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Simulated effects of fire, dispersal and spatial pattern on competition within forest mosaics

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Abstract

Simulations representing tree locations on a rectangular grid (cellular automaton) imply that spatial patterns associated with fire, seed dispersal, and the distributions of plants and resources affect forest dynamics profoundly. Simulated fires ignited at random locations in a uniform environment create non-uniform habitats and lead to patches dominated by different vegetation types. Short-range seed dispersal promotes vegetation clumping; fires cause these clumps to coalesce into vegetation zones separated by sharp borders, especially across an environmental gradient. In simulation of competition within vegetation mosaics, tree populations with a competitive advantage still require the intervention of fire to eliminate rivals. Also, the availability of local seed sources enables established tree populations to exclude invaders, but fires can trigger sudden changes in the composition of such systems. In models of simple succession systems, 'climax' vegetation tends to displace 'pioneer' vegetation, even under harsh fire regimes.

Introduction

Spatial distribution patterns of plants and resources and spatially extensive processes, such as fire and seed dispersal, are crucial elements in forest dynamics. But whereas spatial patterns have been subjected to intensive field study (e.g. Pielou 1969; Greig-Smith 1979; Minnich 1983; van der Maarel 1988), most simulation models of vegetation have ignored spatial patterns. Some models have represented space in a limited way by including environmental gradients (e.g. Kessell 1979), such as soil moisture or elevation, but only a few truly two-dimensional vegetation models have been developed. Most have been single-species models or else closely tied to field studies (e.g. Austin 1980; Hobbs & Hobbs 1987; van Tongeren & Prentice 1986; Wilkie & Finn 1988). However, both analytic models (e.g. Leps & Kindlman 1987; Roff 1974) and simple simulations (De Angelis *et al.* 1985; Green *et al.* 1985) suggest that the between-site interactions caused by spatial proceses profoundly affect the course of community dynamics. Thus the manner in which spatial patterns and processes affect the composition and dynamics of vegetation remains a fundamental question to be addressed by simulation.

This study examines the above question at a very basic level, namely competition between two competing vegetation types. The spatial phenomena examined include fire, seed dispersal, and environmental gradients. In order to address the problem systematically, I proceed in four steps of increasing complexity:

(a) spatial and temporal environmental patterns of fire occurrence and their consequences;

(b) competition between similar 'species' in a uniform environment;

(c) competition between similar 'species' on an environmental gradient;

(d) competition between 'species' that have different responses to fire.

The most telling advantage of this approach is that hypotheses about spatial processes can be abstracted and examined independently of any particular plant community. Thus the models do not simulate particular forests; instead they embody features common to whole classes of communities (e.g. 'rainforest').

The models

A convenient paradigm for spatial modelling is the 'cellular automaton' (Wolfram 1984). A cellular automaton consists of an array of cells ('automata') that interact with their neighbours. These interactions produce a rich variety of unpredictable behaviour (Wilson 1988). A cellular automation model of a landscape consists of a fixed array in which each cell represents an area of the land surface (Green 1983; Green *et al.* 1985). Associated with each cell are 'states' that correspond to environmental features, such as plant cover or topography. This approach is appropriate to environmental modelling as it is compatible with common sources of data, such as pixel-based satellite imagery and quadrat-based field observations. Also it enables processes that involve movement through space to be modelled in 'natural' fashion. For example, cellular models of fire spread show that patchy fuel is responsible for a wide range of observed fire shapes and behaviours (Green 1983).

In the models explored here, space is represented by a 50 × 50 grid of cells. The horizontal scale is arbitrary, but may be taken to lie within the range 10 m–100 m (cell diameter), depending on the biological assumptions that are made. For simplicity, each cell is assumed to contain a single plant (at the smallest spatial scale) or a single plant stand (at large scales). Time steps (taken to be single year intervals throughout) are represented by scanning through the array and updating the information for each cell. The information recorded for each cell includes vegetation type and age, time since the last fire, and values of environmental parameters. For simplicity I refer to the vegetation types in a model as 'species', but these 'species' are only notional and usually apply to community types (e.g. 'rainforest') as readily as real plant species.

The forest simulations described here are implemented using a generic landscape model ('MOSAIC') within which particular simulations are defined using an 'ecosystem modelling language' (Green *et al.* 1988). Features not explicitly defined receive default (usually null) settings. For instance, no fires occur unless a fire regime is specified.

Species life history characteristics

Essential characters for each 'species' s include average longevity, fecundity $F(s)$, and age at which plants start reproducing. If pixels in a model are to represent forest stands, instead of individual trees, then 'age' refers to the length of time that a stand of a given type may be expected to persist once established. Fecundity denotes the relative rates of production of propagules by different modelled species and is used to weight probabilities when randomly selecting propagules to colonize vacant growing sites (see below); juvenile plants (that is, ones whose age is less than the specified adult age) play no part in the weighting procedure.

Reproduction, dispersal and establishment

Two modes of supplying propagules to free growing sites are examined here: 'global dispersal', in which seeds of all species are always present to compete for available growing sites, and 'local dispersal', in which free growing sites are colonized by seeds from nearby sources. For local dispersal the decline in numbers of seeds of species s with distance from source is assumed to follow an inverse square law up to the maximum dispersal distance D_s. Both of the above mechanisms occur in nature. In particular, seed dispersal may appear to be 'local' on a large scale, but on a smaller scale may be 'global' for specific areas. No distinction is drawn here between seed rain and other sources of propagules (seeds stored in the soil, root suckers, lignotubers, etc., which may also be local or global. The case in which the spatial distribution of propagules stored in the soil varies independently of plant distribution is not considered here.

