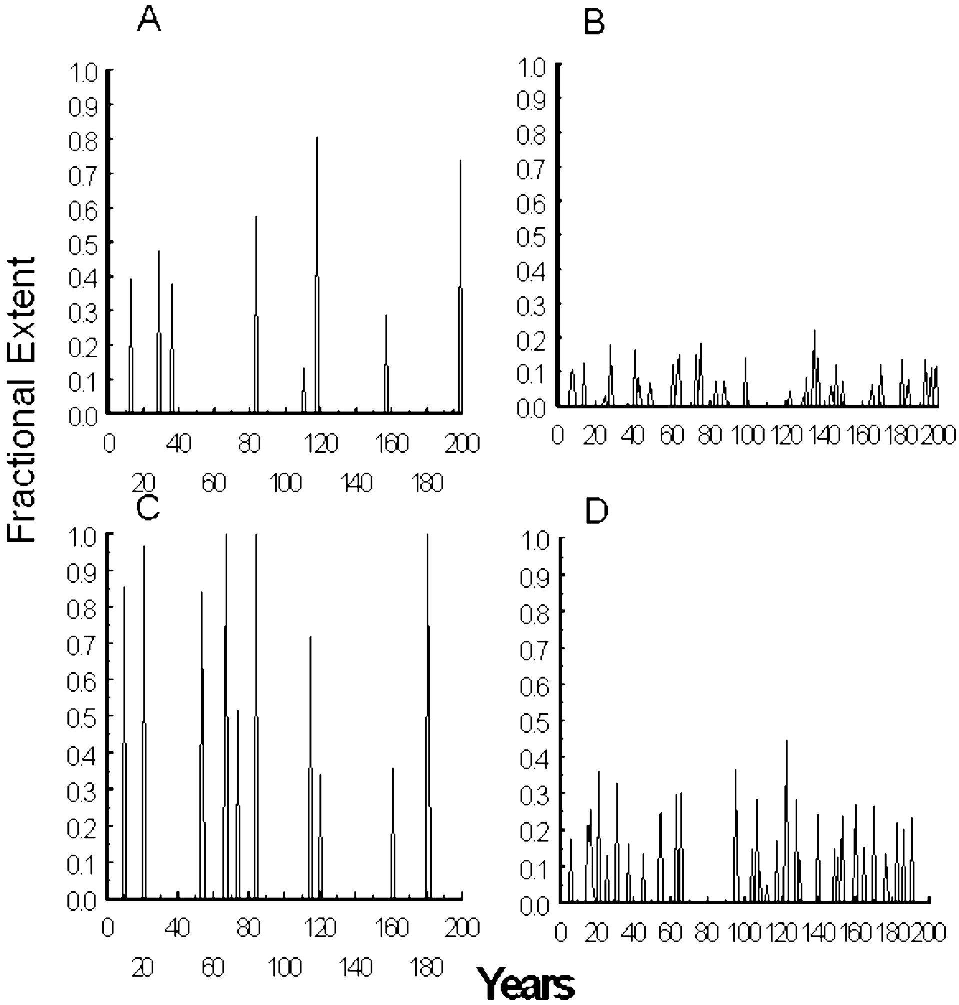

Fig. 3. Disturbance frequency (f_y) and extent (e_y) for the four disturbance types used in the simulations (Table 3). (A) $e_y = 0.02$, $f_y = 0.05$; (B) $e_y = 0.02$, $f_y = 0.2$; (C) $e_y = 0.04$, $f_y = 0.05$; (D) $e_y = 0.04$, $f_y = 0.2$.

tion with a constant amplitude; (3) random disturbance episodes with fixed extent; (4) disturbances random in time and extent (i.e. distributed as white noise); and (5) disturbance frequency and extent following a fractal distribution produced from a 1-dimensional fractional Brownian motion, similar to that used to produce the fractal habitat maps (Plotnick and Prestegaard, 1993; Saupe, 1988). These options cover most conceivable temporal distributions of disturbances. The time series illustrated in Fig. 3 shows disturbance histories of equal total extent (i.e. constant values of e_y) but with year-to-year variance in disturbance frequencies.

The relationships between the frequency, total extent, and the size of disturbances is also illustrated in Table 3. Disturbance frequency and size are parameters that set the proportion of the landscape that is disturbed each year. Average disturbance size is thus: $e_y \times 1/f_y \times n \times m$, making disturbance size directly dependent on extent but inversely dependent on frequency.

The spatial pattern of disturbance (independent of both frequency and extent) can be varied over a continuum ranging from completely random to total aggregated. The continuous pattern of clustered disturbances is produced by a method similar to those used in spatial epidemic models (Plotnick and Gardner, 1993). A random site is selected for the initiation of disturbance and the spread to the eight neighboring sites is randomly propagated with a fixed probability d. When d is < 0.4 the epidemic is likely to die out—in which case a new disturbance is initiated until the total area to be disturbed, as defined by that disturbance scenario, has been reached. The end result of the epidemic process is a contiguous region of disturbed sites with the shape of the fragmented pattern of disturbance a predictable function of d. In general, the higher probability of disturbance growth resulted in more compact and smooth edged disturbance patches. Consequently, these patches have lower edge/total area ratios; as we will see in the following simulations, this attribute has important consequences for re-occupation following disturbance. Disturbances only occur on cells that are occupied by the species being simulated. Thus, a disturbance of a given size X that occurs in a given year will remove exactly X occupied sites from the map. Although this relationship is somewhat arbitrary, it is consistent with a harvesting or herbivory scenario that is independent of species type.

8. Analysis

Three output files are generated by CAPS to record the results of each simulation. The first file records the time-dependent changes in total abundance of each species on the map. The second file is a record (map) of species occupancy at each map site. The second map is usually generated at the end of each simulation, but may be output at specific time-steps during the simulations. The third file is a log of the model input and output, including a statistical summary of the Monte Carlo iterations of the CAPS model.

We analyzed the spatial patterns by input of model results into RULE, a program for the analysis of spatial patterns (Gardner, 1999). A large number of indices have been suggested for measuring fragmentation (Gardner, 1999; Gustafson, 1998; Gustafson and Parker, 1992; McGarigal and Marks, 1994; O'Neill et al., 1988; Plotnick et al., 1993; Riitters et al., 1995), but few of these quantify unique information relative to the process of species establishment and persistence. We chose three indices to measure pattern attributes: the total number of clusters Tc; the total amount of edge Te; and the area weighted average cluster size Sav. Sav equals $\Sigma\, S_i^2/\Sigma\, S_i$, where S_i is the size of cluster i, and the sums are taken over all clusters of the same habitat type. Sav is of interest here because it is less sensitive than the arithmetic average to the presence of a few small clusters that contribute little to landscape-scale changes in population dynamics (Gardner et al., 1993; Li and Archer, 1997; Stauffer and Aharony, 1992). Each metric was calculated separately for each habitat type on each map type and also used to describe species distributions at the conclusion of the simulations.

