POTENTIAL RESPONSES OF LANDSCAPE BOUNDARIES TO GLOBAL ENVIRONMENTAL CHANGE

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Abstract. Global change is likely to affect the location, size, shape, or composition of landscape boundaries. Neutral models were used to study two general mechanisms by which landscape boundaries may respond to global change: (1) disturbance regimes may change in response to climate, leading to rapid alterations in landscape structure, and (2) in the absence of disturbance, suitable habitat for different species may move gradually and directionally. The spread of disturbance was simulated as a function of the proportion of the landscape occupied by a disturbance-prone habitat and the frequency (probability of initiation) and intensity (probability of spread) of a habitat-specific disturbance. The effects of changing disturbance regimes on landscape boundaries were different in connected and fragmented landscapes. In connected landscapes, an increase in disturbance intensity caused landscape boundaries to decrease. In landscapes that were fragmented, an increase in disturbance frequency resulted in a decrease in landscape boundaries. The qualitative change in sensitivity to disturbance intensity and frequency occurred when the proportion of disturbance-susceptible habitat was near the critical threshold, p_c, which is approximately 0.6 in random landscapes. Habitat displacement and species migration were simulated as a function of the proportion of available landscape occupied by a community, migration (probability of colonizing adjacent cells), extinction (probability of the community becoming locally extinct), and the rate at which potential habitat (i.e., climatic conditions suitable for establishment) is displaced. The simulated community could track the movement of habitat when the displacement rate was slow, the extinction probability was low, and the migration probability was at least moderate. Spatial lags (distance of remnants from main front) were greatest when extinction was low and the habitat moved quickly. Simulations such as these can be used to identify combinations of parameters which allow successful colonization and those for which community survival becomes critical. Neutral models can generate quantitative, testable hypotheses which can be used to better understand and predict landscape responses to global change.

Key words: climate change, landscape ecology, disturbance, species migration, boundaries.

INTRODUCTION

Dramatic changes in the global environment are predicted to occur within the next century. For example, the projected doubling of atmospheric CO_2 is expected to alter global climate. Current predictions are for an average rise in global temperature of 1.5 to 4.5°C, with greater warming in winter than summer and increased warming with increased latitude. Increased precipitation in high latitudes and decreased summer precipitation and soil moisture in middle latitudes of the northern hemisphere are also predicted. However, the magnitude, rate, and spatio-temporal characteristics of the climatic response are uncertain. Given the strong relationship between climate, atmosphere, soils, biota, and human activities, there is a solid basis for anticipating changes in terrestrial biomes in response to changes in the global environment.

Global change is likely to have substantial effects on landscape structure and function. Ecological processes (e.g., plant succession, nutrient cycling, dispersal, and disturbance) occur in a spatial context and interact with spatial abiotic factors (e.g., topography and soils) to produce complex

patterns on the landscape. These spatial patterns constrain the biota. For example, suitable habitat and resources for different organisms may be delimited by landscape patterns. In turn, biotic interactions may generate or alter the spatial patterns. This interplay between pattern and process is the key focus of landscape ecology (e.g., Risser et al. 1984; Forman and Godron 1986; Turner 1987, 1989; Urban et al. 1987).

The spatial patterning of landscapes implies the existence of boundaries or ecotones between adjacent ecological systems. Boundaries may influence landscape dynamics by exerting control over the flow of energy, materials, and organisms between landscape components (Risser et al. 1984, Wiens et al. 1985, Forman and Godron 1986, Hansen et al. 1988). It has been suggested that research on ecotones should be prominent in exploring the consequences of global change because interactions between various landscape components will often occur at these boundaries (Hansen et al. 1988).

Landscape boundaries may change in location, size, shape, or composition in response to global change. Specific responses will depend upon a variety of factors at many spatial and temporal scales (e.g., edaphic conditions, local weather patterns, present vegetation mosaic and species composition). However, two general mechanisms by which landscape boundaries may change with the global environment can be considered: (1) disturbance regimes may change in response to climate, leading to rapid alterations in landscape structure; or (2) in the absence of disturbance, suitable habitat for different species may move gradually and directionally. A gradual change in potential habitat may lead to a delayed change in actual landscape boundaries if species' responses exhibit significant time lags. In this paper, we discuss these two mechanisms and explore the potential responses of landscape boundaries to global change by using a neutral modeling approach (sensu Caswell 1976, Gardner et al. 1987). "Neutral models" are used to generate an expected result in the absence of a site-specific process or pattern.

Changing Disturbance Regimes

The patterns of many landscapes are influenced or controlled by disturbance (e.g., White 1979, Mooney and Godron 1983, Pickett and White 1985, Turner 1987, Baker 1989). For example, disturbances create openings within forested landscapes, leading to mosaics of successional patches of different ages (e.g., Runkle 1985, Knight 1987, Baker 1989). Landscape patterns in old-growth forests of New England result from frequent natural disturbances, such as windstorms, lightning, pathogens, and fire (Foster 1988*a*). The diversity of the Yellowstone National Park landscape is controlled by a natural fire regime in which catastrophic fires recur at 200- to 300-year intervals (Romme 1982, Romme and Knight 1982). The susceptibility of individual sites to disturbance may be controlled by edaphic conditions such as slope position and aspect (Foster 1988*a*), and therefore disturbances vary spatially. The spatial patterns of disturbances such as wind damage (Foster 1988*b*) or fire (Sellers and Despain 1976, Romme 1982, Romme and Knight 1982) also may be predictable based on the arrangement of age classes of the vegetation.

The frequency, duration, and severity of both abiotic and biotic disturbances are likely to be altered by climate change. For example, forest fire frequencies should increase where the climate becomes warmer and drier (Sandenburgh et al. 1987). Forest fire regimes may also change in response to species composition shifts induced by elevated CO_2 and climate change. Patterns of biotic disturbances may also be altered. Because their ranges are often limited by climatic factors, the distributions of pests or pathogens may change with climate. For example, spruce budworm populations may expand their range under a warmer climate because they are favored by warm, dry, early-spring conditions (Haynes 1982).

If ecological disturbance regimes are altered, changes are likely in many landscapes and, therefore, in landscape boundaries. Disturbance regimes can be described by a variety of characteristics, including spatial distribution, frequency, return interval, rotation period, predictability, area, intensity, severity, and synergism (e.g., Rykiel 1985, White and Pickett 1985). In this study, we use simulation models to examine changes in two disturbance characteristics, intensity and frequency, and their interactions with landscape pattern. We define disturbance frequency as the probability that a new disturbance will be initiated in a unit of susceptible habitat during the time period represented by the simulation. Intensity is defined as the probability that the disturbance, once initiated, will spread to adjacent cells of the same habitat. We predict the spread of a disturbance across a landscape as a function of (1) the proportion of the landscape occupied by a disturbance-prone cover type, (2) disturbance intensity, and (3) disturbance frequency.

SIMULATION EXPERIMENTS

Two-dimensional m x m landscape maps (100 x 100 cells) were randomly generated for the disturbance-susceptible habitat at different values of p. The variable, m, represents the number of rows or columns in the square matrix. The probability, p, for maps this large represents the proportion of a landscape occupied by a susceptible habitat. The remainder of the landscape is considered unsuitable for propagation of the simulated disturbance. Thus, the maps are composed of 10,000 cells, each of which is randomly designated as suitable or unsuitable for a disturbance. A disturbance that could propagate through susceptible habitat was characterized by frequency and intensity. Disturbance frequency, f, is the probability that a new disturbance will be initiated in a unit of susceptible habitat during the simulation (e.g., the probability that lightning striking a hectare of pine forest during a particular storm event or time period will ignite a fire). Disturbance intensity, i, is defined as the probability that the disturbance, once initiated, will spread to adjacent cells of the same habitat (e.g., the probability of fire or a pathogen spreading to an adjacent cell of susceptible forest). In the first set of simulations (n = 10 replicates), frequency (f = 0.01, 0.1, 0.5), intensity (i = 0.25, 0.5, 0.75), and habitat probability (p = 0.4, 0.8) were all varied. In random landscapes, low values of p yield landscapes with small isolated patches, whereas high values of p yield large connected patches (Gardner et al. 1987). This set of simulations was designed to give a general impression of the interplay of p, i, and f. In a second set of simulations (n = 10), we assumed that disturbances (e.g., lightning strikes or pest outbreaks) would occur at some unavoidable minimum number. Therefore, frequency was held constant at f = 0.01. This permitted a more complete examination of the interplay of the controllable parameters, p and i. In a forest, for example, p could be controlled by old-growth cutting policies and i could be controlled by containing fires.