Colonization of free growing sites is modelled as a Monte Carlo process. Neither regeneration, nor deterministic replacement of species is assumed. The species that establishes itself on a vacant cell $\boldsymbol{x} = (x,y)$ is chosen at random from all available species s, weighted for fecundity $F(s)$, for number $N(s,\boldsymbol{x})$ of available seed sources, and for viability $V(s,e)$ (see 'environmental gradients' below). Thus the probability $P(s,\boldsymbol{x},t,e)$ of establishment of the species s on a vacant site $\boldsymbol{x}$ at time t is a function of $s,\boldsymbol{x},t$, and e and is given by

$$P(s,\boldsymbol{x},t,e) = W(s)/\textstyle\sum_i W(i)\,, \tag{1}$$

where i ranges over all species and the weight $W(s)$ is given by

$$W(s) = F(s)N(s,\boldsymbol{x})\,V(s;e)\,. \tag{2}$$

For global dispersal the factor $N(s,\boldsymbol{x})$ takes the value 1 for all species at all locations; for local dispersal $N(s,\boldsymbol{x})$ follows the inverse law

$$\begin{aligned} N(s,\boldsymbol{x}) = \textstyle\sum \{&n(s,\boldsymbol{x})/d^2(\boldsymbol{x},\boldsymbol{y}) : \\ &: 0 < d(\boldsymbol{x},\boldsymbol{y}) < D_s\}\,, \end{aligned} \tag{3}$$

where $n(s,\boldsymbol{x})$ is the number (either 0 or 1) of plants of species s occupying site $\boldsymbol{x}$ and $d(\boldsymbol{x},\boldsymbol{y})$ is the distance of $\boldsymbol{x}$ from the vacant site $\boldsymbol{y}$. To ensure that vacant cells are always filled, one can assume that global dispersal still operates as a background mechanism even though local dispersal is the predominant process; that is global dispersal occurs if a vacant growing site has no nearby seed sources.

Environmental gradients

Models may include an environmental gradient. That is, the value of an environmental variable e (e.g. rainfall, soil moisture, salinity, altitude) is assumed to vary linearly, either through time or space (as given by position on the x-axis). The exact nature of the variable e is left unspecified, but its effect on the life history characteristics of each species s is explicitly defined by giving limits $(e_{\min}, e_{\max})$ of the species' range, and limits $(e_{\text{low}}, e_{\text{high}})$ of its optimal growth range. These limits allow models to simulate the decreases in fecundity, seed viability, or survivorship that may occur near the edges of a plant species' range. In computation (see above) these decreases are represented by a 'viability factor' $V(s,e)$, which is given by

$$V(s,e) = \begin{cases} 1, & \text{if } e_{\text{low}} < e < e_{\text{high}} \\ (e - e_{\min})/(e_{\text{low}} - e_{\min})\,, & \text{if } e_{\min} < e < e_{\text{low}}\,, \\ (e_{\max} - e)/(e_{\max} - e_{\text{high}})\,, & \text{if } e_{\text{high}} < e < e_{\max}\,, \\ 0, & \text{otherwise.} \end{cases} \tag{4}$$

This viability factor is used to simulate the effect of environment on life history processes. The only processes considered in this study are reproduction and establishment.

Fire regime

Fires ignite at random locations and are elliptical in shape. Their frequency and size have poisson and negative exponential distributions respectively (constant values may also be defined). The fuel code (representing fuel loading) of each species indicates whether or not fires can ignite in that vegetation type. The fire response defines the post-fire time interval (for each cell) during which each species can grow and reproduce. For each individual cell, this feature operates as a local environmental gradient in time (see (3) above).

Boundary conditions

In all model runs used here the initial distribution of plants was defined to be either a uniform cover of a single species, or else a random mixture of all species. To minimize edge effects during model runs, the walls of the cell grid are absorbing. That is, all processes stop at the boundary. Thus the whole grid mimics an isolated region of forest. Models are run for a selected number of simulation years, starting at time zero.

Patterns of fire occurrence

Before looking at vegetation dynamics, we need to understand how fire affects an environment. That is what spatial and temporal patterns of fire occurrence might be expected in a plant community? There are three cases to consider: (a) uniform fuel types, without fuel replacement; (b) uniform fuel types, with fuel replacement; (c) mixed fuel types, with fuel replacement.

Uniform fuel type – no fuel replacement

The area burnt by a series of fires (with no fuel replacement) cannot be predicted exactly, but the following simplifying assumptions yield upper and lower estimates:
(i) that no fuel replacement occurs;
(ii) fires spread if and only if they ignite on sites containing fuel;
(iii) average fire size is a fraction a of the total area in the region (e.g. $0 < a < 1$, and the area actually burnt is reduced if the fire overlaps a previous burn);
(iv) there are no boundary effects.

An upper estimator $B(n)$ of the area that has been burnt after n fires is obtained by assuming that fires never overlap, so the area $a(n)$ burnt out by the n^{th} ignition is either 0 or a, depending on where the ignition occurs. The probability of each value occurring is determined by the total area that has already been burnt, so

$$B(n) = 1 - (1 - a)^n , \tag{5}$$

which is accurate if n and a are both small. A lower estimator $b(n)$ is obtained by assuming that ignited fires always burn out an area that is proportional to the area of unburnt fuel remaining. This assumption (valid if either n or a is large) yields

$$b(n) = 1 - 1/(na + 1) . \tag{6}$$

Equations (5) and (6) provide maximum likelihood estimates for small and large values of n respectively. Simulation confirms the accuracy of the estimates (Fig. 1a) and shows that the true curve drifts from the upper to the lower estimate as n increases.

If areas burnt are compared with numbers of fires, rather than numbers of ignitions, then considerations like those above yield the upper estimator $B'(n)$ of area burnt

$$B'(n) = na , \tag{7}$$

where n now represents the number of fires that have occurred. Equation (5) now gives a lower estimate of the total area burnt after n fires. Simulation (not shown) again confirms these estimates.

If a is small (<0.5), then making fire size random in the above simulations (cf assumption (iii) above) has little overall effect on the frequency/area curve. If a is large (>0.5), then edge effects lead to a wider variation in the number of fires required to burn the entire area than is the case with small fires.