9. Comparisons with previous models

Many of the individual features in CAPS are similar to previous models, especially CA models such as Silvertown et al. (1992), Colasanti and Grime (1993), Etter and Caswell (1995), Dytham (1995), Bascompte and Solé (1998), Grist (1999), and Alonso and Solé (2000). The distinguishing feature of CAPS is the large number of processes that are simulated and the flexibility of the parameters which describe these processes. In this section we compare the individual features of CAPS with similar CA models.

9.1. Size and shape of maps

Map dimensions in CAPS can be as large as to 1024×1024 rows (n) and columns (m). Map dimensions may be either square or rectangular. Maps in other CA applications have generally been small and square, ranging from 30×30 (Colasanti and Grime, 1993) to 256×256 (Etter and Caswell, 1995). Exceptions include Alonso and Solé (2000) who used a rectangular map with m and n of 200×100 and Van Dorp et al. (1997)

who used a linear grid of varying width to simulate dispersal within long, thin corridors.

9.2. Neighborhoods

Neighborhoods in CAPS (the number and distribution of adjacent cells which affect the state of a particular cell) are determined by the dispersal functions of the individual species and may vary for each cell on the map. Neighborhoods in previous CA models include nearest neighbors (four cells; Silvertown et al., 1992; Colasanti and Grime, 1993), next-nearest neighbors (eight cells; Dytham, 1995; Alonso and Solé, 2000), and occasionally as large as 24-neighbors (Grist, 1999). Van Dorp et al. (1997) used a negative exponential seed dispersal function to define a neighborhood, with extreme events truncated in a manner similar to CAPS.

9.3. Heterogeneity

Up to 10 different habitat types may be defined in CAPS, with a wide variety of spatial distributions simulated allowing a detailed representation of landscape heterogeneity. Most CA models have ignored spatial patterns of landscape resources, however Colasanti and Grime (1993) included a gradient of resources, Palmer (1992) and With et al. (1997) used fractal maps as landscape representations; and Lavorel et al. (1993, 1995) represented landscape heterogeneity with hierarchically structured maps.

9.4. Number and types of competing species

CAPS allows as many as 10 competing species to be simulated. Species can differ in their habitat preferences (niche width), dispersal ability, and relative fecundity. Nearly all previous models had far fewer species, generally 2–5, with the exception of Alonso and Solé (2000) who simulated as many as 400 species. Species descriptors generally fall into two general categories: Silvertown et al. (1992) used Markov type transition matrices, while other models differentiated between species based on their competitive abilities (i.e. ability to disperse and utilize resources, usually as a trade-off; see Dytham, 1995; Grist, 1999; Alonso and Solé, 2000).

9.5. Cell state transitions

Cell state transitions in CAPS are determined by a stochastic seed lottery (Chesson, 1981; Lavorel et al., 1994; Shmida and Ellner, 1984), with success in the lottery being a function of the site's neighborhood and the relative fecundity, dispersal ability, habitat preference, abundance, and individual distances of species in that neighborhood. There is only weak dependence on its current state, since each site has a probability of self-seeding. CAPS differs from most other CA models, which are often based on spatial-temporal Markov chains (i.e. STMC, see Balzter et al., 1998) that predict future states based on the former state of the cell and its neighborhood.

9.6. Disturbance

Disturbance in CAPS removes species from affected sites, but does not otherwise alter habitat characteristics. The spatial and temporal distribution of disturbances can be extensively modified in CAPS, allowing a wide variation of forms in space and time. This process is most similar to Etter and Caswell (1995), who simulated disturbance frequency as a Poisson process, with size selected from a skewed frequency distribution. Dytham (1995) and Bascompte and Solé (1998) modeled disturbance as permanent habitat destruction; while Alonso and Solé (2000) and Colasanti and Grime (1993) considered disturbance as the death of individuals at each site.

10. Simulation design

The outcome of competitive interactions in CAPS are affected by three principle factors: variation in landscape heterogeneity; differences between species in their life history characteristics, especially differences in dispersal and fecundity; and temporal and/or spatial variation in disturbance patterns. The possible combinations of parameters affecting these three factors are immense. We have reduced the dimensionality of this problem by considering conditions which vary only two of the three factors at a time. The resulting sets of simulations examine effects due to variation in: (1) life history and landscape pattern (Case 1); (2) life history and disturbance (Case 2); and (3) landscape pattern and disturbance (Case 3).

In Case 1, niche breadth was varied to produce increasing degrees of competition among species coexisting in heterogeneous landscapes. The hypothesis was that large continuous patches of a particular species may result either from wide habitat tolerance or from an unbroken distribution of a preferred habitat type. In Case 2, we compared relative survival of two species, one of which was a superior competitor (i.e. a higher relative fecundity) and the other a superior disperser, under different disturbance regimes. This case evaluates the hypothesis that spatial patterns of disturbance may be an important determinant of competitive success. Case 3 examined the interactive effects of disturbance and landscape heterogeneity on patterns of species abundance, with the hypothesis that disturbance effects are minimal in homogeneous landscapes but become increasingly important as landscapes become more heterogeneous.

Table 2
Habitat optima, iopt$_{j,h}$, for five species differing in habitat preference

[a]Simulation series	Habitat (h)	Species (j)				
		1	2	3	4	5
A	1	1	0	0	0	0
	2	0	1	0	0	0
	3	0	0	1	0	0
	4	0	0	0	1	0
	5	0	0	0	0	1
B	1	3	1	0	0	1
	2	1	3	1	0	0
	3	0	1	3	1	0
	4	0	0	1	3	1
	5	1	0	0	1	3
C	1	3	1	0	1	1
	2	1	3	1	0	1
	3	1	1	3	1	0
	4	0	1	1	3	1
	5	1	0	1	1	3
D	1	3	1	1	1	1
	2	1	3	1	1	1
	3	1	1	3	1	1
	4	1	1	1	3	1
	5	1	1	1	1	3

[a] A, B, C, D are labels for the four patterns of niche breadth used in the model simulations.