The boundaries in the landscape were analyzed for each map before disturbances began. Boundary length was measured by using the side of one grid cell as a unit length. Landscape disturbance was then simulated as follows. Cells were randomly disturbed at a given frequency until exactly fpm^2 disturbances were initiated (m^2 is equal to the size of the map, in this case 10,000). Each disturbed cell was then changed to a state that was no longer vulnerable to disturbance. The disturbance was then randomly propagated with an intensity, i, to an adjacent disturbance-prone cell. The propagation process was repeated until the disturbance could not spread any farther. The disturbed landscape was then analyzed, and the pattern and boundaries between disturbed and undisturbed habitat were summarized.

For this analysis, we distinguish among different types of landscape boundaries that may have ecological significance. We define "habitat boundary" as the edges separating susceptible and nonsusceptible

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habitat (e.g., the boundaries of forest patches susceptible to a pest). We define "disturbance boundary" as edges between disturbed cells and either undisturbed or nonsusceptible cells (e.g., the boundaries of the infested patches). For both habitat and disturbance boundaries, we distinguish between inner and outer edges. An outer edge refers to the outermost perimeter of a cluster of undisturbed (outer habitat edge) or disturbed (outer disturbance edge) habitat. An inner edge is next to a "clearing" or gap within a patch (e.g., inner habitat edges would surround a gap in a patch of undisturbed habitat). Inner disturbance edges surround undisturbed islands that are embedded in a larger disturbed area.

RESULTS

Interaction of disturbance frequency (f) and intensity (i) in fragmented and connected landscapes

Increasing disturbance intensity (*i*) reduces the total amount of habitat boundaries in the landscape (Table 1). Greater intensity leads to larger continuous patches of disturbance and, therefore, fewer habitat boundaries. In contrast, increasing disturbance intensity almost always increases total length of disturbance boundaries. The greater the spread of the disturbance, the greater the opportunity for disturbance boundaries to form. The only exception is for high ***p*** (e.g., ***p*** = 0.8) and high ***f*** (e.g., ***f*** = 0.5). Under these conditions, the high frequency of disturbance creates many small disturbance patches, and further spread of the disturbance causes the small disturbances to coalesce into larger contiguous areas with less boundary length. When ***p*** and ***f*** are high, the percentage of boundary that is inner edge (in parentheses in Table 1) indicates that most of the total boundary length surrounds isolated habitat patches embedded in the disturbed area.

Inner edges are not a significant feature of fragmented (e.g., ***p*** = 0.4) landscapes (Table 1). When the susceptible habitat is scattered on the landscape, there are very few isolated gaps within patches of susceptible habitat, and this pattern is unaffected by disturbance (Turner et al. 1989). However, inner habitat edges become more important when the susceptible habitat covers most of the landscape (e.g., ***p*** = 0.8). Inner habitat edges increase with disturbance if the disturbance is of low frequency (e.g., ***f*** = 0.01, 0.1) and low to medium intensity (e.g., ***i*** = 0.25, 0.5). Under these circumstances, many small gaps are formed, and the inner edges may form the majority of the total landscape boundaries. For disturbances of relatively low frequency (***f*** = 0.01), the ratio of inner to outer habitat edges is maximized for high values of ***p*** (continuous cover) combined with low values of intensity, ***i*** (small pockets of disturbance) (Fig. 1a). However, inner disturbance edges increase with disturbance intensity at all levels of frequency in very connected landscapes (e.g., ***p*** = 0.8). The more the disturbance spreads, the greater the likelihood that small habitat patches will become isolated within the large disturbed areas. The ratio of inner to outer disturbance edges increases as ***p*** and ***i*** increase (Fig. 1b).

Boundaries as a function of the probability of susceptible habitat (p) and disturbance intensity (i)

We now consider the interaction of ***p*** and ***i*** when a fixed low frequency of disturbance (***f*** = 0.01) is assumed. The total habitat boundaries as a function of ***p*** and ***i*** are shown in Figure 2. Maximum habitat boundaries occur at low to intermediate values of ***p*** (dispersed landscapes) and lower values of ***i*** (small disturbances). Under these conditions, the landscape is composed of many small patches with many boundaries. Habitat boundaries on dispersed landscapes are relatively insensitive to changes in disturbance intensity. Because the patches are small and isolated, higher intensity disturbances still tend to be contained within the small patches and have little effect on total boundary. Above a critical threshold

TABLE 1. Mean number (n = 10) of total habitat and disturbance boundaries for various values of the proportion of susceptible habitat, p; disturbance intensity, i; and disturbance frequency, f. Values in parentheses are the percentage of the total edge composed of inner (isolated) edges.

	Habitat Boundaries		Disturbance Boundaries	
Disturbance intensity, i	p = 0.4	p = 0.8	p = 0.4	p = 0.8
		Disturbance frequency f = 0.01		
0.25	9644 *	6885 (90)	205 *	558 *
0.50	9554 *	6708 (78)	286 *	1947 (10)
0.75	9346 *	1999 *	444 *	6269 (88)
		f = 0.1		
0.25	8948 *	8256 (69)	1858 *	4284 *
0.50	8250 *	5739 (6)	2400 *	6169 (43)
0.75	6986 *	1289 *	3281 *	6426 (89)
		f = 0.5		
0.25	5255 *	6243 *	6776 *	8622 (57)
0.50	3870 *	2504 *	7193 *	7222 (87)
0.75	2559 *	511 *	7698 *	6623 (90)

* An asterisk indicates that inner edges are less than 2% of the total.

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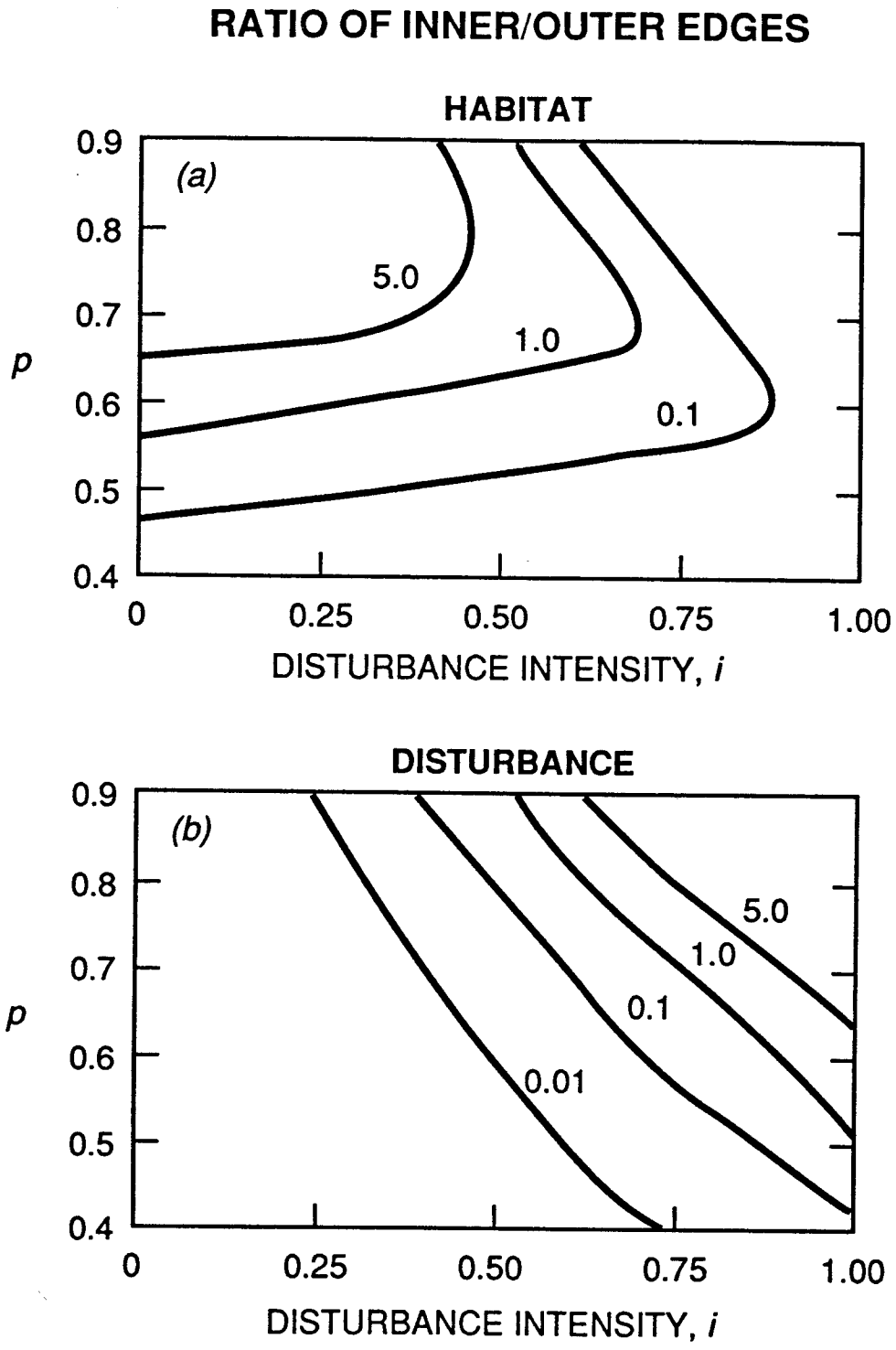

Figure 1. Ratio of inner/outer edges for (a) habitat boundaries and (b) disturbance boundaries as a function of disturbance intensity (i) and the probability of susceptible habitat (p). The figures show isopleths along which the ratio shows the same value.