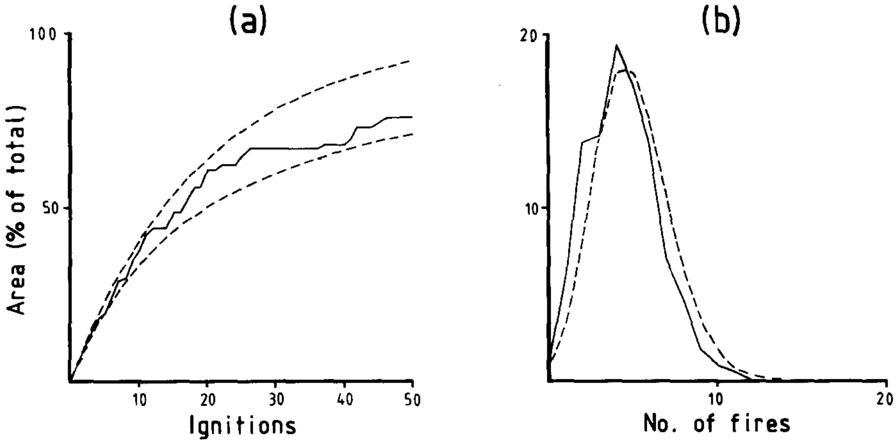

Fig. 1. Fire occurrence patterns in a uniform environment. (a) Proportion of the total area burnt as a function of the number of ignitions that occur before fuel is replaced. Fires burn only if fuel is available at the ignition point; each destroys 5% of the total area. The solid line denotes simulation results; the dashed lines denote statistical estimators (see text). (b) Distribution of fire frequencies after 100 fires are ignited (with fuel replacement). Each fire destroys 5% of the total area. The resulting vegetation distribution is shown in Fig. 2.

Uniform fuel type – fuel replacement

Suppose now that fuel is replaced between fires. Then in the course of a series of fires some locations would be burnt once, others twice or more, and some locations would not be burnt at all. Assuming randomly located ignitions and constant fire size, the distribution of fire frequencies should be binomial with mean na and variance $na(1 - a)$. Simulation (Fig. 1b) confirms that the distribution of fire frequencies is approximately binomial, but the realized mean is slightly smaller than its expected value because of edge effects (cf assumption (iv) above).

Mixed fuel types (with fuel replacement)

The above simulations imply that, even in a uniform environment, many different fire regimes may be experienced by sites within the forest community. Furthermore, the frequency distribution in Fig. 1 implies that within a uniform region, sites experiencing similar fire frequencies occur in patches whose total areas are predictable. The consequences of these results for vegetation pattern can be seen in simulation runs that classify plant cover by its post-fire recovery time. For example, if we assume that burnt sites are at once occupied, then starting from uniform vegetation, the random placement of fires rapidly breaks up the simulated community into patches dominated by stands of different ages (Fig. 2a). The effect of random fire size (Fig. 2b) is to make the size and shape of the patches irregular. In the following sections I consider the dynamics of these patches and the effect of relaxing assumptions, such as non-uniform location of ignitions.

Inter-species competition in a uniform environment

Here I examine how spatial distributions of plants, together with the spatial processes of dispersal and fire, affect inter-species competition, first in a uniform environment, and then in environments that vary in either space or time.

Once a plant occupies a site it normally excludes other plants from that site. This process is a contest ('interference competition') to establish propagules on free growing sites as they become available. Other forms of competition (e.g. 'scramble' for scarce resources) are not considered here. Of course, understorey plants normally coexist under the shade of dominant trees,

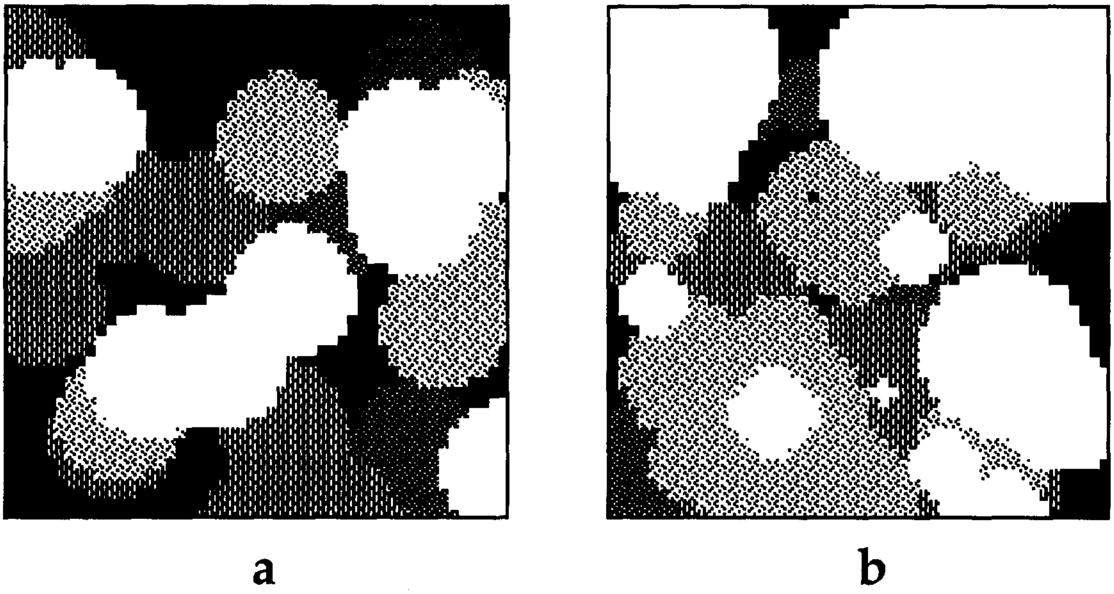

Fig. 2. Maps of simulated environments resulting from the fire frequency distribution of Fig. 1b, assuming that a single fire each year (over a 100 year period) burns 5% (on average of the total area: (a) fire size is constant; (b) fire size is random (follows a negative exponential distribution). The intensity of shading indicates the time that has elapsed since each site was last burnt, ranging from 0–20 years (white) to 80–100 years (black). The spatial scale is arbitrary within the range 10–100 m per cell.

but I consider only competition between, say, overstorey species. Also direct interactions (e.g. shading) between landscape 'cells' usually occur only at the scale of individual plants (say 1–10 m), whereas at the scale of whole forest stands (say 10–100 m), direct competitive interactions between landscape 'cells' are generally minor.