10.1. Case 1: variation in niche breadth and habitat heterogeneity

A series of simulations were performed on maps with 256 rows and columns (65 536 cells) and five habitat types. Each map was generated so that each habitat type was equally represented and no cells were empty (i.e. $p_o = 0.0$). Three map types were used: simple random maps (the RD series), fractal maps with $H = 0.2$ (the H2 series), or fractal maps with $H = 0.8$ (the H8 series). Example images of these map types are shown in Fig. 1.

Five species were simulated on each map type with the relative fecundity of all species set to one. Dispersal distances were drawn from exponential distributions with $\bar{r} = 1$ and $\mathrm{rmax} = 12$. Four alternative patterns of niche breadth and habitat preference were simulated (the A, B, C and D series, Table 2). In the A series all species lived on a single habitat type with no niche overlap. This series was designed to assess the importance of habitat connectivity and initial species distributions in the absence of competition. Series B, C, D represent increasing levels of niche breadth (3, 4, and five habitat types, respectively) and consequently niche overlap. The B, C, D series allow the examination of the role of competition in producing observed patterns.

Initial placement of the species on the maps was random, either along single rows at the edges of the map (series L) or over the entire map (series R). Map boundaries were always wrapped (periodic boundaries), each simulation was run for 200 time steps, and 10 iterations were performed for each simulation case. Because the RD, H2 and H8 maps were generated and saved to a file, all simulations within a single map series use the same sequence of maps.

Table 3
Factorial set of disturbance simulations for two species differing in fecundity and dispersal capabilities

SN	e_y	f_y	e_y/f_y	p_{cg}	Average relative abundance[a](year 200)		
					Species 1	Species 2	# C
1	0.00	0.0	0.00	0.0	0 (0)	100 (0)	0
2	0.02	0.1	0.20	0.4	0 (0)	99.2 (0.2)	0
3	0.02	0.1	0.20	1.0	0 (0)	5.6 (11.4)	0
4	0.02	0.2	0.10	0.4	11.7 (27.9)	87.1 (3.7)	10
5	0.02	0.2	0.10	1.0	59.2 (6.9)	40.7 (10.4)	10
6	0.04	0.1	0.40	0.4	2.9 (316.2)	95.9 (9.3)	1
7	0.04	0.1	0.40	1.0	0 (0)	5.4 (10.2)	0
8	0.04	0.2	0.20	0.4	42.7 (7.7)	57.2 (5.9)	10
9	0.04	0.2	0.20	1.0	94.9 (6.4)	3.9 (149.8)	7

The landscape patterns used for these simulations were 10 fractal maps with five equally abundant habitat types ($H = 0.8$). However, the map may be considered to be homogeneous as habitat preferences for each species was equal for all habitat types (i.e. all $\text{iopt}_{j,h}$ values = 2.5). The relative fecundity (10 and 20) and maximum dispersal (12 and 1) differed between species 1 and 2, respectively. Dispersal distances were drawn from the uniform distribution and seed rain was not simulated. Ten sets of simulations (one for each map) of 200 years were performed for each combination of disturbance parameters. SN, is the simulation number. Average yearly extent (e_y) is the mean fraction of the map disturbed per year, disturbance frequency (f_y) is the fraction of years that a disturbance occurs with average disturbance extent equal to e_y/f_y. p_{cg}, is the probability of cluster growth. When $p_{cg} = 0.4$ dendritic disturbances result while values of 1.0 produce large areas of total disturbance. # C, indicates the number of simulations out of 10 replications that resulted in both species persisting until year 200.

[a] Abundance levels are the percent of the map occupied by that species. The number in parenthesis is the coefficient of variation (mean/S.D.).

10.2. Case 2: interactive effect of disturbance, dispersal, and competition

A second series of simulations were performed to investigate the relationship between varying disturbance regimes and patterns of coexistence among competing species. These simulations 'reused' the 10 replicate fractal maps of the H8 series of the Case 1 simulations. Two species that differ in fecundity and dispersal ability were simulated. The relative fecundity of species 1 was set at 10 and that of species 2 at 20 for all simulations. Thus, in the absence of disturbances, species 2 provides twice as many propagules and always displaced species 1. Dispersal distances for both species were drawn from the uniform distribution. The maximum dispersal distances of species 1 was variable but that of species 2 was always set to a distance of 1 (i.e. dispersal restricted to the four nearest neighboring cells). Seed rain was always set to 0 for both species. The parameters governing disturbance regimes were variable between different sets of simulations. Simulations were repeated 10 times for each unique set of parameter values, once for each map replicate. Species were randomly distributed in year 1 and each simulation lasted for 200 years.

The first set of simulations (a) investigated the trade-off between dispersal and fecundity within a moderately disturbed landscape. The dispersal distance of species 1 was varied from 1 to 24 while disturbance frequency (f_y), extent (e_y) and the probability of cluster growth (p_{cg}) were set to 0.2, 0.02 and 1.0, respectively (disturbances only occur on sites occupied by either species 1 or 2). In the second set of simulations; (b) patterns of coexistence as a function disturbance frequency (f_y) and extent (e_y) were examined. Maximum dispersal distances for species 1 was set to 12 and disturbance parameters were varied in a factorial pattern (Table 3). Nine different combinations of disturbance patterns were simulated. The initial simulations were run without disturbance to determine the effect of competition alone. The remaining eight sets of simulations were performed with disturbances of fixed extent, equally spaced in time. Average yearly extent (e_y) was either 0.02 or 0.04 (2 or 4% of the map, respectively); disturbance frequency (f_y) was either 0.05 (once every 20 years) or 0.2 (once every 5 years); and each disturbance lasted 1 year removing all species from each disturbed site. The selected combinations of e_y and f_y resulted in yearly disturbances that ranged from 10 to 80% of the map (Table 3). The spatial distribution of the disturbances were varied by setting the probabilities of disturbance cluster growth (p_{cg}) to 1.0 (compact disturbance patches) or 0.4 (disturbance patches that were diffuse and dendritic).

