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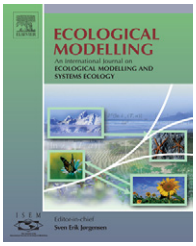

Spatial hyperdynamism in a post-disturbance simulated forest

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ABSTRACT

Competition–colonization models can address the population dynamics of remnants following habitat destruction. Spatially explicit versions have produced qualifications of the extinction debt issue and limited hyperdynamism in populations following habitat destruction. Although spatially explicit, these efforts examined few indicators of the spatial structure of the landscape. An existing model is modified here to represent a difference in niche adaptations as well as the competition–colonization tradeoff. Several landscape metrics are calculated at each iteration. Although the addition of niche differentiation did not change the qualitative outcome of the model, the spatial metrics show that some aspects of landscape structure, i.e., average patch area and proximity, become hyperdynamic and remain so. Small fluctuations in species populations are magnified in their spatial expression because the landscape is simplified.

1. Introduction

The strong influence of the spatial pattern of landscapes on the abundance, distribution, and dynamics of populations and communities inhabiting those landscapes is of central interest to many ecologists. Human activities have increasingly fragmented natural habitats into patches or remnants, subdividing once large populations into smaller groups. Fragmentation can affect population viability and opportunities for the coexistence of species (e.g., Kareiva, 1990; Terborgh et al., 2001), have an important effect on gene flow and the genetic substructure of populations (e.g., Gerlach and Musolf, 2000; Vuilleumier and Fontanillas, 2007), and eventually lead to species extinction (e.g., Rukke, 2000; Marshall et al., 2006). This spatiotemporal heterogeneity has been important in the development of observations and theory of the roles of adaptations for competitive and colonizing abilities among plant species (e.g., Bolker and Pacala, 1999; Turnbull et al., 1999, 2007; Levine and Rees, 2002; Yu and Wilson, 2001; Munkemuller and Johst, 2006; Graniero, 2007). The interest in spatially explicit modeling of fragmentation processes and effects is high (e.g., Echeverria et al., 2008; Hernandez, in press).

The nature of the relative roles of competitive and colonizing abilities is cast in terms of a trade-off, because the adaptations are often for different allocations of resources for the same function (e.g., few large seeds versus many small seeds). Because much of what involves colonizing ability is spatial, such as area to which seeds can be dispersed in terms of numbers and distances, space is an important component of this development. Laurance (2002) proposed that fragmented forests suffer from a chronic increase in the variance of population, community or landscape characteristics following cutting, which he called hyperdynamism; here, we examine variance in specific landscape metrics to focus on spatial hyperdynamism.

Models are one of the primary ways in which colonization and competition trade-offs and their role in ecology has been studied. Competition–colonization (CC) models vary in

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their mathematical sophistication (e.g., Pacala and Rees, 1998) versus their computational basis (e.g., Malanson et al., 2007). Many deal with space abstractly (e.g., Mouquet et al., 2002; Hui et al., 2004) and others more explicitly (e.g., Neuhauser, 1998; Bolker and Pacala, 1999) (cf. Bolker et al., 2003). Much of the work in this area is aimed at assessing conditions for species coexistence and thus diversity (e.g., Matsinos and Troumbis, 2002) and more recently at addressing questions of invasive species (e.g., Arii and Parrott, 2006). Some of the initial work in this type of modeling was done for animal ecology, deriving from metapopulations models (e.g., Nee and May, 1992) and animal CC modeling continues to be important (e.g., Gardner and Gustafson, 2004). The objective of this research is to gain a better understanding of the effects of spatial pattern on species dynamics in the CC class of ecological models. In particular, few models have addressed how the spatial pattern of landscapes is constantly recreated and changed as species reproduce, compete, and die.

Wimberly (2006) used a model of patch occupancy, essentially a multi-species metapopulation model but without competition, and investigated the effects of maintaining a static pattern of habitat versus having the habitat quality altered by repeated disturbances. He found that critical responses in patch occupancy were eliminated in dynamic landscapes with fractal and clumped spatial patterns of habitat, but not in those with random patterns. Landscapes are dynamic, and disturbance is a very important component of all landscapes. To have a dynamic landscape as the simulation baseline is more realistic than using a static one. Malanson et al. (2007) analyzed the patch-per-unit spatial metric (Frohn, 1998) and found that it fluctuated synchronously as species along the competitive hierarchy replaced each other in the iterations following disturbance. We will address outcomes not seen by Malanson et al. (2007) by modifying their model and analyzing different spatial metrics.