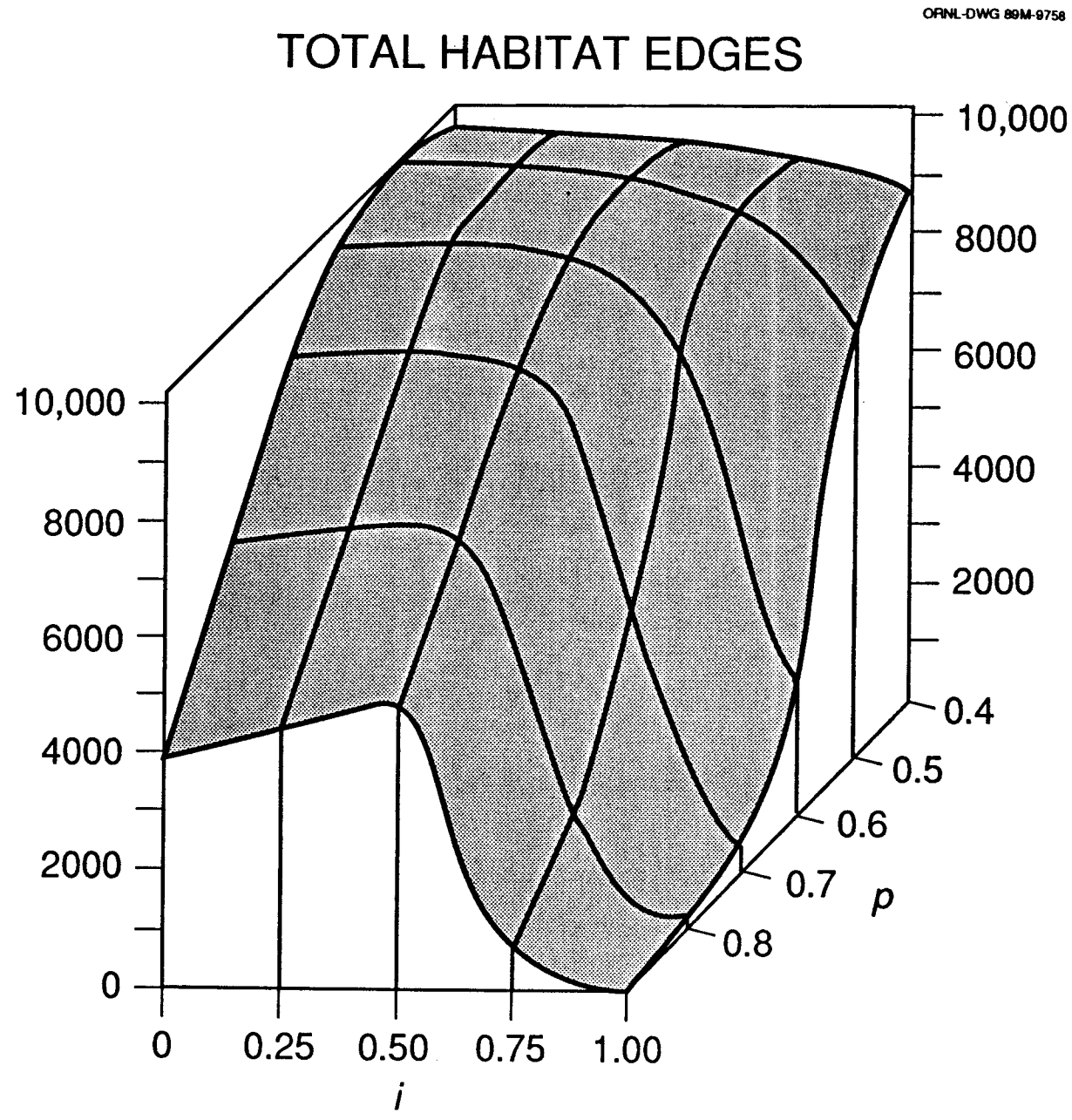

Figure 2. Total habitat boundaries as a function of disturbance intensity (i) and the probability of susceptible habitat (p) for fixed, low-frequency disturbances (f = 0.01).

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(p_c~0.6), patches in random landscapes tend to be connected (Gardner et al. 1987), and habitat boundaries are increased by disturbances of moderate intensity (Fig. 2). (However, this critical threshold of connectivity is a function of the shape of the grid [see Stauffer 1985]). Moderate intensity disturbance breaks up the tight patch structure and creates more edges. The greatest sensitivity to disturbance occurs as p and i increase together (Fig. 2). When this occurs, the landscape is covered by a few large clusters which coalesce at high intensity disturbances.

The total disturbance boundaries as a function of p and i are shown in Figure 3 (note that the p and i axes are rotated from their position in Fig. 2). Disturbance boundaries are insensitive to i on dispersed landscapes (low p) and insensitive to p at low disturbance intensities. In both of these cases, there is very little disturbance edge and therefore very little change with a change in p or i. Maximum disturbance boundaries (see Table 3) tend to occur at higher intensities and at intermediate levels of cover ($0.6 < p < 0.9$).

Maximum outer habitat edges only occur on dispersed landscapes (Fig. 4a). Above p_c, intermediate intensities break up the large clusters and create more outer edges than were present when the landscape was not disturbed. In contrast, maximum inner habitat edges occur only at the lower levels of intensity and intermediate values of p ($0.6 < p < 0.9$) (Fig. 4c). Under these conditions, the disturbances create many small clearings within contiguous habitat clusters.

Maximum values of outer disturbance edges (Fig. 4b) are found along a diagonal running from $p = 0.9$, $i = 0.4$ to $p = 0.6$, $i = 1.0$. As one deviates from this line, conditions become less favorable for producing outer disturbance edges. A minimum occurs when both p and i are very high (disturbances completely cover the large patches, leaving few boundaries of any kind). A second minimum occurs on more dispersed landscapes at low intensity disturbances. Under these circumstances, habitat boundaries are favored rather than disturbance boundaries (see Figs. 2 and 3). Inner disturbance edges are maximized (Fig. 4d) at high intensity and intermediate cover ($0.6 < p < 0.9$). This combination maximizes the probability of an extensive disturbed area surrounding and enclosing undisturbed habitat.

Maximum Landscape Boundaries

In the absence of disturbance, maximum habitat edges on a random landscape occur when $p = 0.5$. An edge is simply the juxtaposition of a susceptible cell (probability p) and a nonsusceptible cell [probability $(1 - p)$]. The probability, **E**, of a cell being located on a habitat edge is simply the product of these two probabilities:

$$\mathbf{E} = p\,(1 - p). \quad (1)$$

Recalling from elementary calculus that a function has its maximum or minimum at the zero of its first derivative, we can take the first derivative of (1) with respect to p,

$$d/dp\,[p\,(1 - p)] = 1 - 2\,p \quad (2)$$

Setting the right hand side of Eq (2) equal to zero and solving for p, we find $p = 0.5$. Again recalling that the solution to Eq (2) is a maximum if the second derivative of Eq (1) is negative, we find that $p = 0.5$ maximizes the probability of edges.