10.3. Case 3: interactive effects of disturbance and landscape heterogeneity

In the final set of simulations the moderating effect of the spatial variability of landscape resources on patterns of species coexistence were examined. The dispersal distance of species 1 was set to 12 and disturbance frequency (f_y), extent (e_y) and probability of cluster growth (p_{cg}) were set to 0.2, 0.02, and 1.0, respectively (the same disturbance regime as Case 2a). Although the spatial variability of maps used in all simulations was constant (i.e. the same 10 fractal maps with five habitat types were used for each simulation set), the response of each species to variation in the distribution of habitat was controlled by differences in the iopt matrix. When all values of iopt matrix are constant the species are unresponsive to variations in pattern—that is, the map is effectively homogeneous. Conversely, the importance of landscape patterns increases as values of iopt differ between habitat types and species. For these simulations the dimensions of the iopt matrix was: j (species) $= 2$ and h (habitat) $= 5$. A homogeneous landscape was first simulated by setting all iopt values to 2.5. Three sets of simulations with progressive increases in spatial heterogeneity were then simulated by altering the $\mathrm{iopt}_{j,h}$ values subject to the constraint that the values for each species must sum to $h \times 2.5 = 12.5$. The first level of heterogeneity was produced by arranging the five values of iopt for species 1 to [3.0, 2.75, 2.5, 2.25, 2.0]; the second level to: [3.5, 3.0, 2.5, 2.0, 1.5]; and the final level to: [4.0, 3.25, 2.5, 1.75, 1.0]. The iopt values for species 2 were the direct opposite of those for species 1. Thus for the final level of heterogeneity, habitat 1 is four times more favorable fore species 1 while habitat 5 is four times as favorable for species 2. In all cases habitat 3 is equally favorable for both species.

11. Results

11.1. Map patterns

The three different map types (Fig. 1) used in the Case 1 simulations have distinctly different arrangements of the five habitat types, even though the proportion of each habitat type, p_h, does not differ between maps. Mean values of p_h for each map and habitat type are near 0.2 (Table 4) with a coefficient of variation (mean/S.D. $\times$ 100) $< 1.0\%$ (range: 0.4 to 0.65%). Because p_h was held constant across map types the method of map generation affected only the spatial heterogeneity of the maps. The random maps were the most fragmented, having the highest number of clusters (Tc), greatest amount of edge (Te), and the smallest average cluster size (Sav). The fractal map with $H = 0.8$ was the least fragmented while the fractal map with $H = 0.2$ had an intermediate level of fragmentation. Landscape metrics are often highly correlated even though maps may differ greatly in pattern (Riitters et al., 1995). The overall correlation of the average cluster size, Sav, with the number of clusters, Tc, and the amount of edge, Te, was -0.71 and -0.86, respectively, and the correlation between Tc and Te was 0.92.

An analysis of variance was performed to test the effect of map and habitat type on Sav using the general linear model of SAS (1993). As expected, the effect of map type was highly significant ($F = 347.6$, $P < 0.001$, $\mathrm{df} = 2135$) accounting for nearly 80% of the variation in Sav. The only expected effect on Sav due to habitat type occurred on the fractal maps where clusters of habitats 1 and 5 were truncated by the map boundaries (Fig. 1, Table 4).

11.2. Case 1: variation in niche breadth and habitat heterogeneity

Simulation results in Table 5 show the mean of species abundances and cluster sizes for species 3 after 200 time steps, averaged over 10 runs, with ANOVA results for all species in Tables 7 and 8. Examination of these results reveals complex interrelationships among habitat preference, niche breadth, map type, and initialization in producing the observed distributions.

As noted above, habitat distributions on random maps (RD series, Table 5) were highly fragmented. As predicted by percolation theory (Plotnick and Gardner, 1993), species confined to a single habitat type cannot spread across the map and remain restricted at or near their initialization sites. This percolation constraint was apparent in the results for simulations with narrow niche on random maps (the *A*:*RD* series, Table 5) where the mean relative abundances were <0.01 and cluster sizes were very small.

In contrast, simulations with broader niches descriptions allow species to achieve an average abundance levels close to the expected value 20%. This is not surprising, since all five habitats were present in equal percentages (Table 4) and all five species had equivalent niche breadths and variation in habitat characteristics is one of several possible mechanisms that allow competitive species to coexistence (Reynolds et al., 1997). Niche breadth had a greater effect on species cluster size than species abundance (Tables 7 and 8). As niche breadth increased, cluster size increased proportionately because the number of contiguous available habitat sites also increased for each species.

As noted above, fractal habitat maps were less fragmented than random maps (Table 4) and the higher fractal dimension maps ($H = 0.8$) were less fragmented than the lower fractal dimension maps ($H = 0.2$). As a result, for corresponding sets of

Table 4
Map characteristics (means with S.D. in parenthesis) for three different map types

Map type	Habitat	p_h	Tc	Te	Sav
Random (RD)	1	0.200 (0.0012)	4760.7 (36.6)	84 076.8 (436.9)	6.08 (0.167)
	2	0.199 (0.0015)	4759.4 (25.3)	83 799.8 (527.4)	5.97 (0.098)
	3	0.200 (0.0015)	4729.9 (52.1)	84 140.2 (582.2)	6.12 (0.181)
	4	0.199 (0.0010)	4741.8 (60.5)	83 849.0 (347.7)	6.05 (0.211)
	5	0.200 (0.0011)	4744.0 (32.8)	84 089.4 (432.7)	6.04 (0.125)
	$\bar{X}$	0.200 (0.0013)	4747.1 (43.2)	83 991.0 (473.9)	6.051 (0.162)
Fractal $H = 0.2$	1	0.199 (0.0007)	721.9 (104.6)	31 177.8 (2899.6)	2873.6 (1545.1)
	2	0.200 (0.0002)	1174.6 (209.1)	60 003.2 (3296.8)	379.7 (263.7)
	3	0.200 (0.0002)	1474.8 (304.7)	63 828.6 (3438.9)	172.4 (100.3)
	4	0.200 (0.0002)	1156.5 (227.0)	58 164.4 (227.0)	825.4 (900.5)
	5	0.199 (0.0009)	689.7 (127.3)	29 103.6 (4805.7)	2720.1 (1050.7)
	$\bar{X}$	0.200 (0.0008)	1043.5 (360.9)	48 455.5 (15708.2)	1394.2 (1480.2)
Fractal $H = 0.8$	1	0.199 (0.0007)	54.5 (15.7)	6291.2 (497.5)	5921.9 (1990.7)
	2	0.200 (0.0004)	93.3 (22.9)	1277.6 (1852.5)	8351.3 (2447.4)
	3	0.200 (0.0003)	93.4 (21.7)	1356.7 (2679.8)	7256.7 (2732.2)
	4	0.200 (0.0003)	76.3 (26.6)	11 571.2 (3042.1)	7898.6 (2624.3)
	5	0.198 (0.0009)	44.7 (27.8)	5895.0 (1517.7)	6224.5 (1446.5)
	$\bar{X}$	0.200 (0.0010)	72.44 (30.1)	10 019.4 (3877.1)	7130.6 (2396.2)

The three different maps (random, fractal with $H = 0.2$, and fractal with $H = 0.8$) described in the text and illustrated in Fig. 1. $\bar{X}$, indicates averages across all habitat types; p_h, the proportion of the map occupied by each habitat type; Tc, the number of clusters; Te, the amount of edge; Sav, the area weighted average cluster size. Statistics are based on 10 iterations of each map type.