Simulations show that the dynamics of competition in vegetation mosaics can be complex. Consider two similar species competing in a uniform habitat (Fig. 3). Despite the restrictive assumption that only one species may occupy any individual site at a given time, neither species is eliminated. The assumption that seed dispersal is global – that is, propagules of both species are always available to colonize vacant growing sites (empty cells in the model) – leads to uniformly random distributions of the two species (Fig. 3a), whereas local dispersal gives rise to clumped distributions (Fig. 3b). However, in both systems, the populations quickly become roughly equal in size, even if one starts out much larger than the other. Although the spatial patterns slowly change, with patches growing, moving, or breaking up in random fashion, the population sizes fluctuate only slightly after reaching equilibrium (not shown). The only difference in the dynamics of the two systems (not shown) is that if dispersal is global (either for both species or for the invader only), then a community composed initially of just one species can be successfully invaded by the other, but if dispersal is local (either for both species or for the invader only), invasion is impossible because no seed sources are available for the invader.

In a series of model runs (not shown), simple changes to the above models changed the equilibrium, but did not lead to the elimination of one or other species. Because either species can always reappear on freshly cleared sites, competitive exclusion is demonstrably impossible with global dispersal, so I confine this discussion to local dispersal. If one species has greater fecundity than its competitor, then the system soon settles into an equilibrium with the population sizes roughly proportional to the relative fecundities (not shown). In these runs, the rival's fecundity had to be more than 100 times greater

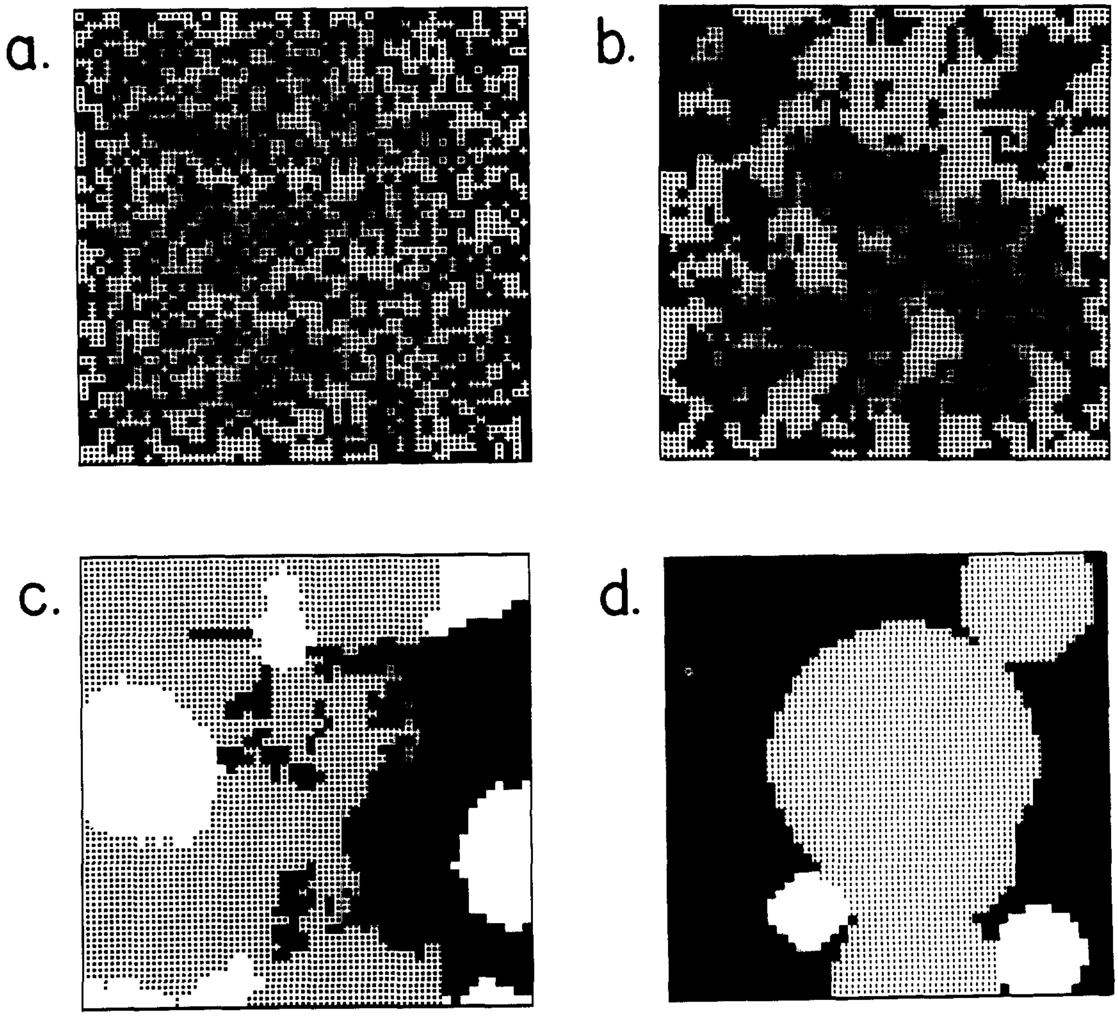

Fig. 3. Distribution patterns (after 200 simulation years) of two vegetation types competing in a uniform environment. The two species are represented by black and by shading The blank areas have been burnt recently. (a) seed dispersal is 'global' and no fires occur; (b) seed dispersal is 'local' and no fires occur; (c) seed dispersal is 'local' and fires occur regularly; (d) as in (c), but fires can ignite in one vegetation type only. The spatial scale is arbitrary within the range 10–100 m per cell. See the text for further explanation.

before the suppressed species was eliminated. That is, a small 'competitive advantage' allows one species to outnumber its rival, but not to eliminate it. The suppressed population is able to survive because it forms clumps. Within such clumps its lower fecundity is offset by the proximity of seed sources to any sites within the clump that fall vacant when individuals die.