The situation changes slightly as we add a point disturbance (i.e., disturbance intensity $i = 0.0$ and the disturbance does not spread). Now an edge is the juxtaposition of remaining susceptible habitat [probability $p(1-f)$] with either nonsusceptible habitat [probability $(1 - p)$] or disturbed habitat (probability fp). The probability of a random point being an edge becomes:

$$p(1-f)(1-p) + p(1-f)(fp) = p(1-f)(1-p+fp) \quad (3)$$

The zero of the first derivative with respect to p of Eq(3) for $f \neq 1$ (because we are not

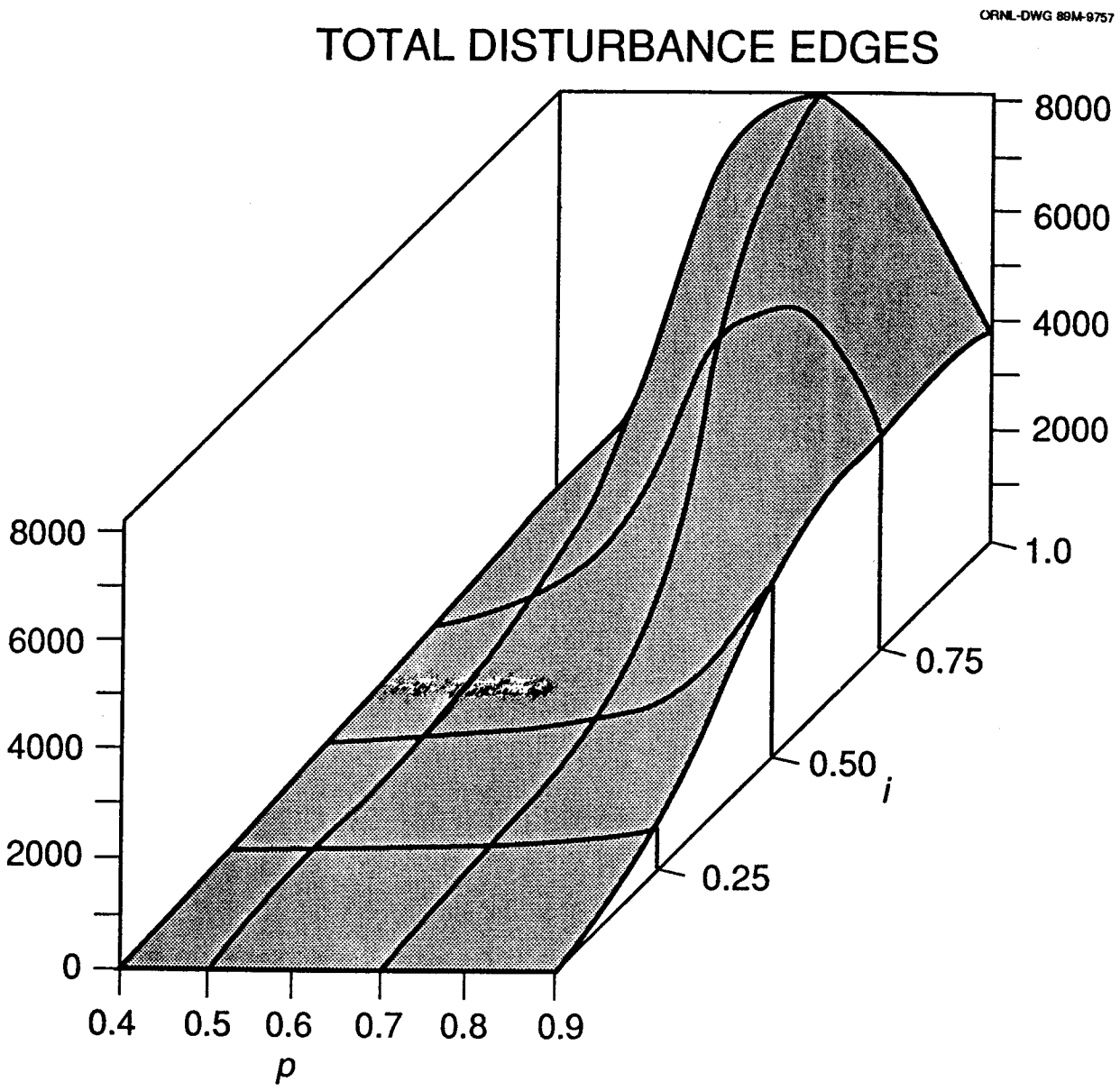
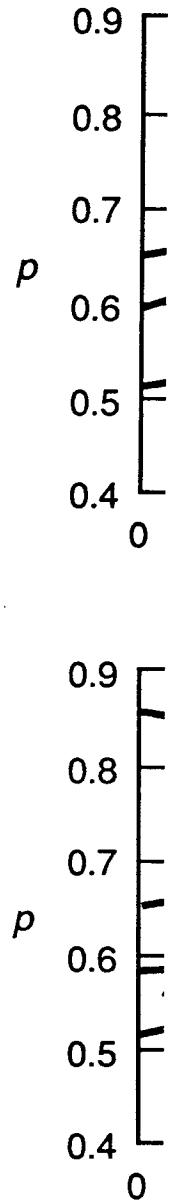


Figure 3. Total disturbance boundaries as a function of disturbance intensity (i) and the probability of susceptible habitat (p) for fixed, low-frequency disturbances (f = 0.01).



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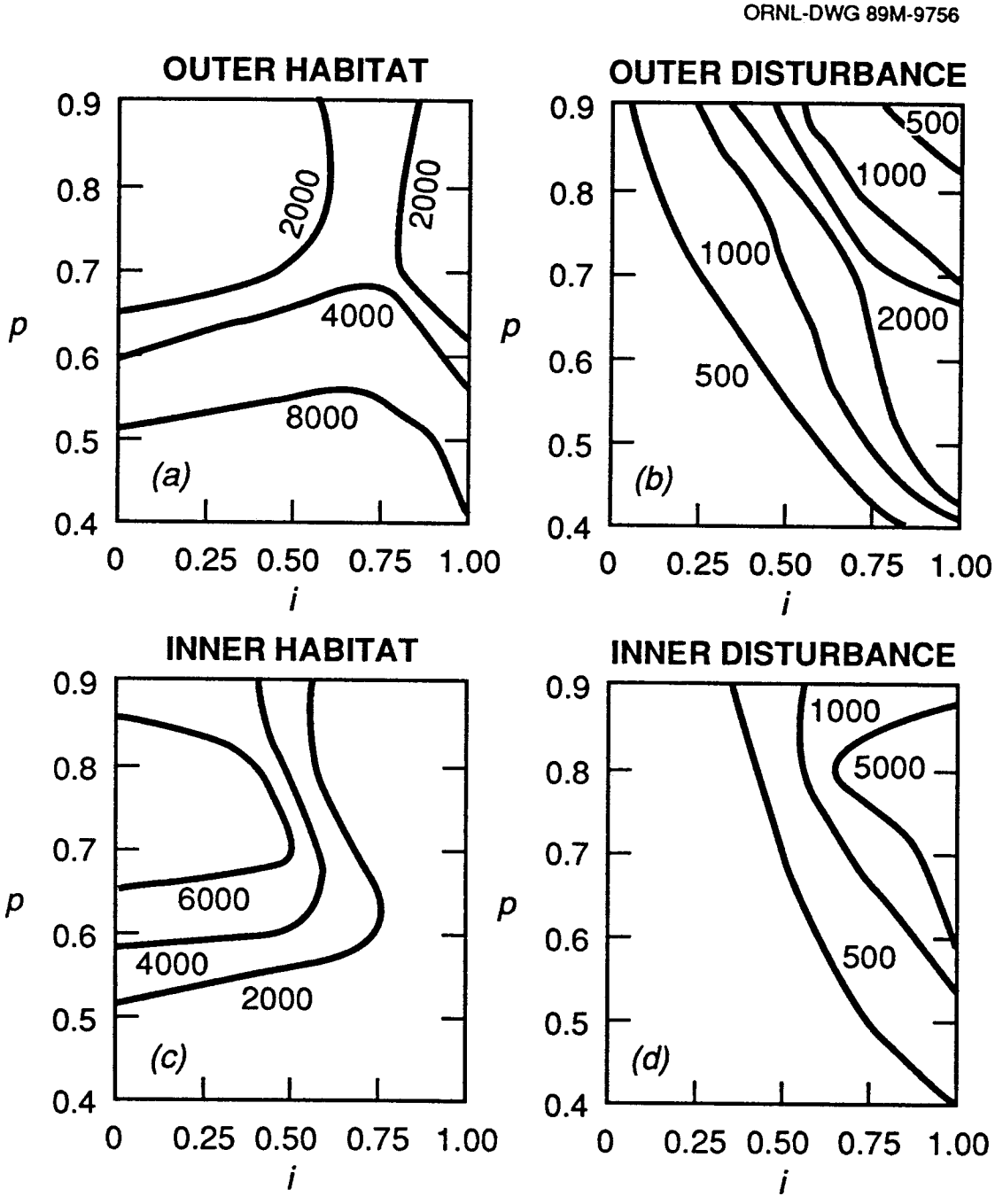

Figure 4. Isopleths showing equal amounts of edge as a function of the probability of susceptible habitat (p) and disturbance intensity (i) for (a) outer habitat edges, (b) outer disturbance edges, (c) inner habitat edges, and (d) inner disturbance edges. Disturbance frequency was fixed at f = 0.01.

interested in the singularity when all cells are disturbed) becomes:

$$1 - 2p + 2fp = 0 \quad (4)$$

Equation (4) indicates that the value of p giving the maximum edges is a function of disturbance frequency, f. Table 2 gives values for p that satisfy Eq (4) at values of f from 0.01 to 0.5. Because $f < 1.0$ for practical situations, the second derivative of Eq (3) will always be negative and the solution of Eq (5) will be a maximum.