Table 5
Results of the habitat Case 1 simulations

Habitat optima	Map type	Init	RA		CS	
			Mean	CV	Mean	CV
A	RD	E	<0.01	173.2	0.6	177.9
A	RD	R	<0.01	38.3	4.8	25.3
A	H2	E	6.8	38.9	44.6	58.8
A	H2	R	11.0	13.6	40.9	49.9
A	H8	E	17.0	22.6	6841.2	37.4
A	H8	R	19.4	0.9	6843.9	36.3
B	RD	E	20.5	18.5	446.3	52.9
B	RD	R	20.1	5.3	137.8	19.7
B	H2	E	18.1	22.2	1494.7	35.7
B	H2	R	18.7	6.7	475.9	45.3
B	H8	E	20.9	32.6	9186.5	57.9
B	H8	R	20.1	1.0	7711.1	32.2
C	RD	E	13.1	29.6	871.2	61.3
C	RD	R	13.1	29.6	871.2	61.3
C	H2	E	17.9	34.2	3095.8	98.6
C	H2	R	19.1	2.5	535.6	40.3
C	H8	E	23.2	44.7	9797.5	88.6
C	H8	R	20.1	0.7	7041.7	34.6
D	RD	E	22.1	49.2	7158.1	79.7
D	RD	R	22.1	49.2	7158.1	79.7
D	H2	E	20.8	42.6	6157.1	74.5
D	H2	R	19.2	2.6	753.9	33.3
D	H8	E	19.6	20.6	7287.8	36.3
D	H8	R	20.1	0.9	7495.2	29.6

Mean relative abundances (RA) and cluster size (CS) for species three averaged over 10 iterations.

simulations the average species cluster sizes were greatest on H8 maps and least on the random maps (Table 5). Simulations with random initialization were less variable for both relative abundance and species cluster size. The initialization effect was particularly noticeable in the narrow niche breadth simulations (series *A*, Table 5) because the limited niche width does not allow species to reach all available sites. The effect of initialization were strictly spatial and the ANOVA on abundance levels (Table 6) shows that the method of initialization had a negligible effect on overall levels of abundance. Although the method of initialization was of no consequence for species cluster sizes for cases *C* and *D* on random maps, it remains important for fractal maps when species were initialized from the edge. In these cases, the final species distributions are characterized by consistently larger cluster sizes. Habitat contiguity also had a significantly greater effect on species cluster sizes than niche breadth (Table 7), but this pattern was reversed for species abundance (Table 6).

Table 6
Analysis of variance of mean abundance levels for Case 1 simulations ($N = 120$, $R^2 = 0.78$)

Source	df	Mean-square	*F*-ratio	*P*
N	3	764.1	65.8	0.0001
M	2	213.6	18.4	0.001
I	1	12.4	1.1	0.3
N × M	6	206.4	17.8	0.001
N × I	3	8.8	0.8	0.5
M × I	2	2.8	0.2	0.7
N × M × I	6	2.7	0.2	0.7
Error	96	11.6		

N, niche breadth (the number of habitat types potentially occupied by each species); M, map type; I, species initialization method. See text for details.

Table 7
Analysis of variance of mean cluster size for Case 1 simulations ($N = 120$, $R^2 = 0.88$)

Source	df	Mean-square	F-ratio	P
N	3	39 080 720	14.2	0.001
M	2	290 520 000	105.7	0.0001
I	1	69 265 713	25.2	0.001
N × M	6	6 801 042	2.5	0.03
N × I	3	8 802 324	3.2	0.03
M × I	2	11 993 198	4.4	0.02
N × M × I	6	2 064 421	0.8	0.61
Error	96	2 749 855		

N, niche breadth (the number of habitat types potentially occupied by each species), M, map type, I, species initialization method. See text for details.

Table 8
Effect of variation in dispersal distance on patterns of coexistence for two species differing in their relative level of fecundity

Dispersal radius for species 1	Abundance levels[a] (Year 200)		# C
	Species 1	Species 2	
1	0 (0)	4.8 (54.4)	0
3	43.3 (13.4)	45.4 (10.3)	10
6	54.1 (9.3)	42.9 (12.9)	10
12	59.2 (6.9)	40.7 (10.4)	10
24	61.4 (6.3)	38.6 (10.0)	10

Dispersal radius is the number of cells that may be reached by species 1. Dispersal distances were drawn from the uniform distribution and seed rain was not simulated. The relative fecundity of species 1 was 10 and that of species 2 was 20. The disturbance regime for all simulations was: $e_y = 0.02$, $f_y = 0.2$, $p_{cg} = 1.0$ (see Table 3). # C, indicates the number of simulations out of 10 replications that resulted in both species persisting until year 200.

[a] Abundance levels are the percent of the map occupied by that species. The number in parenthesis is the coefficient of variation (mean/S.D.).

11.3. Case 2: interactive effect of disturbance, dispersal, competition and landscape heterogeneity

11.3.1. Case 2a

When lottery models are used to simulate plant competition, even slight differences in fecundity between otherwise similar species will result in the eventual displacement of the less fecund species. However, differences in dispersal may off-set this disadvantage if the landscape is periodically disturbed. A series of experiments with two species that differed in relative fecundity (10 versus 20 for species 1 and 2, respectively) and variable levels of dispersal were performed on a landscape with a fixed disturbance regime ($e_y = 0.02$, $e_f = 0.2$, $p_{cg} = 1.0$; Table 8). The greater fecundity of species 2 resulted in the displacement of species 1 when dispersal distances were equal (radius of 1, Table 8). However, a slight increase in dispersal for species 1 (radius = 3) resulted in the coexistence of the 2 species. Additional increases in the level of abundance of species 1 occurred with increasing dispersal range, with abundance levels a monotonic function of dispersal distance (Fig. 4). Because the simulation of disturbance in CAPS requires that grid cells be occupied before they can be disturbed (e.g. a harvest scenario), the slow rate of recovery of species 2 from disturbance results in a decline in their abundance after species 1 goes extinct (see first case in Table 8).

11.3.2. Case 2b

Simulations with variable levels of disturbances (Table 3) showed that species 2 was the superior competitor in the absence of disturbance, causing in the rapid extinction of species 1. Extinction of species 1 also occurred for the four sets of simulations where disturbances were infrequent ($f_y = 0.05$, disturbances occurring once every 20 years) because species 1 had declined to very low levels before the first disturbance occurred in year 21.

