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Research article

Species dynamics in disturbed landscapes: when does a shifting habitat mosaic enhance connectivity?

Michael C. Wimberly
Warnell School of Forest Resources, University of Georgia, Athens, GA 30602, USA; (e-mail: wimberly@forestry.uga.edu)

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Abstract

Although landscape ecology emphasizes the effects of spatial pattern on ecological processes, most neutral models of species–habitat relationships have treated habitat as a static constraint. Do the working hypotheses derived from these models extend to real landscapes where disturbances create a shifting mosaic? A spatial landscape simulator incorporating vegetation dynamics and a metapopulation model was used to compare species in static and dynamic landscapes with identical habitat amounts and spatial patterns. The main drivers of vegetation dynamics were stand-replacing disturbances, followed by gradual change from early-successional to old-growth habitats. Species dynamics were based on a simple occupancy model, with dispersal simulated as a random walk. As the proportion of available habitat (p) decreased from 1.0, species occupancy generally declined more rapidly and reached extinction at higher habitat levels in dynamic than in static landscapes. However, habitat occupancy was sometimes actually higher in dynamic landscapes than in static landscapes with similar habitat amounts and patterns. This effect was most pronounced at intermediate amounts of habitat ($p = 0.3 - 0.6$) for mobile species that had high colonization rates, but were unable to cross non-habitat patches. Differences between static and dynamic landscapes were contingent upon the initial metapopulation size and the shapes of disturbances and the resulting habitat patterns. Overall, the results demonstrate that dispersal-limited species exhibit more pronounced critical behavior in dynamic landscapes than is predicted by simple neutral models based on static landscapes. Thus, caution should be exercised in extending generalizations derived from static landscape models to disturbance-driven landscape mosaics.

Introduction

Simulation modeling has been instrumental in the development of general hypotheses about species responses to landscape patterns (Fahrig 1991). Early research used neutral models and percolation theory to demonstrate that habitat connectivity exhibits non-linear responses to habitat loss when spatial pattern is explicitly taken into account (Gardner et al. 1987). A fundamental phase shift in landscape structure occurs at a critical threshold where a single large habitat cluster is suddenly fragmented into many smaller, isolated patches. When recolonization is critical for metapopulation persistence, this sudden decrease in connectivity can precipitate the extinction of dispersal-limited species (Bascompte and Sole 1996). The magnitude of these effects depends upon habitat pattern, with spatially aggregated habitats having more connectivity and greater probability of species persistence than spatially random habitats (Hill and Caswell 1999; With and King 1999b). Although some research indicates that species dynamics are much more sensitive to habitat amount than to habitat pattern (Fahrig 1998), other work suggests that habitat pattern may be especially important in highly fragmented landscapes where small populations are at a high risk of extinction (Flather and Bevers 2002).

Most landscape modeling to date has focused on spatial and temporal dynamics of organisms or metapopulations, while assuming that the amount and configuration of habitat remains static. Dynamic habitats are the norm in real landscapes, however, and may be manifested in two ways. Directional landscape change occurs as a gradual trend over decades or centuries, resulting from climate shifts, human population expansion, or the recovery of natural communities following land abandonment. When habitat decreases over time, models predict a temporal lag before the onset of population and community responses (Tilman et al. 1994; Brooks et al. 1999; Cowlishaw 1999). Where habitat fragmentation has recently occurred, observed species patterns may thus represent legacies of past landscapes, and future loss of species diversity may be inevitable.

Landscape dynamics also occur in shifting patch mosaic landscapes, where the spatial configuration of habitats varies over time but the amount of habitat remains relatively constant in a dynamic equilibrium (Pickett and White 1985). For example, disturbances such as fire, wind, or timber harvesting continually reset forest patches to early successional stages which then change over time as a result of forest succession. Although the phenomenon of patch dynamics has been recognized for decades (e.g. Watt 1947), it has only recently been embraced as an overarching paradigm for linking spatial and temporal variability in ecological systems (Wu and Loucks 1995). Patch dynamics models integrating disturbances, shifting habitats, and species responses have demonstrated that complex dynamics at the landscape level are not necessarily predictable from the behavior of individual patches, and that these emergent properties are sensitive to the spatial and temporal patterns of disturbance (Wu and Levin 1994; Moloney and Levin 1996). Simple neutral models based on landscape grids have similarly been important in the development of ecological theory related to landscape pattern, connectivity, and species persistence (Gardner et al. 1991; Hill and Caswell 1999; With and King 1999a, b), but these models have almost exclusively considered static landscapes. Does our understanding of the linkages between habitat amount, habitat pattern, and species responses change when these factors are reexamined in a dynamic context?

Although several researchers have developed models of metapopulations in dynamic habitats (e.g. Hanski 1999; Johnson 2000; Gu et al. 2002; Johst et al. 2002), only a few studies have explicitly addressed how species respond to different rates of habitat dynamics. Analyses of generalized spatial (Keymer et al. 2000) and nonspatial (Boughton and Malvadkar 2002) models have demonstrated that for a given habitat amount, an increasing rate of habitat turnover decreases habitat occupancy and results in extinction at higher amounts of habitat. Akcakaya et al. (2004) likewise found that the predicted carrying capacity of a landscape decreased when habitat dynamics resulting from timber harvests were incorporated into a detailed spatial metapopulation model of Sharp-tailed Grouse (*Tympanuchus phasianellus*). These results have been attributed to direct mortality resulting from habitat destruction, time lags before newly created habitat is colonized, and environmental stochasticity in the form of fluctuating habitat amounts.