As the frequency of point disturbances increases, the maximum edges are achieved on more connected landscapes, i.e., $p > 0.5$ (Table 2). In essence, for the maximum edges after disturbance, the value of p prior to disturbance must be large enough so that following the disturbance, the final landscape has $p = 0.5$. For example with $p = 1.0$, we have a landscape completely covered with susceptible habitat. With a disturbance frequency of $f = 0.5$, one half of the cells will be disturbed and the final result is the same as having an initial landscape with $p = 0.5$.

The situation becomes more complex when we allow the disturbance to spread at intensity, i, and we want to distinguish between inner and outer edges. Table 3 shows the disturbance intensity at which maximum habitat and disturbance boundaries occur for each value of p when disturbance frequency is low ($f = 0.01$). Even with disturbance spread, maximum habitat boundaries still occur near $p = 0.5$ for small values of f and monotonically decrease as p moves away from that value.

On dispersed landscapes ($p = 0.4, 0.5$) the maximum habitat edges are found at $i = 0.0$ (i.e., the point disturbances). Higher disturbance intensities simply open up more contiguous areas of disturbance and decrease the total habitat edge. As p approaches 0.6, we know from percolation theory (Gardner et al. 1987) that the habitat clusters tend to coalesce. As the habitat patches become more contiguous, disturbances of moderate intensity break up the patches and create more edge. The disturbance intensity that creates the most boundary increases from $i = 0.25$ to $i = 0.50$ as proportion of the landscape occupied by susceptible habitat increases from $p = 0.6$ to $p = 0.9$ (Table 3).

The values in parentheses in Table 3 indicate the percent of the boundary that is inner edge. On dispersed landscapes, the majority of the edges are always outer edges (see also Table 1 and Fig. 1a). But at intermediate values of p (e.g., 0.6 to 0.8), the disturbances occur in the center of contiguous patches of habitat and the majority of the edges are inner edges. At $p = 0.9$, maximum edges occur at $i = 0.5$. At this higher intensity, the disturbance tends to break through the enclosing habitat to form outer edges.

The maximum number of disturbance boundaries tend to occur at the highest disturbance intensity ($i = 1.0$) when $f = 0.01$ (Table 3). At $i = 1.0$, a disturbance spreads until it covers the entire habitat cluster within which the disturbance begins. It is only at $p = 0.9$ that intensities above $i = 0.6$ tend to disturb the entire landscape, leaving few or no edges. As with habitat boundaries, inner disturbance edges (values in parentheses) dominate when p is equal to or greater than 0.6. In these cases, high intensity causes the entire habitat patch to be disturbed, surrounding and entrapping undisturbed areas.

Gradual Movement of Suitable Habitat

We have seen how landscape boundaries may change in response to alterations in disturbance frequency and intensity. Landscape boundaries also may change in response to interactions between global change and habitat displacement. As climate changes, for example, there may be a gradual movement of potentially suitable conditions for different species, and species may migrate to track hospitable environments. However, migration rates are

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TABLE 2. Values of the proportion of susceptible habitat ***(p)*** that produce maximum habitat boundaries when point disturbances (i.e., disturbance intensity = 0) occur at different levels of disturbance frequency ***(f)***.

Disturbance frequency ***f***	Proportion of susceptible habitat ***p***
0.00	0.50
0.01	0.50
0.1	0.56
0.2	0.62
0.3	0.71
0.4	0.83
0.5	1.00

TABLE 3. The value of disturbance intensity, *i*, that creates maximum habitat and disturbance boundaries at $f = 0.01$ for different values of p. Numbers in parentheses represent the percentage of the maximum that is composed of inner edges.

	Maximum habitat boundaries		Maximum disturbance boundaries	
p	Disturbance intensity *(i)*	Amount	Disturbance intensity *(i)*	Amount
0.4	0.0	9709 (2)	1.0	858 (5)
0.5	0.0	10110 (11)	1.0	2757 (20)
0.6	0.25	9750 (52)	1.0	7397 (71)
0.7	0.25	8718 (85)	1.0	8128 (91)
0.8	0.40	6906 (87)	1.0	6575 (91)
0.9	0.50	4861 (45)	0.6	4669 (93)

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difficult to predict because the projected rate of climate change is an order of magnitude faster than previous climate changes. Davis (*in press*) suggests that the spatial displacement of habitats can be visualized if one assumes the same general configuration of climate as today. With a latitudinal lapse rate in the Great Lakes region of about 100 km/°C, isotherms would be displaced northward 300 km in the next 100 years. This rate is 10 times greater than the documented range extensions for trees in a similar time interval (Davis *in press*). Furthermore, there are now new barriers to migrations (e.g., cities, agriculture, and roads) and new modes of migration (e.g., cars, trains, transplants for horticulture, forestry, or agriculture.) Range extension in the future may be less efficient than in the past because advance disjunct colonies have been extirpated by human disturbances, and propagule sources have often been reduced (Davis 1989). The current spatial distribution and abundance of a species will influence its ability to migrate successfully to regions of suitable climate and soils (Peters and Darling 1985).

A variety of modeling approaches have been used to explore the potential redistribution of habitats in response to changes in climate and atmospheric CO_2 (e.g., Davis and Botkin 1985; Emanuel et al. 1985*a*, 1985*b*; Solomon and Webb 1985; Solomon 1986). Diffusion models have been used to explore alternative modes of species migration in which (1) species may migrate as a continuous front, or (2) discontinuous populations may be established far in advance of the main species front (Davis 1987). Individual-based forest stand models have been used to simulate responses to global climate change (e.g., Davis and Botkin 1985, Solomon 1986, Pastor and Post 1988), although species dispersal/migration is not included. Simulation results suggest that species abundances are not always in equilibrium with climate; biotic interactions or other environmental factors (e.g., soil heterogeneity) can have strong effects and may obscure or delay observed responses; and time lags of up to 1000 years may occur in biome shifts.

The rate of movement of potential habitat and the rate of species dispersal/migration will influence landscape boundaries, especially if time lags occur (e.g., Davis 1984, Webb 1986, Pennington 1986). Time lags in species responses to historical climatic changes have been documented. For example, beech has animal-dispersed seeds and tends to move as a front. Beech showed a time lag of 500 to 1000 years in crossing from the eastern to the western shore of Lake Michigan (Davis 1989). In contrast, hemlock, whose wind-dispersed seeds can travel 100 km beyond the main species front, showed no time lags attributable to crossing the Great Lakes (Davis 1989). Davis (1989) also proposes that time lags in the adjustments of species abundances to climate will be small (~10 - 20 yrs) in the heavily disturbed communities that cover most of the landscape. The most common species will be dispersed to new habitats by humans, but time lags will be a problem for unmanaged forests, natural areas, and preserves. The climate change during the next century may not be enough to kill dominant species directly. Thus, the landscape may appear superficially unchanged even though a different community is becoming established in the understory.

The migration of species and the redistribution of community types in response to global change and the associated effects on landscape boundaries are complex issues (c.f., Brubaker 1986, Pennington 1986). Some organisms track climate change closely, reacting to conditions each year, while others respond so slowly that only long-term climatic trends have any observable impact (Davis 1984). In a new set of simulation experiments, we examine potential changes in landscape boundaries by focusing on: (1) the rate of movement of conditions that are potentially suitable for a community type; (2) the probability of local extinction of the community; and (3) the probability of migration. The term "community" is used here

to represent the group of organisms of interest, but the model can be developed for a species or population. We use a model very similar to the one described previously, but we modify the parameter ***i*** and add new parameters. We define the interval of movement of potential habitat, ***t***, as the number of time steps required for a new row of the landscape matrix to become potentially available for colonization while an old row at the bottom becomes unsuitable for new colonization. Extinction, ***e***, is defined as the probability of the community becoming extinct at a particular cell and is based upon the longevity of the community. For example, a community that exhibits a longevity, ***l***, of 10 years would have ***e*** = 1/10 = 0.1. This inverse relationship is similar to turnover time and turnover rate. Migration, ***i***, is defined as the probability of successfully colonizing an adjacent cell of potential habitat. Migration can occur in any of the four cardinal directions (up, down, left, right) from an occupied cell. Thus, the spread of the community is simulated as a continuous front, rather than as establishment of disjunct colonies.