A more interesting pattern was seen when disturbance frequency was 0.2 (once every 5 years). In all four of these cases species 1 survived until year 200. Because species 1 could disperse 12 times further then species 2, species 1 was able to quickly occupy space cleared by disturbance. As a result, survival of species 1 was enhanced by a higher disturbance frequency and extent. The spatial pattern of the disturbance was also an important determinant of observed levels of coexistence. More highly aggregated disturbances ($p_{cg} = 1.0$) have a higher ratios of interior area to edge than less aggregated disturbances ($p_{cg} = 0.4$). Since species 2 can only disperse to adjacent cells along the edge, it is at a disadvantage when disturbances are

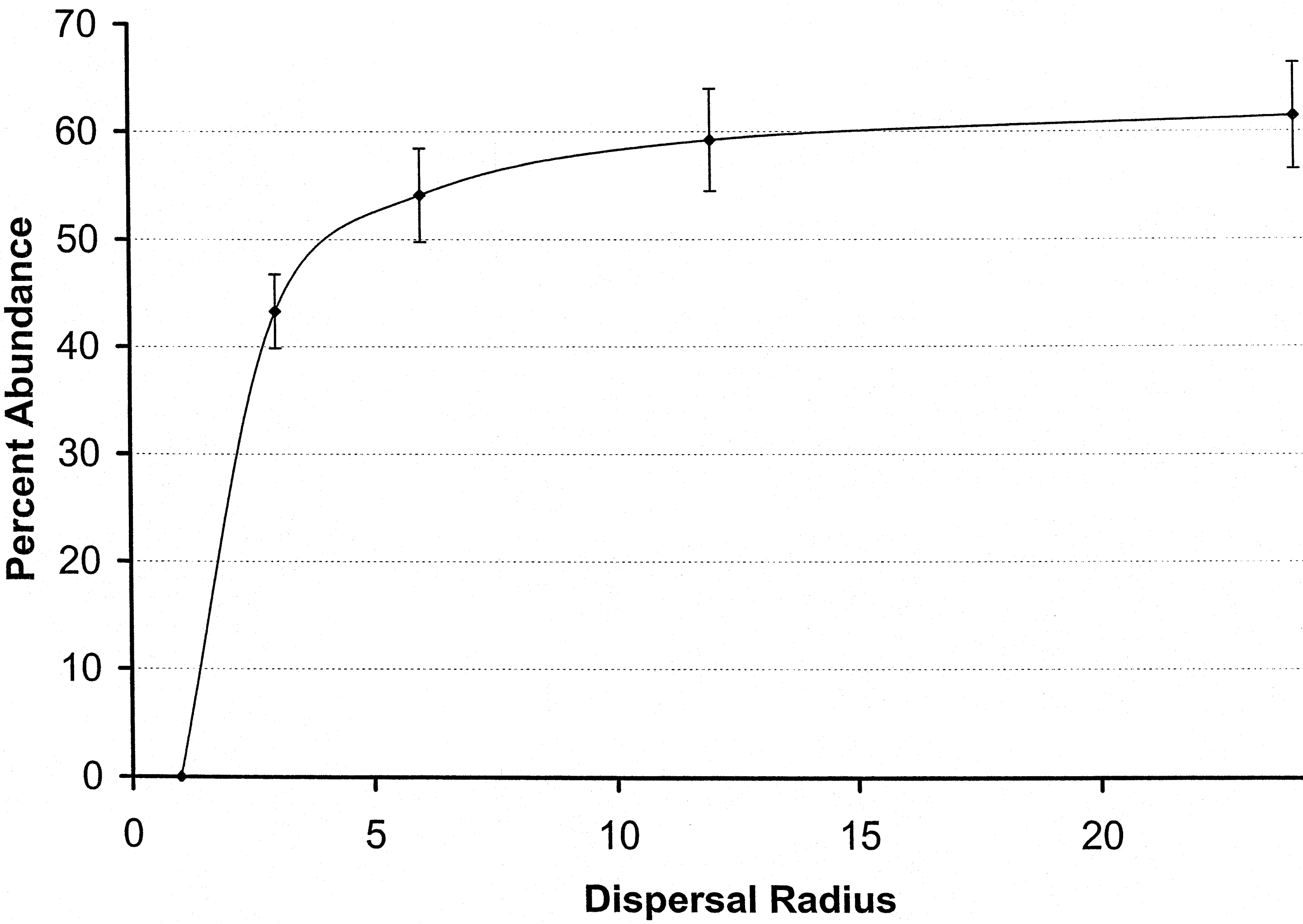

Fig. 4. The simulated increase in abundance of species 1 as a consequence of increasing dispersal distances. All simulations occurred on maps with two species in their relative levels of fecundity (species 1 = 10, species 2 = 20), and periodic disturbances ($e_y = 0.02$, $f_y = 0.2$, $p_{cg} = 1.0$). See text for additional details.

large and contiguous. In the extreme case, with high extent ($e_y = 0.4$), frequency ($f_y = 0.2$), and probability of cluster growth ($p_{cg} = 1.0$) species 2 was greatly reduced in abundance and became extinct in 3 of 10 simulations. As shown in the Case 2a simulations, repeated large disturbances resulted in the progressive loss of territory for species 2 after species 1 had gone extinct.

11.4. Case 3: interactive effects of disturbance and landscape heterogeneity

The simulations in Case 2a and 2b did not consider the effect of the heterogeneity of landscape pattern on species abundance levels. To assess possible effects of landscape patterns on species coexistence, four sets of simulations with variable levels of habitat optima were performed on the 10 $H = 0.8$ fractal maps. All simulations were performed with the same disturbance regime as Case 2a ($e_y = 0.02$, $f_y = 0.2$, $p_{cg} = 1.0$, Table 9). The two species that were simulated had the same life history parameters as the Case 2b simulations. The differences between each set of simulations was the habitat optima values contained within the iopt matrix. When the iopt values are constant across species and habitat types (the first set of simulations in Table 9) the outcome of the seed lottery in CAPS is unaffected by the underlying heterogeneity of the landscape. However, as differences in iopt are increased between species and across habitat types the heterogeneity of the landscape may play a more dominate role in the outcome of competition and the patterns of species abundance. The three sets of simulations with increasing differences in habitat optima show progressive increases in the level of abundance of species 1. In the most extreme set of simulations (last line of Table 9) the habitat optima values of species 1 are four times greater than species 2 on habitat type 1 (the reverse situation occurs for species 2 on habitat type 5). These differences result in large areas of the map being dominated by a single species. Because species 1 can quickly invade and hold areas that are disturbed, the combination of landscape heterogeneity and disturbance provides an additional advantage that allows abundance levels of species 1 to increase with increasing impact of habitat heterogeneity.