A major elaboration of the competition–colonization idea is within the narrative of extinction debt (ED). When habitat is destroyed, some species in remnants are doomed to go extinct through loss of area and increase in isolation (Tilman et al., 1994; see MacArthur, 1972, p. 110). But these doomed species may not go extinct immediately; they may remain on the remnant for some time and then become locally extinct gradually. So there will be a difference between diversity when the habitat becomes a remnant and diversity when the ecosystem achieves its theoretical future equilibrium, which is defined as ED (Tilman et al., 1994). Tilman et al. (1997) built a spatially explicit ED model to examine one single large patch and a checkerboard pattern in an infinite non-habitat. Results show that after habitat destruction, superior competitors become extinct before superior colonizers. From that study we know that aggregated landscape patterns can help superior competitors persist in the simulation model. Klausmeier (1998) used a simple spatial representation that limited dispersal and allowed more coexistence in less habitat. Malanson (2002a) developed a more spatially detailed ED model including hierarchical competition and species-specific reproduction, dispersal, and mortality to further study the changes of abundance for each species with both two-phase and continuous representations of landscape. The results show the thresholds are not evident among different amounts of extant habitat or across a range of spatial patterns. Better competitors are more sensitive to the initial stage of destruction and leave a more dispersed pattern of habitat; while better colonizers have the opposite trends. Lin (2005) found that extinctions in and ED model could alternate along the hierarchy as the species started going extinct and releasing their closest competitors from pressure. Lin et al. (2005) found that defining the species relationship to the habitat could alter the entire ED outcome. Lin (2003) also used ED as a starting point to analyze habitat restoration.

Much prior research assumed the existence of a binary landscape of habitat and matrix (non-habitat), and most research about species dynamics has been mainly focused on habitat (remnant), especially in modeling (e.g., Wu and Vankat, 1991). The matrix, viewed as uniform background surrounding the habitat patches, is often ignored as being unsuitable to sustain species. The matrix is the most extensive and connected patch type (Turner et al., 2001), but it can be just the land cover type surrounding the patches of immediate interest (Kupfer et al., 2006). Recently there has been a growing awareness of the importance of matrix quality in affecting the dynamics of population and community-level processes in fragmented landscapes (e.g., Jules and Shahani, 2003; Dunford and Freemark, 2004; Debinski, 2006; Kupfer et al., 2006). Some recent models have included the landscape matrix more explicitly (e.g., Pichancourt et al., 2006; Hoyle, 2007). Malanson (2002b) developed a simulation of ED on a more continuous surface as a representation of habitat quality for five species on a hierarchy of competition–colonization tradeoffs and found that changes in quality equivalent to binary destruction had even greater effects but that spatial pattern per se mattered less. Malanson et al. (2007) extended this analysis to examine patterns of resilience and found only short-lived hyperdynamism following habitat destruction

2. Methodology

2.1. *Landscape models*

Following Malanson et al. (2007), we generated synthetic landscapes as grids representing an environmental gradient based on virtual elevation of a surface in three dimensions created using the random midpoint displacement method (Saupe, 1988; Gardner, 1999), which is the most common method of generating fractal landscapes. The process started from a single large grid cell, which was quartered into four identical smaller cells by connecting the midpoint of the parallel edges. The elevation of the first four cells was randomly assigned using a Gaussian probability function. This cell quartering process is repeated for six iterations, and a grid with an extent of $2^6 \times 2^6$ (4096 cells) was created. The elevation of each newly generated grid cell was determined from adjoining cells with a Gaussian displacement factor added, computed according to the given fractal dimension D. After this process, a 3D landscape consisting of 4096 cells was generated. Then the corresponding 2D landscape with virtual elevation as habitat character was used as a baseline to run the simulations.

For these analyses all landscapes were generated with a 3D fractal dimension of 2.5. The initial habitat values ranges from