Fire acts as a space-creating mechanism in the above systems. For global dispersal, the only effect is to increase the variance in population sizes about their equilibrium values, since burnt patches are soon filled by a mixture of the two competing species (not shown). However, with local dispersal, the species have to invade cleared areas by gradually spreading inwards from the fringes. This process creates larger patches, which coalesce into regions dominated by one or other of the two species (Fig. 3c). Moreover, fires allow a species with a competitive advantage to eliminate its rival, since a single fire can wipe out the patches within which the smaller population becomes concentrated (not shown).

A crucial change to the above fire-prone system is to restrict ignitions to sites occupied by just one of the species (but once ignited, fires still spread through sites occupied by either species). With this change, fire generated patches grow much larger, so that the whole community breaks up into solid regions occupied by one or other of the competing species (Fig. 3d), although the regions themselves gradually shift in size, shape and location.

Competition on environmental gradients

Environmental gradients may occur either in space or in time. Spatial gradients include such environmental features as altitude, soil moisture, salinity, and nutrient levels. Environmental gradients in space have been of great interest to ecologists because they create spatial patterns that expose the mechanisms of inter-species competition to view (Pielou 1969). Environmental gradients in time include such well-known phenomena as climatic change (e.g. increasing temperature or rainfall), increasing aridity, and encroaching salinity.

Gradients in space

Here I examine ecosystems consisting of two competing plant populations that are identical in all respects, except for their range of tolerance to some environmental factor that changes in space. The environmental gradient is represented by a variable e that varies linearly in value (along the x-axis) from 0 to 100 (arbitrary units). On this scale, the range of species 1 has the limits $e = 0$ to 80, with its optimum range being $e = 0$ to 60; the range of species 2 has the limits $e = 20$ to 100, with its optimum being $e = 40$ to 100. Thus the modelled system contains environments ($e = 0$ to 20 and $e = 80$ to 100) in which only one of the two competing species can survive and environments ($e = 20$ to 80) in which they compete against one another. The effects of this gradient on fecundity and viability of propagules for each species are combined into the single parameter V (equations 1 and 2). Also I assume that established trees survive unless e is outside their allowable range, whereupon the trees automatically die.

If we assume that dispersal is 'global', then the two populations intermingle freely and their ranges merge smoothly into one another (Fig. 4a). This pattern results irrespective of whether or not fires occur. A similar pattern results from a system in which dispersal is local (with or without

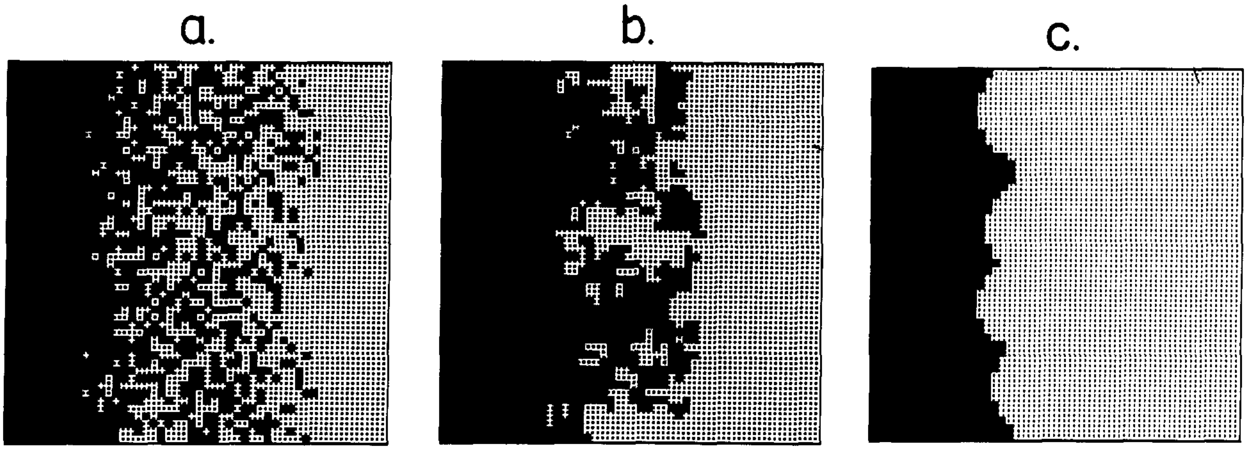

Fig. 4. Distribution patterns (after 200 simulation years) of two vegetation types competing on an environmental gradient in space (running from left to right on the figure) and with fires occurring at regular intervals: (a) seed dispersal is 'global' and fires can ignite anywhere; (b) seed dispersal is 'local' and fires can ignite anywhere; (c) as in (b), but fires can ignite only in the vegetation type on the right. See the text for further explanation.

fire), except that the transition zone is patchier and the sites occupied by a particular species tend to be connected (Fig. 4b).