Table 9
Effect of variation in habitat preferences ($\text{iopt}_{j,h}$) on patterns of coexistence for two species that differ in their relative level of fecundity

SN	iopt_{1h}	Abundance levels[a] (Year 200)		# C
		Species 1	Species 2	
1	[2.5 ... 2.5]	59.2 (6.9)	40.7 (10.4)	10
2	[3.0 ... 2.0]	63.6 (9.6)	36.4 (15.2)	10
3	[3.5 ... 1.5]	66.9 (9.4)	33.1 (19.6)	10
4	[4.0. .. 1.0]	70.3 (9.3)	29.2 (21.4)	10

Only the first and last elements of the row in the iopt matrix, corresponding to the habitat preferences for species 1, are shown in column 1. The elements of iopt matrix for species 2 are the reverse of those for species 1. The disturbance regime for all simulations was: $e_y = 0.02$, $f_y = 0.2$, $p_{cg} = 1.0$ (see Table 3). SN, is the simulation number; # C, indicates the number of simulations out of 10 replications that resulted in both species persisting until year 200.

[a] Abundance levels are the percent of the map occupied by that species. The number in parenthesis is the coefficient of variation (mean/S.D.).

12. Discussion

Contemporary changes in the structure of plant communities, and the increasing uncertainty in the response of these communities to a variety of new disturbances, has become a pressing concern as human alteration of the environment has reached global dimensions (Chapin et al., 1998; Naeem et al., 1995; Sala et al., 1999). Although it is clear that species assemblages—and changes in these assemblages with time—are a complex function of a large number of physical and biological variables, little progress has been made in our ability to make unambiguous predictions of change in space and time. Part of the problem is simply the scope and scale of the issues. Local communities are often shaped by specific spatial arrangements of ecological resources, are subjected to a diversity of disturbance regimes and composed of unique species assemblages. Because of the practical limitations of empirical studies, it is rare that more than 2 or 3 of these factors can be investigated in a single study (Caswell, 1988).

Ecological models, which have fewer practical constraints, have either concentrated on the details of specific systems or provided general results for a limited subset of the relevant variables. Thus the determination of the controls of community structure remains one of the most important questions in ecology (Tanner et al., 1994).

CAPS was developed as a general model for the exploration of the response of diverse species to the effects of the spatial variation of ecological resources, and the changes in the frequency, extent and pattern of disturbances on the subsequent formation of plant communities. CAPS was especially formulated so that large spatial arrays could be rapidly simulated and the variables which control dynamics systematically altered to determine the importance of spatial interactions on patterns of species coexistence. We have used CAPS here to examine three sets of questions: (1) How are different species affected by the spatial variation of landscape resources? (2) What effect does the disturbance regime (including spatial patterns of disturbance) have on the outcome of competitive interactions among species? and (3) Is there a significant interaction between landscape heterogeneity and disturbance on the outcome of competitive interactions?

12.1. The effect of spatial variation of landscape resources

Species are distinguished in CAPS by differences in their life-history characteristics which include: habitat preferences, levels of relative fecundity, and dispersal characteristics including seed rain (Table 1). Small differences in fecundity provide a competitive advantage that results in species displacement when habitat heterogeneity is absent (e.g. simulation 1, Table 3). However, conditions may exist where separation of species in space produces patterns of coexistence not predicted by non-spatial (mean-field) models.

The interaction of species life-history characteristics with the distribution of landscape patterns were systematically varied to provide a range of conditions over which the effects of competition could be analyzed. Three types of maps were generated (i.e. random, fractal with $H = 0.2$, and fractal with $H = 0.8$, Fig. 1). Each map was composed of five different habitat types with each habitat type occupying exactly 20% of each map (see values of p_h, Table 4). This method of map generation allowed the investigation of pattern effects independent of those due to differences in amount of habitat. Analysis of map patterns showed that the random maps were more fragmented than the fractal maps and, among the fractal maps, the $H = 0.2$ maps were more fragmented than the $H = 0.8$ maps (Table 4).

Simulations of species differing in their habitat optima (Table 5) showed that habitat fragmentation had a significant impact on species abundances and spatial distributions, especially when species habitat optima were set at the narrowest level (i.e. each species restricted to a different, single habitat type). Random maps had the lowest level of species abundance and cluster sizes because suitable habitat was distributed in a manner that prevented species from reaching all sites. For this set of simulations wide distances between areas with suitable habitat prevented species from achieving their expected levels of abundance as predicted by percolation theory (Gardner et al., 1992; Plotnick and Gardner, 1993). Under these conditions the results of a non-spatial model would not apply. However, as the range of habitat optima of each species increased (the B, C, and D series of simulations, Table 5), increasing amounts of habitat became available and the levels of species abundance approached the expected value of 20%. Nevertheless, the distribution of species cluster sizes (Tables 8 and 9) still reflect the underlying patterns of the landscape, with the greatest effect noticeable for the fractal maps with $H = 0.8$.

Two methods of setting initial species distributions were employed for these simulations: random initialization (species placed at random throughout the map and edge) or edge initialization (species randomly placed along the map edge). Random initialization resulted in species distributions that were highly fragmented, but usually guaranteed that all species were placed near an optimal habitat type. Edge initialization required species to disperse across the map, making characteristics of species dispersal and habitat connectance important. For the narrowest niche (case A, Table 5) only 20% of the landscape is available to each species. The organized patterns of fractal maps (Fig. 1) makes the optimal habitat relatively accessible and species abundances are highest on these landscapes. The method of map initialization remained significant even after 200 years, with all 2-way interaction terms of the ANOVA (Table 7) between the method of map initialization, species life-history characteristic and map type significant. However, the observed effect of initialization were strictly spatial, and abundance levels were unaffected by the method of initialization (Table 6). Thus, above the percolation threshold habitat contiguity had a significantly greater effect on species cluster sizes than did differences in niche breadth.

12.2. The effect of disturbances on patterns of species coexistence

Competitive exclusion, and thus the reduction in biodiversity, is the inevitable consequence of competition among species if they reside in the same place at the same time. However, disturbances may allow coexistence of competitors, as predicted by the intermediate disturbance hypothesis (Allmon et al., 1998; Connell, 1978; Denslow, 1985; Tilman, 1999) when disturbances are of sufficient frequency and size. Unfortunately theory does not provide an unambiguous definition of ‘intermediate’ for different species assemblages. However, the systematic variation of the disturbance regime can be performed with CAPS to identify sets of disturbance parameters that allow coexistence among competing species.