SIMULATION EXPERIMENTS

Two-dimensional landscape maps (100 x 100 cells) were randomly generated to contain the community of interest only in the lower half of the map (e.g., rows 51 to 100) at probability ***p***. Initially, the upper half of the map is considered to be unsuitable for the community. Spatial patterns and boundaries are analyzed on the initial landscape. At each subsequent time step during the simulation, a community cell can become extinct at probability ***e***, and new community cells can become established within the suitable range (e.g., initially only within rows 51 to 100) at migration probability ***i***. The movement of potential habitat (i.e., suitable range) is then simulated as follows. At each interval of time ***t***, the lower-most row of potential habitat becomes unsuitable for the establishment of new community cells, and a new row of potential habitat becomes available at the upper edge of the range (Fig. 5). Community extinction and establishment continue, and the range of suitable habitat continues to move at intervals of ***t***. The simulation is concluded when the suitable habitat has been displaced to the other half of the map (i.e., rows 1 to 50). The new landscape patterns are then analyzed.

Communities may exhibit spatial and temporal lags if habitat displacement is rapid relative to the longevity of the community. This occurs because long-lived remnant populations may persist even though the habitat is no longer suitable for reestablishment. As a result, landscape patterns may appear to change very slowly. To quantify this phenomenon in the simulations, we defined the spatial lag to be the maximum distance of a remnant population from the current range of suitable habitat. The maximum spatial lag in our simulations was 50, reflecting half the linear distance in the 100 x 100 arrays. Spatial lag was measured at the end of each simulation.

These simulations were all done with the initial proportion of habitat occupied by the community fixed at ***p*** = 0.8. This proportion established a landscape that was connected rather than fragmented (Gardner et al. 1987), permitting the community to migrate as a front. (Frontal migration could not occur if the potential habitat were fragmented). Rows of potential habitat added during the simulation also had 80% of their cells available for colonization. Simulation experiments were conducted with factorial combinations of the parameters: extinction (***e*** = 0.1 and 0.5) corresponding to longevity values of ***l*** = 10 and 2 time steps, respectively; migration (***i*** = 0.1, 0.5, and 1.0); and the interval of movement of potential habitat (***t*** = 1, 2, and 10 time steps). For each combination of parameters, 10 simulations were conducted.

RESULTS

The proportion of the newly available habitat that was colonized by the community increased with increased

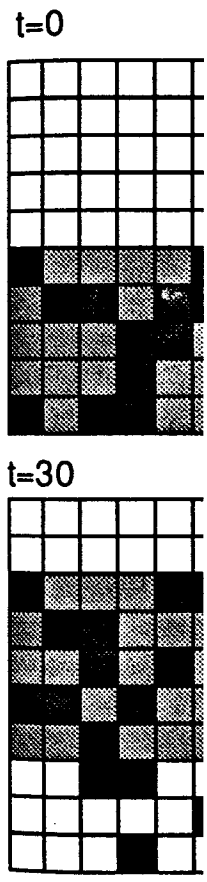

Figure 5. Illusti
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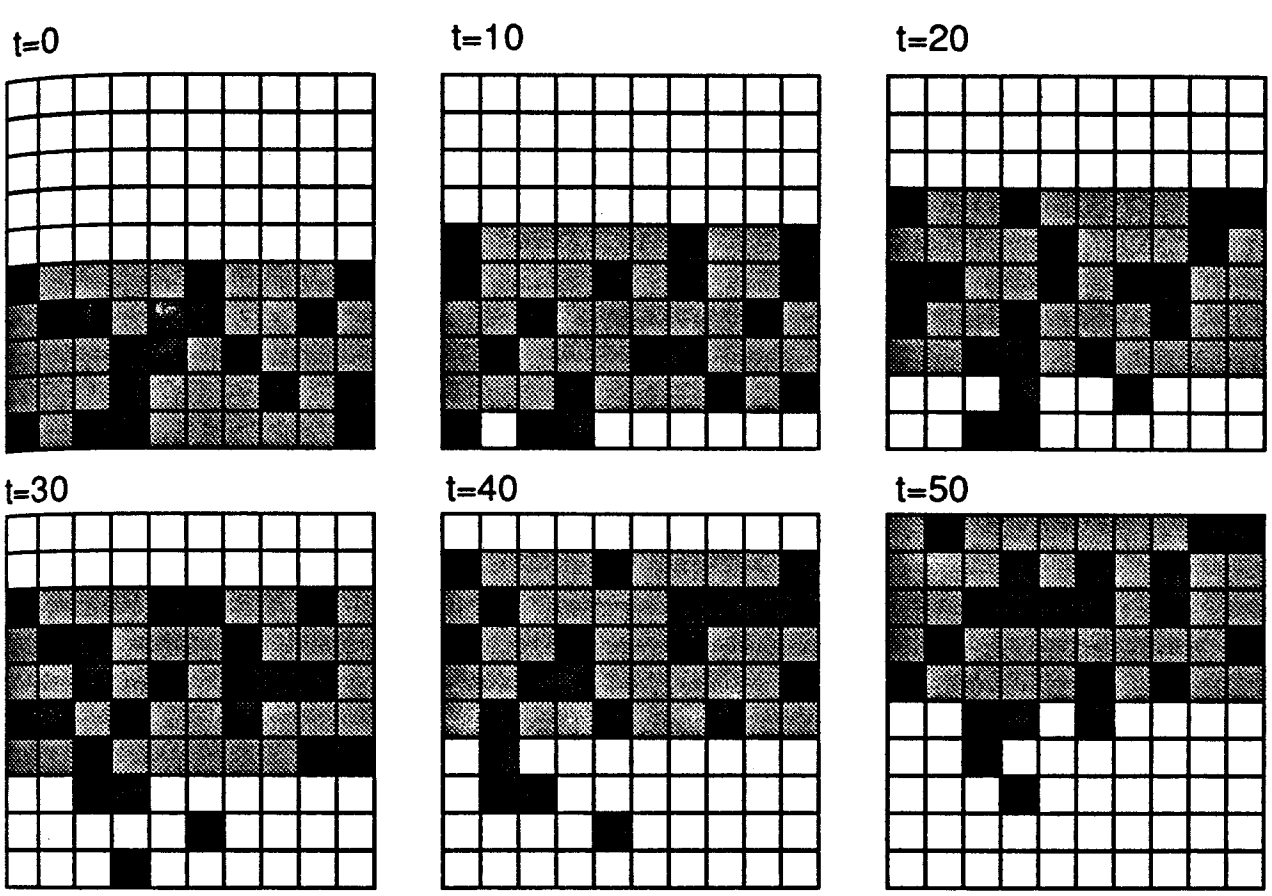

Figure 5. Illustration of the hypothetical movement of potential habitat and the response of a community. The grey area represents habitat that is suitable for colonization by a community type. Black cells are occupied by the community, and white areas are not suitable for colonization. At intervals of 10 time units, the potential habitat moves one row north. Remnant populations may remain behind, but colonization can only occur in the gray areas. The simulation concludes when the potential habitat reaches the last row of the map.

probabilities of migration (higher *i*) and slower rates of habitat movement (higher *t*) (Fig. 6). Provided that the probability of migration exceeded the probability of extinction, more new habitat was colonized at higher *i* values. The maximum distribution (*p* = 0.8) was approached when extinction was low and the probability of migration was greater than or equal to 0.5. For a given combination of *e* and *i*, more new habitat was colonized when the potential habitat moved more slowly (e.g., increasing *t* in Fig. 6). When the potential habitat moved very rapidly (e.g., *t* = 1), high values of *i* were necessary for the community to colonize only 40% of the available habitat. At high values of *t* and *i* and low values of *e*, the community could track the migration of suitable habitat. However, when extinction values were high, the proportion of the new habitat occupied by the community never exceeded 0.5 (Fig. 6).

The spatial lag in remnant populations was greatest when longevity of the community was high (longevity *l* = 10, corresponding to the lower extinction rate) and the potential habitat moved quickly (*t* = 1) (Fig. 7). At low extinction rates, the lag distance of the remnant populations decreased as the movement rate of the habitat slowed (higher values of *t*), reflecting increased opportunities for remnant populations to become extinct. When the community lifespan was short (*l* = 2, corresponding to the higher extinction probability), the spatial lag was very small (Fig. 7). For given values of *t* and *e*, an increased probability of migration generally increased the spatial lag because it allowed more community cells to become established.

The total amount of boundary in the landscape changed in response to the habitat displacement (Fig. 8). Initially, the total boundary length was approximately 4000, shown by the dashed line in Figure 8. The total amount of boundary was maintained or increased with particular combinations of *e*, *i*, and *t* (Fig. 8). With low extinction values, the amount of landscape boundary in the new habitat was similar to the initial habitat when the displacement rate was slow (higher *t*). This indicates a similar landscape structure and successful migration of the community. However, total landscape boundary decreased with low migration probability (*i* = 0.1) and rapid habitat displacement (low values of *t*) (Fig. 8). At higher extinction rates, the boundary increased by as much as 25%. As *i* increased, however, the total boundary in the landscape increased rapidly. At higher values of *i* and *t*, the amount of landscape boundary exceeded the initial conditions. This occurred because the proportion of the landscape occupied by the community approached 0.5 (Fig. 6), which is the value for which maximum boundaries are observed (Gardner et al. 1987).