The above system can be changed in three ways to create sharp borders between the species ranges; all require that seed dispersal be local. First, if fires can ignite in only one of the two vegetation types, then the system resembles that which produced the large regions of Fig. 3d. But in this case the environmental gradient fixes the regions in space, giving rise to the familiar phenomenon of zonation, that is a sharp boundary separates regions dominated by each population (Fig. 4c). Note that the border trends to be pushed towards the extreme environmental limit of the fire-prone population (Fig. 4c). Second, if the overlapping portion of the two species' potential ranges is reduced, then the region within which they compete becomes narrow, thus producing a 'sharper' boundary (not shown). In the limit (no overlap), the boundary is inevitably a straight line, reflecting the effect that scale can have if the environmental tolerances of species are narrow and the environmental gradient is steep. Third, sharp boundaries also occur when one species has a competitive advantage (greater fecundity, way) over its rival. In this case, the boundary is pushed closer to the limits of the favoured species, so that it occupies more territory. In this sense, fire-prone vegetation may be said to have a competitive advantage.

Gradients in time

To examine the dynamics of simulated systems on a time gradient, the model setup was identical to that for a spatial gradient, except that the environmental parameter e changed in time instead of space. Another essential change was to allow global dispersal to occur if no local seed sources were available; otherwise an invading population would not even be able to colonize an empty model grid. The models thus represent the case of an established population that is increasingly 'stressed' by a changing environment, which favours an invading competitor. This 'stress' is here represented by propagule viability, which decreases in response to changes in the environmental parameter e (see equation 4).

In the absence of fires global dispersal allows the invader to establish itself freely anywhere and the relative sizes of the two competing populations are simple functions of the changing viability of their seeds in response to the gradient (Fig. 5a). If local dispersal applies, then the competitive advantage of the established population is so great that the invading species cannot become established until the environment is so severe that all of the existing plants die (Fig. 5b). There is then a sudden switchover from one population type to the other.

Adding fire to the system makes virtually no difference to the overall behaviour pattern in the case of global dispersal (Fig. 5c). If local dispersal

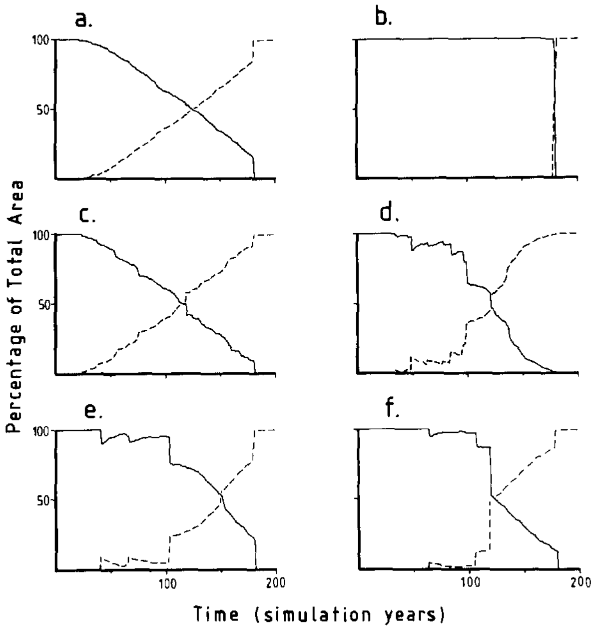

Fig. 5. Populations competing on environmental gradients in time. Solid lines indicate size of an established population; dashed lines indicate the size of an invading population. Both populations behave identically, apart from their environmental preferences, which overlap. (a) global dispersal, no fires; (b) local dispersal, no fires; (c) global dispersal, fires small but frequent; (d) local dispersal, fires small but frequent; (e) local dispersal, fires intermediate in size and frequency; (f) local dispersal, fires large and rare. See text for further explanation.

predominates, then frequent small fires still permit a more or less smooth transition in population numbers (Fig. 5d), but during the early stages the invading population is suppressed between fires by its more abundant competitor. This suppression of the invading population becomes more pronounced as fires become less frequent and bigger in size (Fig. 5e, 5f). Also, in the course of the invasion the community becomes patchy, with the two populations dominating different areas (cf Fig. 4). An important aspect of the transition in dominance is that the switchover occurs after halfway through the model run. That is, the invading population is always at a disadvantage because it must achieve clear competitive superiority over the established population before its population can 'explode'. This is exactly the pattern (Fig. 5f) that has been observed in pollen studies of plant invasions (Bennett 1985; Green 1987).

As with competition on a spatial gradient, 'sudden' changes in community composition can also be produced by reducing the environmental overlap of the two populations or by giving one species a competitive advantage (not shown). The nature of ecosystems in which populations compete on temporal or spatial gradients are thus analogous, with the important difference that the directionality of time confers on an established population a distinct advantage over any invader. In both cases, fire and the mechanism of propagule dispersal have a great bearing on the resulting dynamics.

Competition between 'species' with different responses to fire

Competition between species takes on a completely new form if the species differ in their post-fire responses. In this section I examine the case of a simple 'successional' system in which one vegetation type (a 'pioneer' species) can establish on newly burnt sites, whereas the competing type (a 'climax' species) can grow only on sites that have been left unburnt for some years. Once again we have two vegetation types competing for space, but the difference is that vacant sites are now recolonized in orderly fashion: the 'pioneer' species always appears first after a site is burnt and is inevitably replaced by the 'climax' species, provided no further fires occur on the site. Examples of such systems abound and include sclerophyll/rainforest woodland in eastern Australia and New Guinea (Gill *et al.* 1981; Gillison 1969; House 1986), forested islands in the Florida swamps (Glasser 1985), and birch-spruce-poplar/beech-maple forests in eastern Canada and USA (Green 1981).

In successional systems such as these, the 'pioneer' vegetation is often fire-prone, whereas the 'climax' vegetation is often fire-sensitive. That is, fires tend to ignite in stands of 'pioneer' vegetation rather than 'mature' forest. Also, 'climax' vegetation that is removed by fire does not regenerate until many years afterwards. We can view simple successional systems of this kind as a competition for space in which the two vegetation types employ different strategies. The 'pioneer' species promotes fire, which creates space for it to occupy, whereas the 'climax' species gains space by displacing the 'pioneer' species. In the following simulations, I try to identify conditions necessary for 'pioneer' and 'climax' vegetation to coexist indefinitely within the same community.