In contrast to these studies, Matlack and Monde (2004) analyzed a simulation model incorporating habitat dynamics and the responses of dispersal-limited, sessile organisms such as forest herbs. They found that habitat occupancy was highest at intermediate rates of habitat turnover in fragmented landscapes, and attributed this result to the effects of short-lived habitat patches that served as ‘bridges’, providing temporary connectivity for rapidly-moving species. Similarly, Keymer et al. (2000) described the phenomenon of ‘direct percolation’, in which a dynamic landscape mosaic that is spatially fragmented at a single point in time remains connected over multiple time steps as patches continually fragment and coalesce. If shifting habitats actually enhance long-term connectivity, it might be possible to increase the populations of some species through the management of dynamic landscapes. Conversely, reductions in the rate of habitat dynamics could reduce connectivity and be detrimental to some species.

Possible differences in species responses to static and dynamic habitats also have implications for the application of spatial datasets and ecological models in conservation planning. As remote sensing-derived maps of land cover become widely available, they are being integrated with spatial population models to assess the impacts of land management on biodiversity (e.g. Richards et al. 2002; Schumaker et al. 2004). If these types of analyses fail to account for the destruction and creation of habitats over time, they may lead to misleading inferences about the population levels that can be supported by the landscape, and ultimately to flawed management decisions (Akcakaya et al. 2004). In light of these possibilities, the main objective of this research was to contrast the responses of simulated species in dynamic, age-structured landscapes vs. static landscapes. The following major research questions were addressed: (1) Does habitat occupancy differ in static and dynamic landscapes with similar habitat amounts and patterns? (2) How do responses vary for species with different habitat associations, colonization and extinction rates, and dispersal distances? (3) How do responses vary with disturbance patterns?

Methods

Landscape dynamics model

Landscape dynamics were simulated using the Landscape Age-class Dynamics Simulator (LADS), a spatially explicit model of disturbance and forest age structure. For a detailed description see Wimberly (2002). The simulated landscape was a 100×100 lattice of square cells. Cell size was not explicitly specified, but was assumed to represent patches large enough to support subpopulations of the hypothetical species described in the next section. Similarly, the time step of the model was not explicitly specified, but was assumed to be scaled to the demographic rates of each species. Habitat structure in each cell was indirectly modeled based on the number of time steps since the last disturbance. Grid cells younger than 40 time steps were classified as early-successional habitat, cells between 40 and 199 time steps were classified as mid-successional habitat, and cells 200 time steps or older were classified as old-growth habitat.

Disturbance simulation was based on parameters describing the disturbance cycle (b) and the mean disturbance size (s). The disturbance cycle was the mean number of time steps between disturbances for any point on the landscape. The mean disturbance size was the mean number of clustered grid cells that comprised a single disturbance event, expressed as a proportion of the total number of cells in the landscape. To generate a given disturbance cycle for disturbance events of a particular mean size, it was necessary to compute the mean frequency of disturbance events occurring in each time step as:

$$f = (sb)^{-1}.$$

The number of disturbance events was generated independently for each time step as a Poisson random variable with mean equal to f. This disturbance modeling approach was a spatial extension of the negative exponential model, which has been widely used to characterize fire cycles and forest age-structure in fire-prone ecosystems (VanWagner 1978; Boychuk et al. 1997).

Disturbance events were initiated in a random cell, and disturbance spread was modeled using a cellular automata-based algorithm. This algorithm could be parameterized to generate a variety of disturbance shapes, ranging from circular clusters to more complex fractal shapes with a high edge to interior ratio (Wimberly 2002). The landscape was assumed to be physically homogeneous and disturbance spread was independent of forest age. All disturbances were stand-replacing events that killed the majority of vegetation in the disturbed cells, thereby resetting the ages to zero. Individual cells were allowed to burn more than once during a single time step. These simplifying assumptions allowed the disturbance cycle for an expected habitat proportion (p) to be computed analytically based on the assumption of a negative exponential distribution of forest age classes (VanWagner 1978; Boychuk et al. 1997).

Appropriate disturbance cycles were simulated to generate landscapes with p ranging from 0.1 to 0.9 at intervals of 0.1. Three disturbance patterns were simulated for each level of p. In the random scenario, all disturbances were a single cell in size, with the probability of disturbance in any pixel independent of the surrounding cells. This scenario served as a neutral landscape model comparable to previous studies of random landscapes (e.g. Gardner et al. 1987). In the clumped scenario, disturbance events occurred as approximately circular clusters of cells, with cluster size modeled as a normal random variable with a mean of 50 cells and a standard deviation of 10 cells. This scenario produced more realistic, aggregated disturbance patches similar to clearcuts in a managed forest. In the fractal scenario, disturbance clusters had high edge-to-interior ratios, and disturbance event size was modeled as a lognormal random variable with a mean of 50 cells and a standard deviation of 10 cells. This scenario was most comparable to a natural fire regime, with more complex shapes and greater variation in disturbance sizes than the clumped scenario.