DISCUSSION

Two potential means by which global change may affect landscape boundaries have been explored by using a "neutral model" approach (Caswell 1976, Gardner et al. 1987). Global climate change can alter the frequency and intensity of disturbances such as fires or pest outbreaks. In addition, global climate change can alter the spatial arrangement of species tolerance limits and change the location of boundaries between community types. Changing disturbance regimes were simulated in both fragmented and connected landscapes. The effects of potential habitat displacement were simulated only in landscapes with sufficient connectivity to allow migration to adjacent cells of suitable habitat.

The frequency and intensity of disturbances can be expected to change with the global climate, but the effects of changing disturbance regimes on landscape boundaries will be different in connected and fragmented landscapes. In landscapes that are connected (high *p*), an increase in disturbance intensity (probability of spreading) will cause landscape boundaries to decrease in total length. In landscapes that are fragmented (low *p*), an increase in

Figure 6. The p
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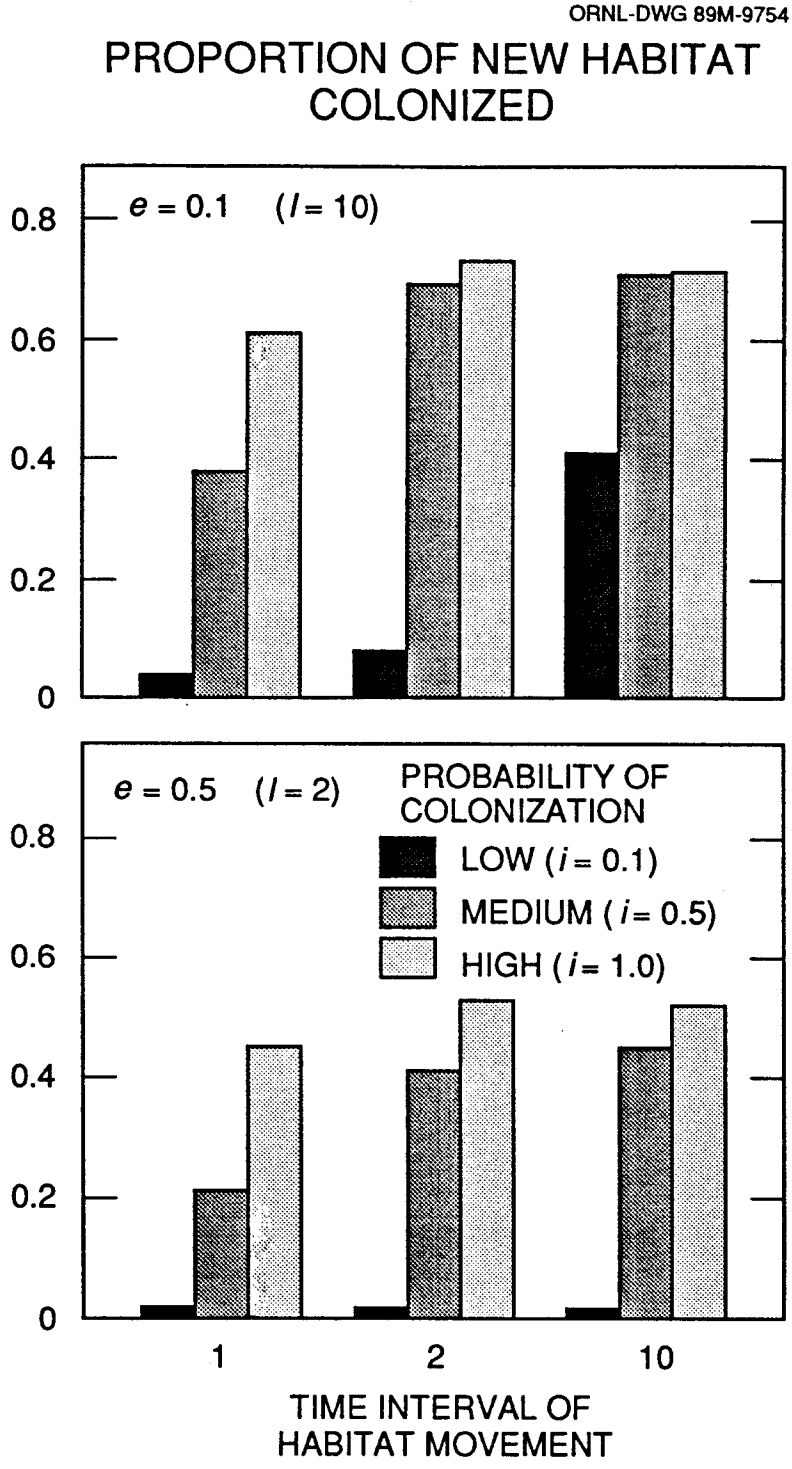

Figure 6. The proportion of newly available habitat that is successfully colonized by the community as a function of the rate of habitat movement and probability of dispersal, i, for (a) low probability of extinction and (b) high probability of extinction. When t = 1, habitat movement is rapid, and when t = 10, habitat movement is slow. The maximum possible community colonization is 0.8.

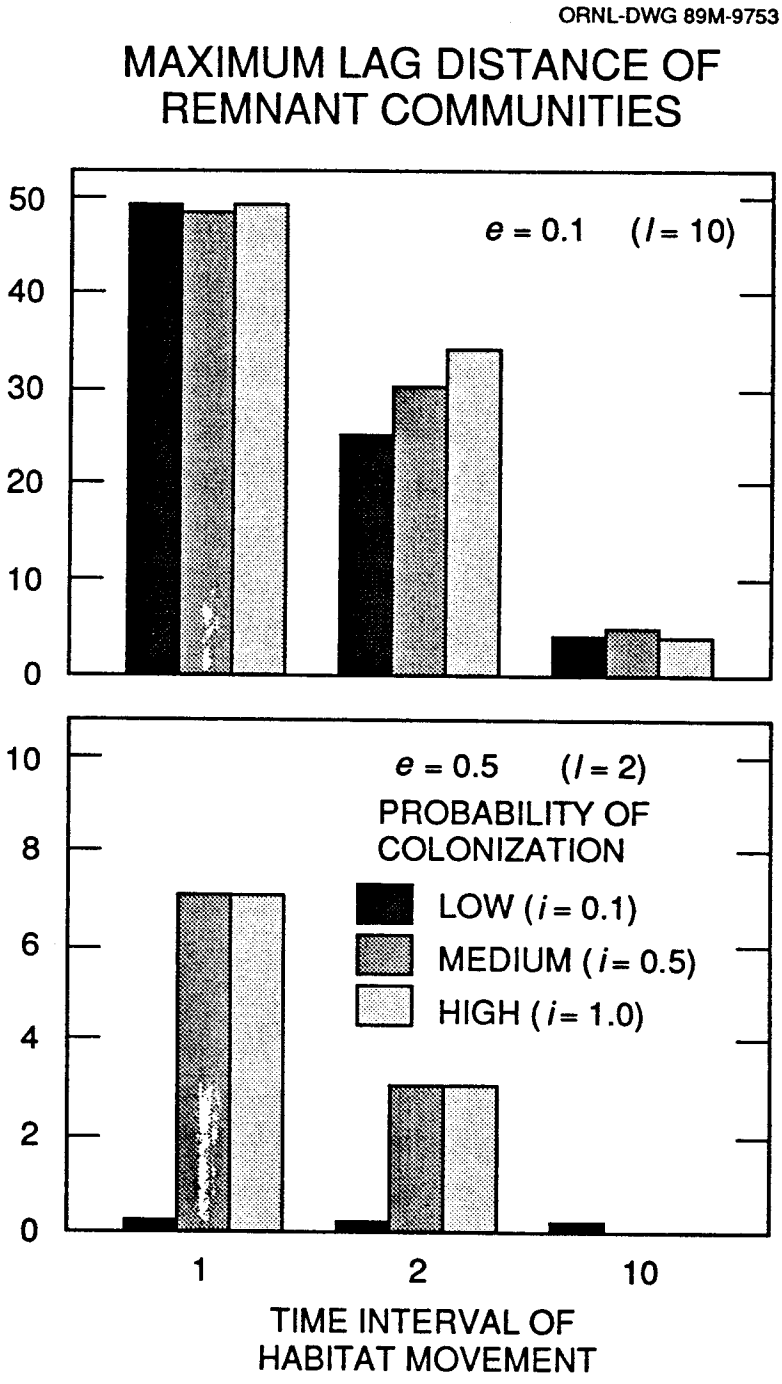

Figure 7. The maximum spatial lag distance of remnant communities from the suitable habitat as a function of the rate of habitat movement and probability of dispersal, i, for (a) low probability of extinction and (b) high probability of extinction. When t = 1, habitat movement is rapid, and when t = 10, habitat movement is slow. The maximum possible lag distance is 50, or half the size of the landscape maps.