Randomly located ignitions

The starting point for this study was a simple 2-species model comprised of 'pioneer' vegetation, which establishes itself on any site immediately after fire occurs, and 'climax' vegetation, which displaces the 'pioneer' vegetation 50 yr after fire occurs. Further initial assumptions were that fires could ignite in either vegetation type, that on average fires occurred once in 10 years and burnt out 10% of the total area. Other assumptions were that the environment was uniform, that both species had equal fecundity (that is, all individuals produced the same number of seeds per year), that seeding was 'global' (that is, seeds are dispersed over the entire model area), and that the 'climax' vegetation displaced the 'pioneer' vegetation on any site where fire had not occurred for 50 or more 'years'.

After an initial period of adjustment, the average long-term abundances of both 'pioneer' and 'climax' species in the above system (Fig. 6a) is a function of the area burnt per year and of the time that the 'pioneer' species survives before being replaced on individual sites. An important consequence of the random location, size and timing of fires is the inherent unpredictability of short-term population changes. Even if fires of fixed size are made to occur at fixed intervals, they still ignite at random locations, so the effect of each fire on each population cannot be predicted. In many cases, the resulting trends in population size are effectively random walks, with the future course of a trend being unpredictable at any time.

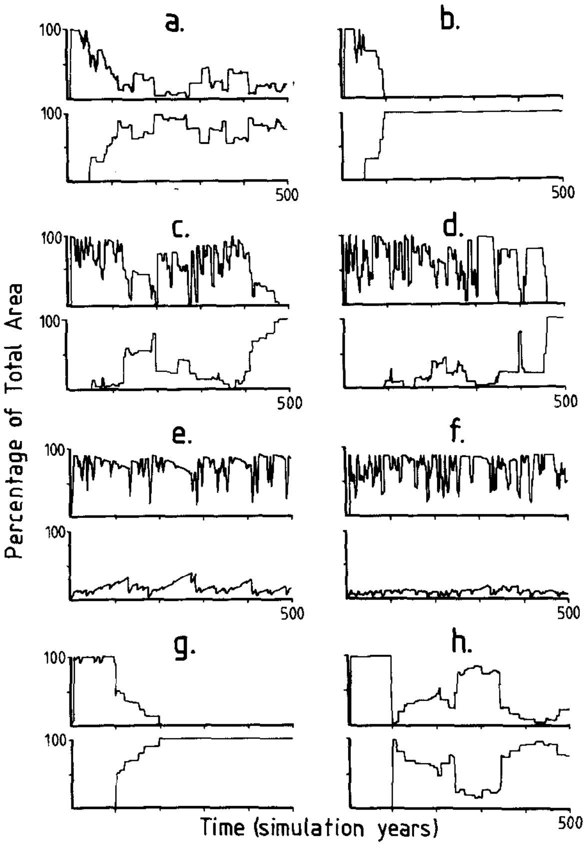

Fig. 6. Population dynamics over a 500 year period in a simulated successional system. Each pair of curves shows abundances of 'seral' vegetation at the top and of 'climax' vegetation below. The assumptions for each run are given in Table 1. Maps showing the final states of runs (a) and (b) are given in Fig. 2c and 2d respectively. (a) Initial run with setup as described in the text. (b) As in (a), but fires do not ignite in 'climax' vegetation. (c) As in (b), but with increased fire size and frequency. (d) As in (c), but with 'local' dispersal. (e) As in (c), but the post-fire time ranges of 'pioneer' and 'climax' vegetation overlap. (f) As in (e), but with local dispersal. (g) As in (f), but with reduced fire size and frequency, and increased fecundity for 'pioneer' vegetation. (h) As in (g), but fires can ignite in juvenile 'climax' vegetation.

No ignitions in 'climax' vegetation

The assumption in the initial model that fires can ignite anywhere is often not echoed in nature, since 'climax' vegetation is often less fire-prone than 'pioneer' vegetation. A series of alternative models, varying the above assumptions (Table 1), was therefore tested. Each of these variant models assumed that fires do not ignite on sites occupied by the 'climax' species (Figs. 6b–6g).

In most cases the model systems are not resilient; that is they lose species after a disturbance. In some cases, the systems are not even viable; that is, the 'pioneer' species disappears even in the absence of disturbance. In nature, regular fires tend to eliminate 'climax' species, yet in the model it is the 'pioneer' species that is eliminated (Fig. 6b). The 'pioneer' population survives for a certain length of time, after which it dies out. This 'survival time' increases as fires are made bigger and more frequent, but even under a harsh fire regime (Fig. 6c) the 'climax' vegetation still eventually eliminates the 'pioneer' vegetation. The instability of the system arises from the high variance in population size of both 'pioneer' and 'climax' species. The only change in the dynamics of the system produced by switching to local rather than global dispersal (Fig. 6d) is that the initial dominance of the 'pioneer' species can be prolonged, but the 'pioneer' vegetation is still eliminated eventually.

On the other hand, allowing the post-fire species time ranges of 'pioneer' and 'climax' species to overlap does permit the 'pioneer' vegetation to survive indefinitely (Fig. 6e), and the

Table 1. Assumptions made in simulations of simple succession[1].