Species dynamics model

Metapopulation dynamics were simulated using a simple occupancy model, in which cells were classified as either occupied or unoccupied by a population of a hypothetical species. Occupied cells had a fixed probability of local extinction, e, during each time step. For all species, extinction also occurred following a disturbance, based on the assumption that organisms in disturbed cells either suffered direct mortality from disturbance or were unable to reestablish following the disturbance. For early-successional species, extinction also occurred when early-successional habitat was lost to vegetation regrowth (when the cell reached an age of 40 time steps). During each time step, the number of colonization attempts from an occupied cell was modeled as a Poisson random variable with mean equal to c. Each colonization attempt was modeled as a random walk assuming nearest-neighbor dispersal, with a maximum distance of d cells. Dispersers reaching the edge of the map were reflected off the map boundary. If suitable unoccupied habitat was reached in less than the maximum dispersal distance, then the first unoccupied cell encountered was colonized. Otherwise, the colonization attempt was unsuccessful and no new cells were occupied.

Because of computational limitations and the desire for adequate replication over a range of habitat patterns and amounts, this study focused on four hypothetical species. A full factorial design was not used because not all parameter combinations were ecologically reasonable. For example, it would be unrealistic to model an early-successional species with a very slow rate of dispersal-limited colonization. High-mobility species represented generalists with relatively high rates of metapopulation turnover that recolonized frequently and over relatively long distances ($c = 1$, $e = 0.1$, $d = 10$). High-mobility species were simulated for both early-successional (HMES) and old-growth (HMOG) habitats to allow comparison of species with similar life-history characteristics but different habitat associations. Restricted-mobility species had the same parameters as high-mobility species, but were restricted to movement only within their associated habitat. Low-mobility species had low rates of extinction and colonization, as well as limited dispersal distances ($c = 0.1$, $e = 0.01$, $d = 1$). Both the restricted-mobility species (RMOG), and the low-mobility species (LMOG) were simulated for old-growth habitats, allowing a comparison of species with similar habitat associations but different colonization rates and dispersal modes.

Simulation experiments

We carried out two types of simulation runs: dynamic and static (Figure 1). In the dynamic runs, both habitats and species changed over time. To initialize each simulation, landscape dynamics were modeled for 1000 time steps starting from a random landscape to allow the disturbance-generated patterns to overwrite the initial conditions. Once the initialization was finished, populations were established in random habitat cells. Simulations were carried out with two initial metapopulation sizes: 10 populations and 250 populations. In the dynamic runs, both landscape dynamics and species dynamics were simulated for 10,000 time steps (Figure 1). Preliminary analyses indicated that this length was sufficient to allow the metapopulations to either decline to extinction or reach a dynamic equilibrium. In the static runs, the landscape pattern at the end of the initialization period was held constant and only species