The disturbance regime is defined in CAPS by three parameters: The disturbance frequency (f_y) or the fraction of years that a disturbance occurs; the average yearly extent of disturbances (e_y); and the spatial pattern of the disturbance which is controlled by p_{cg}, the probability of cluster growth. When p_{cg} is small then dendritic disturbances will result, while larger values of p_{cg} produce contiguous areas that are totally disturbed.

Identification of disturbance parameters that allows coexistence was achieved by a factorial set of simulations for two competing species differing in relative fecundity and dispersal. The results showed that species 2 (higher relative fecundity) always displaced species 1 (the better disperser) for simulations that either lacked disturbances or where the disturbances were infrequent (simulation numbers 1–3 in Table 3). However, more frequent disturbances ($f_y = 0.2$) resulted in coexistence of both species (simulations 4, 5, 7 and 9). When disturbances were large, frequent, and the pattern of the disturbances were spatially contiguous ($p_{\mathrm{cg}} = 1.0$, simulation 9 in Table 3). Under these circumstances species 1 was far more abundant than species 2.

These factorial set of experiments resulted in an ‘intermediate’ disturbance regime for coexistence that was near $f_y = 0.02$, $e_y = 0.2$ and $p_{\mathrm{cg}} = 1.0$. Coexistence was enhanced when disturbances were frequent and the spatial patterns were contiguous. However, other sets of disturbance parameters also produced coexistence for all 10 sets of simulations (simulations 4 and 8 of Table 3). The average size of disturbances (e_y/f_y in Table 3) was not predictive of coexistence, differing among successful sets of simulations by a factor of 2. Thus, even for the this simple two species case a range of parameter values may allow coexistence and satisfy the requirements of an ‘intermediate disturbance regime’ that allows coexistence. Determination of these multiple parameter sets can, at present, only be accomplished by trial and error. Identification of patterns of coexistence among multiple species may be even more problematic, particularly if the criterion for success is to maximize biodiversity. Under these circumstances, multiple sets of disturbance parameters may exist with equal levels of diversity but distinctly different sets of species assemblages. Hopefully, the brute force approach used in CAPS will allow the systematic exploration of disturbances regimes and, eventually, the emergence of a more predictive theory.

12.3. Interactive effects of disturbance and landscape heterogeneity

A final set of simulations were performed to examine the interactive effect of landscape pattern, disturbances and species competition. Once again, 2 species were simulated with the disturbance regime set to the optimal case for coexistence (simulation 5, Table 3). Four sets of simulations were performed with progressively increasing degrees of habitat preference as defined by iopt, the habitat preference matrix. In the first case all values of iopt were constant across species and habitat types. Thus, competitive interactions did not differ by habitat type, and the landscape may be regarded as homogeneous. As the iopt values are progressively altered the nature of competitive interactions will become more dependent on habitat type. In the most extreme case considered (the [4.0 ... 1.0] case, Table 9) the greatest 'niche separation' occurs—and species 1 is twice as likely to succeed on habitat type 1 as species 2. Because the row sum of the iopt matrices were fixed, the spatially averaged competitive interaction was constant across simulations. Although the appropriate mean-field model might predict competitive results similar to simulation 1 in Table 9, the general trend of increase in abundance of species 1 with increasing niche separation would not be predicted by a non-spatial model.

Although the general principles of disturbance effects on patterns of species coexistence are generally understood (Petraitis et al., 1989), there remains insufficient theoretical and empirical insight that can relate landscape heterogeneity, varying disturbance regimes, and species life-history differences to the process of competition mediated coexistence. An example of this difficulty is that general theory predicts that systems that are more diverse should be more resistant to invasion (Levine and D'Antonio, 1999; Stachowicz et al., 1999). However, recent evidence suggests that spatial variation in propagule supply (Levine, 2000) and habitat quality (Stohlgren et al., 1999) can interact to make species-rich sites the most likely candidates for invasion by exotics. It is exactly these relationships which can be easily examined by CAPS to establish the likely patterns of community change.

The simulations presented here have illustrated the importance of spatial dynamics as determinants of patterns of species coexistence. The fact that spatial interactions can be important is, of course, not surprising as many studies have shown that local interactions can have broad range effects (see discussions in Tilman and Kareiva, 1997). These simulations have also shown that in many situations spatial patterns need not be explicitly considered. This trade-off between detail and generality is important and has been the focus of a variety of studies as well (Bascompte and Solé, 1998; Pacala and Levin, 1997). Currently, our ability to identify the conditions were spatial interactions are likely to be important require simulations with models such as CAPs that simultaneously consider a broad spectrum of variables affecting species interactions. Hopefully such investigations will allow scaling relationships to be developed so that changes in pattern and process at local scales can be used to anticipate changes at much broader scales (Levin and Pacala, 1997).

Ultimately, models such as CAPS are most useful when applied to real world situations. Model parameters which describe actual landscapes, the temporal and spatial dynamics of disturbances that have occurred in these landscapes, and the subsequent changes in patterns and abundance of resident species are now being estimated from a series of empirical studies. The amount and distribution of habitat types are being determined using decision tree models (i.e. CART analysis; Clark and Pregibon, 1993; Venables and Ripley, 1994). Key abiotic descriptors (soil type, moisture, elevation, light availability, etc.) that affect plant establishment following disturbances are entered into the CART analysis and ordinal descriptors of habitat patterns are predicted. Habitat preferences (i.e. the iopt values in CAPS) are being estimated from the frequency distribution of plant establishment at previously unoccupied sites within each species dispersal range. Experimental data required for the estimation of the probability distributions of plant dispersal are not available for most species. Therefore, dispersal parameters will be estimated from seed size (Harper et al., 1970), morphology (Sheldon and Burrows, 1973; Greene and Johnson, 1989; Okubo and Levin, 1989), and dispersal mechanism (e.g. wind versus surface transport, vander Wall, 1992). The appropriate dispersal kernel will then be selected and tested against observed distances and patterns of seedling establishment (Clark et al., 1999). Differences in fecundity between species, represented in CAPS in relative terms, will be estimated from the variation in seedling densities occurring in close proximity to the parent plant.

Improvements in CAPS are now underway to consider a broader set of species characteristics. This changes include the simulation of rare, long distance dispersal events including those associated with fat-tailed distributions (Clark, 1998; Clark et al., 1999); dispersal from a fixed species pool outside the simulated landscape (Drake, 1990a,b); and inclusion of long-lived species (e.g. biannual and perennials) with age-dependent variation in fecundity.

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