Model run	Fire regime			Fecundities	Dispersal mechanism	Post-fire time ranges of taxa
	Freq.	Size	Ignition site			
(a)[1]	0.1	0.1	anywhere	equal	global	disjoint
(b)	0.1	0.1	not 'climax' veg.	equal	global	disjoint
(c)	0.2	0.5	not 'climax' veg.	equal	global	disjoint
(d)	0.2	0.5	not 'climax' veg.	equal	local	disjoint
(e)	0.2	0.5	not 'climax' veg.	equal	global	overlap
(f)	0.2	0.5	not 'climax' veg.	equal	local	overlap
(g)	0.1	0.1	not 'climax' veg.	unequal	local	overlap
(h)	0.1	0.1	not mature 'climax' veg.	unequal	local	overlap

[1] The full model setup for run (a) is described in the text. The other runs are variants of run (a), with the changes indicated by this table.

combination of both overlapping time ranges and local dispersal makes the system very resilient (Fig. 6f). However, the 'climax' vegetation is still not eliminated from the system. If fires are reduced to their original size and frequency, then even giving the 'pioneer' vegetation several times greater fecundity and dispersal range fails to inhibit the 'climax' vegetation, and the 'pioneer' vegetation is quickly eliminated once again (Fig. 6g).

Ignitions in immature 'climax' vegetation

As the above tests show (Fig. 6a–6g), the assumption that fires will not start in 'climax' vegetation has a destabilizing effect on the dynamics of the successional system. One difficulty in the model lies in the way vegetation is classified. In forest stands, for example, transitions from 'pioneer' to 'climax' vegetation can take years, during which time a stand has intermediate composition. Thus patches of 'climax' vegetation may be ignitable for some time after it becomes established. When this assumption is made, the 'pioneer' vegetation becomes more competitive and is able to persist even under a mild fire regime (Fig. 6h).

Discussion

Studies of spatial pattern in forest communities usually consider only the effects of site-related factors, such as landscape and substrate. The simulations developed in this study show that more attention needs to be paid to dynamic interactions between sites. The results imply that spatial patterns and processes affect forest dynamics profoundly. Moreover, they suggest that a small number of processes, notably fire and dispersal may account for many of the large-scale spatial patterns seen in forest communities.

An important conclusion to be drawn from the simulations of competition in uniform environments is that clumping promotes the persistence of established vegetation. In the absence of disturbance, populations that are at a competitive disadvantage in (say) fecundity tend to persist because they form tight clumps, which offset their disadvantage. On the other hand, populations that invade an established community are at a disadvantage because they lack seed sources within the area.

These results have implications for conservation. For instance, they imply that clumped populations have better chances of survival than scattered populations, that it is important to isolate clumps of species to be conserved from likely competitors, and that circular reserves are better than long thin ones. Moreover, the evident importance of spatial patterns to the persistence of rare species means that models used to plan or evaluate management practices should embody spatial pattern explicitly.

The above results may also help to explain the species richness of undisturbed rainforest communities. Rainforests are often dominated by a few, very abundant populations and scores of rare species (Connell *et al.* 1984), most of which have clumped distributions (Hubbell, 1979; House 1985). Many mechanisms have been proposed for clump formation in tropical rainforests, including post-dispersal predation of seeds (Janzen 1970), density-dependent survival of seedlings (Hubbell 1979), and dioecy and pollination (House 1985). The results of this study suggest that short dispersal range of the seeds of rainforest trees may also be an important mechanism. Field studies confirm that this mechanism causes clumping in at least some types of plant population (Westelaken & Mann 1985). The simulation results also suggest that the prevalence of clumped distributions may be caused by the tendency of clumps to persist once they appear. Thus the tendency to form clumps may enable rare species to survive despite the presence of superior competitors.

The simulations of competition on environmental gradients in space demonstrate several mechanisms by which zonation can occur. The case in which fires ignite in one of the two vegetation types is common in many forest ecosystems. For example, the results are consistent with observations of sharp boundaries between rainforest and sclerophyll forests in North Queensland (House 1986) and New Guinea 1969), between birch and conifer forests in Labrador (Foster & King 1986), and between hardwood/mixed pine forests and sand pine scrub in Florida (Myers 1985).

The simulations of competition on environmental gradients in time suggest a mechanism for the abrupt changes in vegetation composition often seen in palaeoecological studies. For instance in the northward migrations of tree populations in Europe and North America following the retreat of the last great ice sheets about 11000 years ago (Davis 1976), migrating tree populations tended to 'explode' and attain very high abundance levels soon after they first appeared at each site. Pollen studies of the dynamics involved imply that invading species were often suppressed or excluded by populations already present and that major fires, which removed the competitive advantage of populations already present, often triggered 'explosions' by the invading populations (Green 1982, 1987; Ritchie 1985). The results obtained here suggest that it was the prevalence of local seed sources that provided extant populations with an advantage over invaders.

The simulations of succession raise questions about the causes of instability in fire-sensitive vegetation. Fire-sensitive vegetation (which I have called 'climax' vegetation here) is usually thought of as particularly 'fragile' (non-resilient). For example, a patch of mature rainforest that is removed by burning may take several human generations to reappear. In the succession models however, the fire-sensitive 'climax species' not only persisted, but usually succeeded in ousting the fire-tolerant 'pioneer species', even in harsh fire regimes. Three factors appear to explain why real ecosystems behave differently from the simulations. First, real fire regimes are extremely harsh by the standards of the models, especially in any area where fires are set by humans. Second, fire-tolerant and fire-sensitive vegetation may have different site preferences. For instance, fire-sensitive species are often adapted to moist sites where fires usually do not reach. Such site preferences make the dynamics of a successional system more like those of competition on an environmental gradient. Finally, different vegetation types may not be as mutually exclusive as the models assume. In northern Australian rainforests, for example, remnant eucalypts often coexist with rainforest trees and may act as seed sources for regeneration (House 1986).

This study only begins to address the influence of spatial processes on vegetation dynamics. For instance the next logical step would be to extend the present models to multi-species communities. Also, many ideas about community processes are based on models of small plots. The effect on these models of inter-site interactions needs to be examined. The models tested here necessarily contain many restrictive assumptions, such as the absence of soil seed storage, which need to be examined, especially before developing spatial models for management purposes. Other issues that need to be addressed include characterizing the dynamics associated with different types of plant distributions (cf van der Maarel 1988) and with different spatial scales.

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