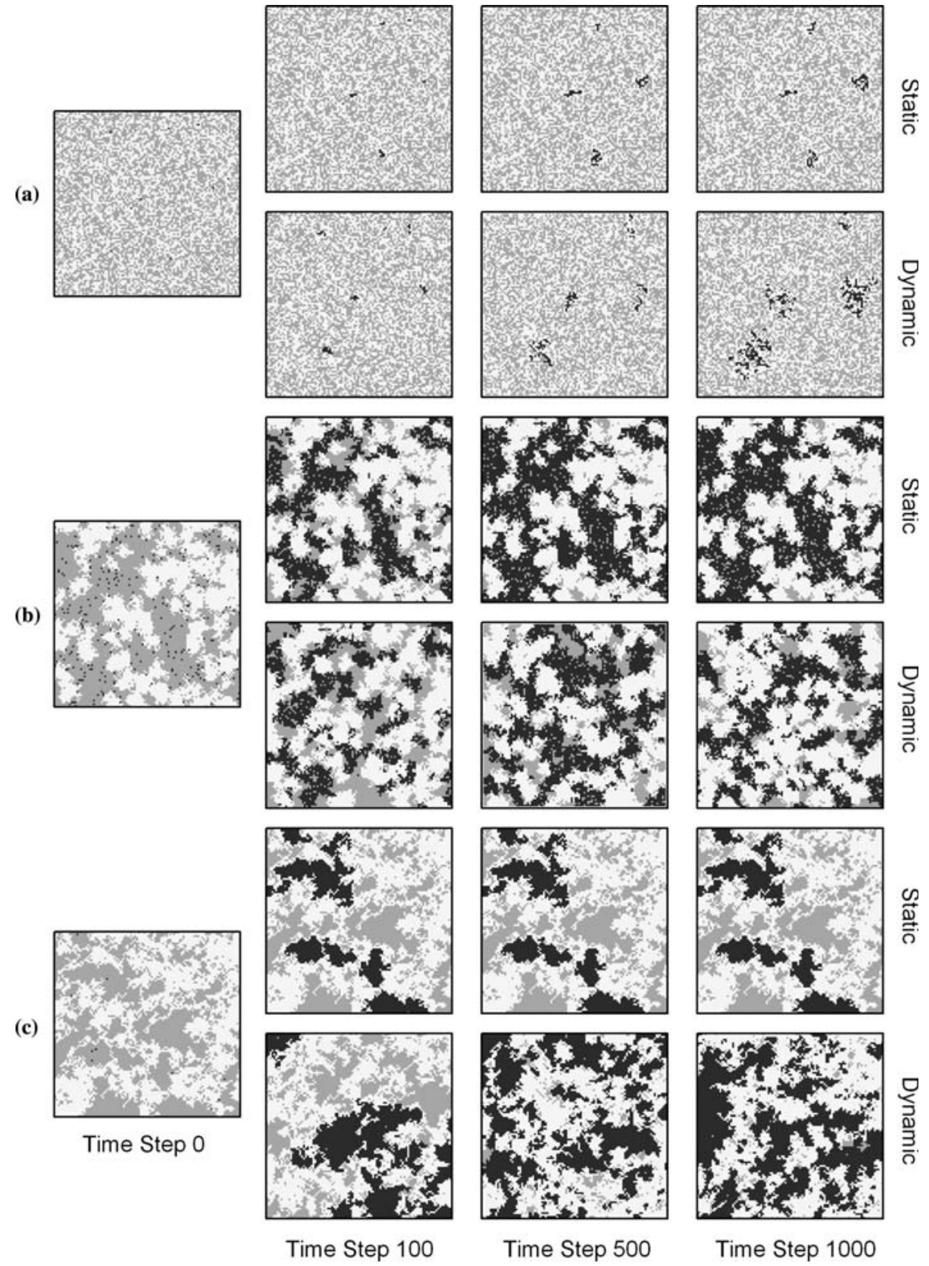

Figure 1. Sample graphical model output for (a) LMOG species in a random landscape with $p = 0.5$ and 10 initial populations, (b) LMOG species in a clumped landscape with $p = 0.5$ and 250 initial populations, and (c) RMOG species in a fractal landscape with $p = 0.5$ and 10 initial populations. Each set of two sample runs (static and dynamic) started with the same initial configurations of habitat and populations. In the static run, only species dynamics were modeled. In the dynamic run, both habitat and species dynamics were modeled. White cells represent non habitat, gray cells represent unoccupied habitat, and black cells represent occupied habitat.

dynamics were simulated. Thus, the landscape patterns in the static runs represented independently-generated iterations of the disturbance-generated habitat patterns from the corresponding dynamic runs.

To verify the disturbance algorithm and assess temporal variability in habitat amount, the simulated proportions of early-successional and old-growth habitats were computed using 50 landscapes for each combination of p and disturbance pattern. Landscape pattern indices, including the proportion of the landscape occupied by the largest patch, the total number of patches, and the standard deviation of patch sizes, were also computed for early-successional and old-growth habitats in each of these landscapes. Habitat patches were defined as clusters of connected grid cells based on an eight-cell adjacency rule.

To compare habitat occupancy in static and dynamic landscapes, 50 static and 50 dynamic runs were carried out for each combination of habitat proportion, disturbance pattern, and species. The total number of habitat cells and the proportion of occupied cells were recorded at the end of each simulation. Time series of individual model runs were also examined to explore temporal trends in habitat occupancy.

Results

Landscape dynamics

Mean simulated habitat amounts were all very close to the expected values of p. Mean habitat proportion was always within 0.006 of the expected p, and standard deviations were all less than 0.033. Differences among static landscapes generated for a given habitat amount and pattern, and among time steps in the dynamic simulations, were thus primarily manifested as variability in habitat arrangement rather than large fluctuations in habitat amount.

Changes in the largest patch index with habitat amount were similar for early-successional and old-growth habitats (Figure 2a). In the random landscapes a single large patch consisting of most of the habitat was fragmented when p was reduced to 0.4, and all patches became very small when p was further reduced to 0.3. Clumped and fractal landscape followed a similar trend, but had larger clusters of habitat than random landscapes at low values of p. The coefficient of variation of patch size was highest at intermediate levels of p (Figure 2b), whereas the number of patches generally decreased with p (Figure 2c).

In random landscapes, there was no difference in the patterns of early-successional and old-growth habitats for any of the landscape indices. Early-successional habitat in clumped and fractal landscapes had fewer patches and less variability in patch size than in random landscapes with the same p. Old-growth habitat in clumped and fractal landscapes had more patches and higher variability in patch size than in random landscapes when p was greater than 0.4. Old-growth habitats in clumped and fractal landscapes also had higher variability in patch size and more patches than early-successional habitats with similar patterns and the same p.

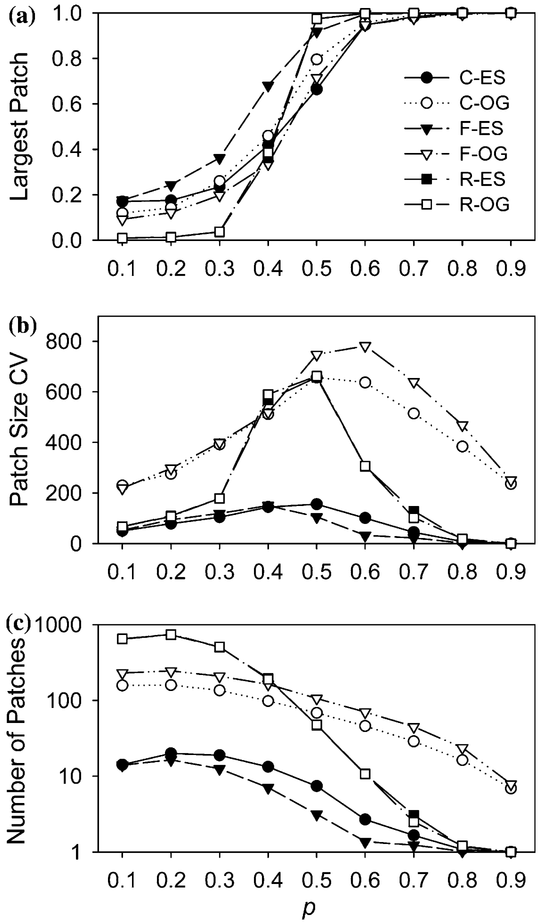

Figure 2. Patch metrics at varying levels of p for different habitats (ES = Early Successional, OG = Old Growth) and disturbance patterns (C = Clumped, F = Fractal, R = Random). Patches were defined as contiguous areas of habitats based on an 8-cell neighborhood. (a) Largest patch size expressed as a proportion of the total landscape, (b) Coefficient of variation of patch sizes, (c) Total number of patches.