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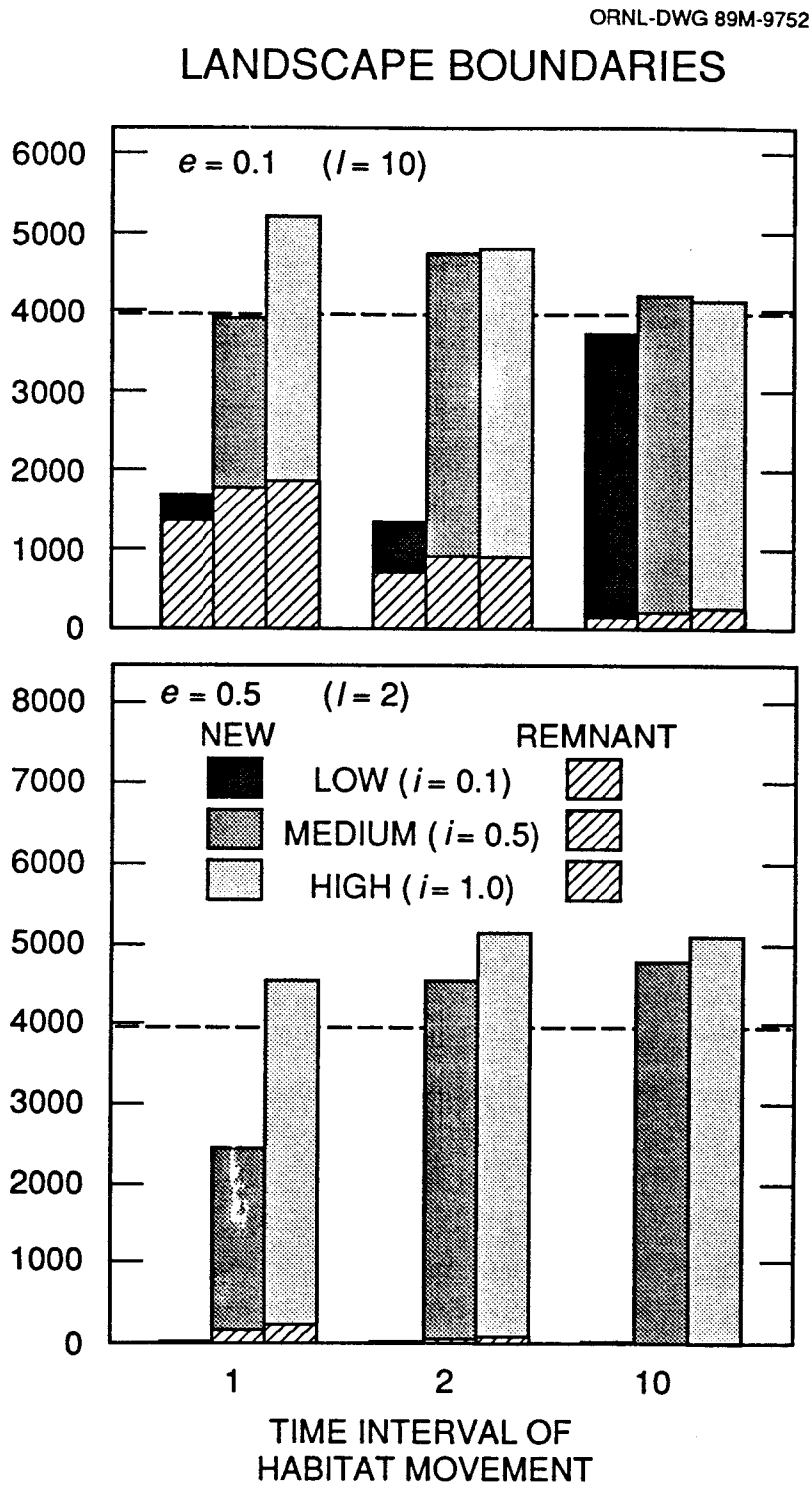

Figure 8. Landscape boundaries as a function of the rate of habitat movement and probability of dispersal, i, for (a) low probability of extinction and (b) high probability of extinction. Extinction probability is indicated by the variable, e, which is the inverse of longevity, l. The total boundary is the sum of boundaries in the newly available habitat and those of the remnant communities. When t = 1, habitat movement is rapid, and when t = 10, habitat movement is slow.

disturbance frequency (probability of disturbance initiation) will result in a decrease in landscape boundaries. The qualitative change in sensitivity to ***i*** and ***f*** occurs at the percolation threshold, p_c which is approximately 0.6 in random two-dimensional maps and will be different in more complex landscapes. This suggests different strategies for mitigating the effects of changing disturbance regimes in habitats that occur above and below p_c in the landscape. When a habitat is rare, the fragmented spatial distribution tends to inhibit disturbance spread, and the persistence of the habitat depends less on disturbance intensity than disturbance frequency. Therefore, management should focus on potential changes in disturbance frequency if the habitat is rare. In contrast, when a habitat is common, the contiguous spatial distribution enhances the spread of disturbances of low frequency but high intensity. Therefore, management should focus on potential changes in disturbance intensity if the habitat is common.

The conditions that maximize landscape boundaries can be determined, allowing general predictions about whether boundaries will increase or decrease with changing disturbance regimes. Habitat boundaries will be greatest in fragmented landscapes with disturbances of low intensity. Disturbance boundaries will be greatest in landscapes having intermediate values of ***p*** and disturbances of high intensity. As conditions depart from those that maximize either type of boundary (e.g., increasing ***i*** in fragmented landscapes), the simulations predict that the amount of boundary will decline.

Changes in the relative abundances of outer edges (perimeters of patches) and inner edges (gaps within larger habitat patches) may influence the distribution and abundance of wildlife species. Therefore, responses of inner and outer edges to global climate changes should be considered. The ratio of inner to outer edges was sensitive to the interaction between disturbance frequency and intensity in both fragmented and connected landscapes. Because these types of edge are qualitatively different (i.e., gaps or perimeters), changes in their relative abundance may have indirect effects on species or ecological processes. Predictions about the combination of ***i*** and ***f*** that maintain a particular inner/outer edge ratio might be useful in managing landscapes for the persistence of particular species.

Landscape boundaries are also controlled by the spatial distribution of species tolerance limits. Range limits are likely to be displaced from their current distributions in a changing climate, leading to new landscape patterns. The effects of habitat displacement on landscape boundaries will vary with the rate of movement and the probabilities of community extinction and migration. Climatically-induced habitat displacement may lead to time lags in the response of landscape boundaries. Spatial lags in the simulations were greatest when extinction was low and the habitat moved quickly. If this occurs in real landscapes, a time lag would be observed in the response of the landscape to habitat displacement. The present landscape could appear unchanged superficially, even though substantial changes occurred (e.g., community reestablishment is no longer possible). However, species responses are likely to be individualistic. By estimating parameters for this model for some key species, habitat displacement might be simulated by using predicted climatic changes through the next century.

Habitat displacement simulations might be used to guide mitigation by identifying the combinations of parameters which allow successful colonization and those for which community survival becomes unlikely. The simulated community could track the movement of habitat when the displacement rate was slow, the extinction probability was low, and the migration probability was at least moderate. Clearly, the more rapid the rate of habitat displacement, the more difficult it is for a community to migrate to its new range of

potential habitat. Species with slow migration rates could be targeted for transplanting. An important topic for additional study is the influence of current landscape patterns on the ability of a species to successfully migrate to suitable habitat. Barriers such as urban centers or agricultural tracts may exert a dominant influence on species colonization.

CONCLUSIONS

The responses of landscape boundaries to global change undoubtedly will be complex. The simulations described in this paper predict interactions between landscape pattern, disturbance characteristics, and community migration characteristics. Because these predictions are quantitative, they provide testable hypotheses which can be evaluated for actual landscapes and used to examine the effects of different parameters. For example, a change in disturbance regimes can be simulated on real landscapes with disturbances of known frequencies and intensities. Similarly, habitat movement can be simulated for species with known lifespans and dispersal abilities and perhaps tested by modeling the range changes that accompanied past climatic change. A combination of theoretical and empirical work is necessary to better understand and predict the responses of landscape boundaries to global change.

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