Species dynamics

Simulation results were summarized as the mean habitat occupancy from 50 model runs for each combination of species, habitat pattern, static vs. dynamic habitat, and *p*. In 91% of these cases the standard error of the resulting mean was less than 0.01, and in all cases the standard error was less than 0.03. Based on these results, 50 model runs were deemed sufficient for comparing trends in habitat occupancy across the experimental factors. Because of their small sizes, error bars were not displayed in the graphs of model results.

In static simulations, the HMES species occupied nearly all available habitats when *p* was 0.3 or greater, with habitat occupancy declining slightly when *p* was less than 0.3 (Figure 3a, b). Habitat occupancy was always lower in the dynamic simulations, especially in clumped and fractal landscapes which had extinction thresholds at $p = 0.1$. Results were not appreciably different between the two initial metapopulation sizes, except that habitat occupancy in the static simulations was slightly higher at low values of *p* when the number of initial populations increased from 10 to 250. The HMOG species occupied the majority of available habitat across all values of *p*, and only minor differences were observed between static vs. dynamic simulations, different landscape patterns, and different initial conditions Figure 3c, d).

For the LMOG species with a small initial metapopulation, habitat occupancy was similar for static and dynamic simulations when *p* was 0.7 or greater (Figure 4a). When *p* ranged from 0.4 to 0.6, LMOG habitat occupancy was highest in the dynamic simulations for fractal and random landscapes, but similar in the dynamic and static simulations for clumped landscapes. When *p* decreased below 0.5, habitat occupancy began to decline more rapidly in the dynamic simulations. When *p* ranged from 0.1 to 0.3, habitat occupancy approached zero for all of the dynamic simulations, as well as for static simulations of random landscapes. However, static simulations of clumped and fractal landscapes remained above the extinction threshold even at $p = 0.1$.

Results for the LMOG species changed dramatically when the number of initial populations was increased to 250 (Figure 4b). Habitat occupancy in the static simulations was much higher than at the low initial population size, and with the exception of random landscapes at $p = 0.5$, was

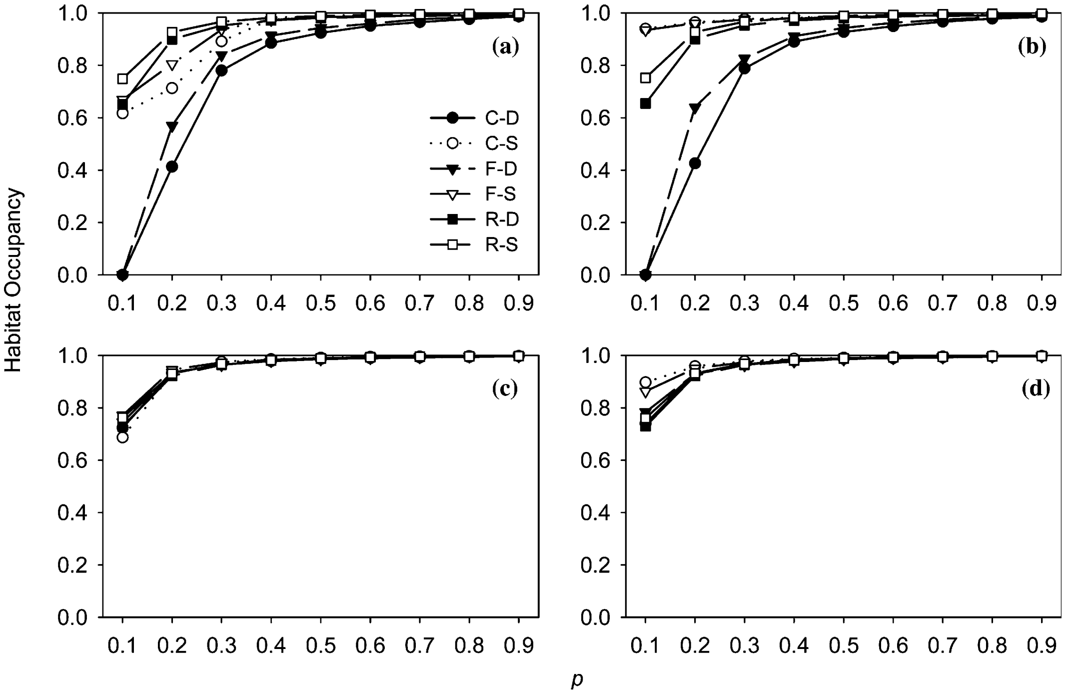

Figure 3. Habitat occupancy at varying levels of *p* for different scenarios (D = Dynamic Habitats, S = Static Habitats) and disturbance patterns (C = Clumped, F = Fractal, R = Random). (a) HMES species with 10 initial populations, (b) HMES species with 250 initial populations, (c) HMOG species with 10 initial populations, (d) HMOG species with 250 initial populations.

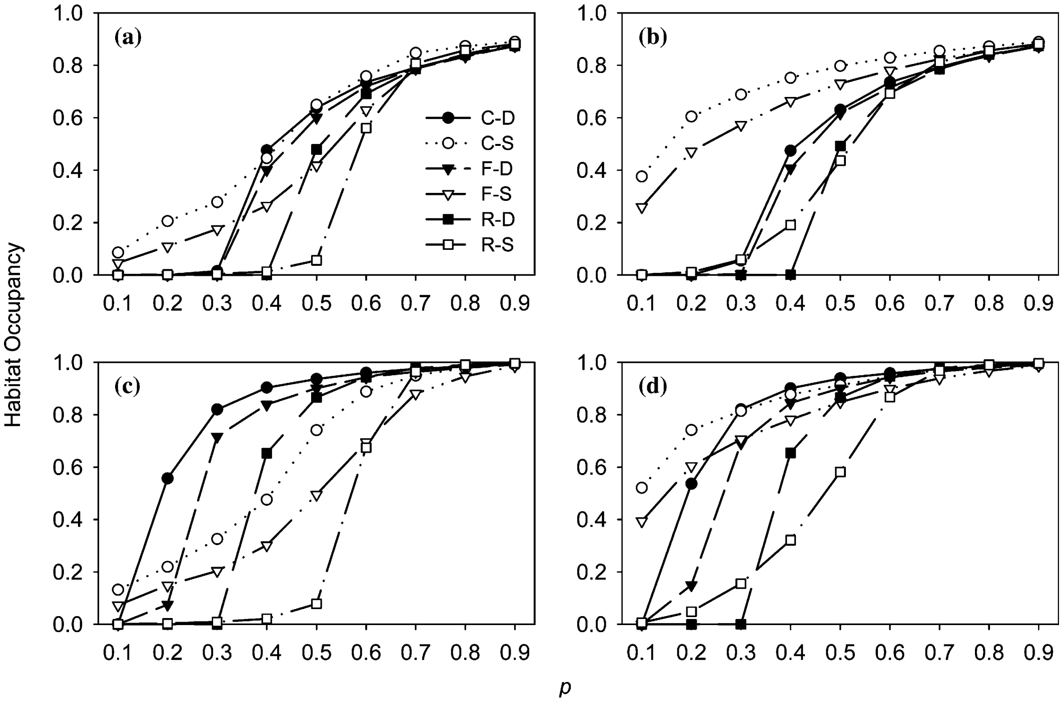

Figure 4. Habitat occupancy at varying levels of *p* for different scenarios (D = Dynamic Habitats, S = Static Habitats) and disturbance patterns (C = Clumped, F = Fractal, R = Random). (a) LMOG species with 10 initial populations, (b) LMOG species with 250 initial populations, (c) RMOG species with 10 initial populations, (d) RMOG species with 250 initial populations.

always greater than or equal to the corresponding dynamic simulations. These differences were generally larger for clumped and fractal landscapes than for random landscapes. For both the small and large initial metapopulations the LMOG species exhibited a more precipitous decline to extinction over a narrower range of *p* in the dynamic landscapes.

For the RMOG species with a small initial metapopulation, mean habitat occupancy was almost always higher in dynamic simulations when *p* was 0.6 or less (Figure 4c). This effect was more pronounced in random landscapes than in clumped or fractal landscapes. At high levels of *p*, initial decreases in habitat occupancy with declining habitat were more rapid in static simulations. However, as with the LMOG species, habitat occupancy in dynamic landscape began to decrease more rapidly once *p* dropped below 0.5, and dynamic simulations of clumped and fractal landscapes reached extinction thresholds at higher values of *p* than static simulations with similar patterns. When initial metapopulation size was increased to 250, habitat occupancy in static simulations of clumped and fractal landscapes was usually higher than or equivalent to the corresponding dynamic simulations (Figure 4d). Habitat occupancy in random landscapes was higher in dynamic simulations when *p* was 0.4 or 0.5, and higher in static simulations when *p* was 0.3 or less.

The preceding results were all based on simulations in which the species had reached a dynamic equilibrium with their habitats. However, different species required markedly different amounts of time to reach these equilibria. The HMES and HMOG species always reached equilibrium very rapidly, (< 50 time steps) from either the low or high initial metapopulation size. The RMOG species also reached a dynamic equilibrium fairly rapidly, although it took several hundred time steps to reach high levels of equilibrium occupancy from 10 initial populations (Figure 5a). The LMOG species, in contrast, required several thousand time steps to reach equilibrium habitat occupancy from the low initial condition (Figure 5b). With a small initial metapopulation size, *p* equal to 0.5, and a random landscape pattern, the equilibrium habitat occupancy was much larger

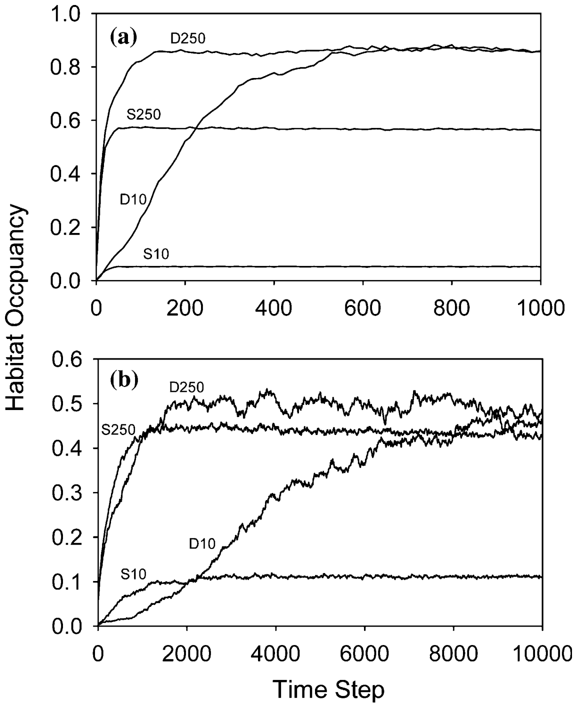

Figure 5. Temporal trends in habitat occupancy for species associated with old-growth habitat under different scenarios (D = Dynamic Habitats, S = Static Habitats) and different initial conditions (10 or 250 initial populations). (a) RMOG species for $p = 0.5$ and random habitat pattern. (b) LMOG species for $p = 0.5$ and random habitat pattern.

for dynamic than for static habitats (Figure 4a). However, the dynamic simulations required nearly 9000 time steps to reach this value, and for the first 2200 time steps habitat occupancy was actually higher in the static landscape. Both simulations reached equilibrium habitat occupancy in less than 2000 time steps when the initial metapopulation size was 250.

Discussion

Assumptions and limitations

To derive a suite of generalized hypotheses about species responses to habitat dynamics, this study was carried out using a relatively simple model (Fahrig 1991). The landscape dynamics simulations were based on the exponential model of disturbance frequency, with spatial and temporal clustering of disturbances and patch-age based habitat transitions. Although the model incorporates numerous simplifying assumptions, it has considerably more ecological realism than other models that are either not spatially explicit (Boughton and Malvadkar 2002) or incorporate random disturbances and constant probabilities of habitat creation and destruction (Keymer et al. 2000). In particular, the different results from random, clumped, and fractal disturbance patterns emphasize the importance of considering the spatial patterns of disturbances and habitats. However, it is likely that factors not considered in the present model, such as spatial variability in disturbance regimes (Heyerdahl et al. 2001) and successional pathways (Wimberly and Spies 2001) also influence the relationships between habitat dynamics and populations in real landscapes.

Another fundamental assumption was the treatment of habitat as a binary variable. This decision greatly simplified parameterization and increased the efficiency of the simulations. In the case of early-successional habitat, which can be lost to canopy closure of shrubs or trees within a few growing seasons, this assumption may be realistic. The successional transition between young forest structure and old-growth habitat is more gradual, however, and old-growth species likely view habitat as a continuum rather than as discrete classes (Glenn et al. 2004). In addition, species with restricted dispersal were assumed to only move within cells classified as habitat. Although forest species often exhibit strong preference for movement within closed-canopy forest rather than across gaps, many will also occasionally cross open areas (Desrochers and Hannon 1997; Bakker and Van Vuren 2004). In real landscapes, both habitat patches and the intervening matrix will exhibit some degree of spatial heterogeneity, which can significantly impact dispersal success (Gustafson and Gardner 1996).

Simulation-based studies of fragmentation in static landscapes are also sensitive to the specification of the underlying population model. Patch occupancy models, such as the one used in this study, exhibit higher extinction thresholds (i.e. are more sensitive to habitat fragmentation) than models that explicitly track the demographics of individuals within each patch (Fahrig 2002). Similarly, sensitivity to dispersal distance is much greater for metapopulations of species with high population growth rates (the implicit assumption in patch occupancy models) than in species with lower population growth rates (Johst et al. 2002). The influences of these myriad assumptions were beyond the scope of the current study. In the future, additional sensitivity and uncertainty analyses of linked landscape- and species-dynamics models should focus on identifying key assumptions that model results are contingent upon (e.g. Fahrig 2002; Wimberly 2004).

Contrasts between static and dynamic habitats

Species in dynamic landscapes exhibit more pronounced critical behavior as a function of decreasing habitat amount than species in static landscapes. Even in situations where habitat occupancy was higher in the dynamic landscapes at intermediate levels of habitat, habitat occupancy always declined more rapidly with decreasing habitat and reached extinction at higher habitat amounts than in the static landscapes. A previous study similarly found that habitat occupancy in simulated dynamic landscapes exhibited threshold responses to declining habitat even though spatial metrics of habitat connectivity exhibited nearly linear responses (Hanski 1999). Thus, assessments of habitat connectivity based on relatively simple neutral models (Gardner et al. 1987) or even more sophisticated spatial analyses (Keitt et al. 1997) may underestimate rates of species decline with habitat loss when landscapes are in fact dynamic.

High-mobility species are insensitive to landscape dynamics at moderate to high amounts of habitat. Rapid colonization rates and long-distance dispersal effectively saturate all available habitats, compensating for the additional mortality caused by habitat destruction. However, even high-mobility species exhibit markedly different responses to early-successional vs. old-growth habitats. These differences result primarily from the distinctive spatial patterns of these age classes. Early-successional habitat clusters are created by disturbance and resemble the sizes and shapes of individual disturbance events. In contrast, old-growth patches are created indirectly when habitats survive for 200 time steps without being disturbed. During this time lag, subsequent disturbances gradually fragment age-classes, resulting in a few large and many small old-growth habitat clusters. This spatial pattern is likely to be advantageous for metapopulation persistence in dynamic landscapes because the larger patches can support large, stable population clusters, whereas the numerous smaller patches serve as ‘stepping stones’ that allow new habitat patches to be quickly colonized. Previous research demonstrated that these patterns were characteristic of old growth in pre-European landscapes of the coastal Pacific Northwest (Wimberly 2002), and the present study further suggests that small habitat fragments can play an important role in maintaining species in dynamic landscapes.

Low-mobility and restricted-mobility species associated with old-growth habitats can exhibit either higher or lower habitat occupancy in dynamic landscapes. At intermediate habitat amounts, temporary connections in dynamic habitats allow species to disperse among the shifting habitat patches, even if the configuration of patches is highly fragmented at any single point in time. This effect was most pronounced in random landscapes, least pronounced in clumped landscapes, and intermediate in fractal landscapes. In the random landscapes, individual disturbance patches are a single cell in size, matching exactly the spatial grain of the metapopulation model. In comparison, clumped disturbances are much larger than the grain of the metapopulation model, and fractal disturbances create a mixture of small and large disturbance patch sizes. Thus, the potential for enhanced connectivity and increased habitat occupancy in dynamic landscapes seems to be greatest when the spatial scale of habitat fragmentation is similar to spatial scale of metapopulation dynamics.

In addition, habitat occupancy is higher in dynamic landscapes than in the corresponding static landscapes only when the initial metapopulation size is very low. In these cases, founder populations in the static landscapes are essentially trapped within their habitat patches by dispersal limitation, and isolated patches that do not receive an initial population have no chance of colonization. At higher initial metapopulation sizes, populations are seeded across nearly all of the patches, and the additional connectivity provided by habitat dynamics is no longer advantageous. When habitat amount decreases below a threshold level, patches remain isolated even in the dynamic landscapes. In these cases, species in dynamic landscapes reach extinction more rapidly than in static landscapes because of the additional mortality caused by disturbance and habitat turnover.

These results differ from prior modeling experiments which found that increased habitat dynamics always resulted in decreased habitat occupancy and higher probability of extinction (Keymer et al. 2000; Boughton and Malvadkar 2002). Boughton and Malvadkar (2002) used a non-spatial model, whereas the present study used a spatially explicit model in which ephemeral patches could be linked through dispersal. Keymer et al. (2000) simulated a dispersal-limited species that was similar to the LMOG species in the present study, using a spatially explicit model that simulated habitat dynamics as a Markov process with constant probabilities of habitat creation and destruction. In contrast, the present study used an age-structure habitat dynamics model in which destruction of old-growth habitat had a fixed and constant probability, and habitat creation occurred at a fixed time following disturbance. Thus, different results may be attributable to differences in the underlying habitat dynamics model. This assertion is supported by Johnson (2000), who found that simulated population dynamics in successional landscapes are sensitive to variability in the rate of patch succession.

Matlack and Monde (2004) used a Markov model of landscape dynamics similar to that of Keymer et al. (2000), but found that in dynamic landscapes habitat occupancy peaked at intermediate rates of habitat dynamics. This phenomenon was most pronounced for species with rapid dispersal rates, and was not apparent at very low dispersal rates that were comparable to those used in Keymer et al. (2000). The present study similarly found that RMOG species exhibit higher levels of habitat occupancy than LMOG species in dynamic landscapes with similar habitat amounts and patterns, further supporting the idea that a high rate of mobility, relative to the rate of landscape change, is necessary to allow a species to take of advantage of spatio-temporal connectivity in dynamic landscapes. In contrast, sessile organisms with limited dispersal such as understory plants are less likely to benefit from enhanced connectivity in frequently-disturbed landscapes.

Conclusions

The major insight from this work is that species with either low colonization rates or dispersal restricted to habitat patches can exhibit higher habitat occupancy in dynamic landscapes than in static landscapes with similar habitat patterns. This phenomenon occurs at intermediate levels of habitat availability when patches are spatially fragmented at a single point in time, but remain connected over multiple time steps. The potential for species responses to this spatio-temporal connectivity is likely to be greatest when metapopulation processes and disturbance regimes operate at similar spatial and temporal scales. However, habitat occupancy in dynamic landscapes also declines more rapidly as habitat approaches zero and reaches extinction at higher habitat amounts than in corresponding static landscapes. The consequence of these two effects is a more pronounced critical behavior in the dynamic landscapes, with habitat occupancy exhibiting a more precipitous decline to extinction with decreasing habitat than in static landscapes.

The results of this simulation experiment are contingent upon numerous simplifying assumptions, and it remains to be seen whether similar effects are manifested for species in real landscapes. Even so, the general prediction that species will have greater sensitivity to changing habitat amounts in dynamic patch mosaics strongly suggests that landscape-level ecological assessments should explicitly consider the spatial and temporal dynamics of habitats as well as organisms. In particular, caution should be exercised in extrapolating results from population assessments based on static habitat maps to real landscapes.

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