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Locally dispersing populations in heterogeneous dynamic landscapes with spatiotemporal correlations. II. Habitat driven by voter dynamics

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HIGHLIGHTS

- We study a spatially explicit population model on dynamic heterogeneous landscapes.
- Population dispersal and habitat dynamics are studied at local and global scales.
- The spatial scale of habitat dynamics affects segregation of disturbances.
- Dynamic habitat can induce spatial clustering in populations with global dispersal.

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ABSTRACT

We examine a spatially explicit population model on a dynamic landscape with suitable and unsuitable habitat driven by voter or contagion dynamics. We consider four cases, consisting of all combinations of local and global interactions for both population dispersal and habitat dynamics. For both local and global population dispersal, using local habitat dynamics always increases population density relative to the case with global habitat dynamics, due to the resulting segregation of habitat turnover, decrease in effective habitat turnover rate, and presence of stable habitat corridors. With global habitat dynamics, a population using local dispersal exhibits lower density than one with global dispersal due to local crowding as well as frequent disturbance due to habitat transitions. On the other hand, with local habitat dynamics, a population using local dispersal can exploit suitable habitat patches and use dynamic corridors to colonize new regions. The latter effect is not seen with static landscapes, where clustered habitat can lead to the isolation of suitable patches due to surrounding unsuitable habitat.

1. Introduction

The relative importances of loss, fragmentation, and heterogeneity of habitat are widely known (Andrén, 1994; Bodin et al., 2006; Bonin et al., 2011; Debinski and Holt, 2000; del Castillo, 2015; Didham et al., 1998; Fahrig, 1997; Lande, 1987; Santos et al., 2015; Wiegand et al., 2005). Habitat heterogeneity in space and time has a wide variety of effects, including species composition in benthic communities (Munguia et al., 2011), seed production and dispersal and seedling establishment in forests (Uriarte et al., 2010), and the movements of organisms among patches (Collinge and Palmer, 2002; Diffendorfer et al., 1995). The effects of habitat heterogeneity may even vary over time within the lifetime of a particular organism (Bonin et al., 2011; Hovel and Lipcius, 2001).

Heterogeneities in space and time are intrinsically linked, with the variability in one dependent upon the scale within which the other is observed (Hiebeler and Michaud, 2012). Spatial and temporal variability, as well as their interactions, impact the structure of populations as well as communities (Chesson, 1985; Cleland et al., 2013; DeWoody et al., 2005; Fahrig, 1992; Jacquemyn et al., 2003; Johnson, 2004; Keymer et al., 2000; Loehle, 2007; Moloney and Levin, 1996; Snäll et al., 2005). For example, the spatial scale of disturbances influence species diversity, either by driving local extinction of species, or by leading to greater spatial variability in the densities of various species among communities (Limberger and Wickham, 2012).

Spatial or temporal variation are typically studied separately, although some investigations have addressed habitat that is both time-varying and spatially structured (Matlack, 2005; Matlack and Monde, 2004). It has been found that dynamic habitat can change the importance of features such as patch connectivity and patch quality, as compared with static habitat (Hodgson et al., 2009). In

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some cases, the effects of spatial features such as fragmentation are reversed in dynamic landscapes relative to static landscapes (Roy et al., 2004).

Temporal variation in habitat may arise from human land use, abiotic factors such as wind and rain, or the presence of other species that either promote or inhibit growth of a focal species. In all cases, the dynamics of habitat change may have a spatially local component. Here we explore the role of spatial scale of population dispersal and habitat dynamics on population density. Local habitat dynamics are modeled via a cellular automaton voter or contagion model. Variations of cellular automaton voter models have seen applications to the spread of Müllerian mimicry in predator–prey systems (Sherratt, 2006), maintenance of species diversity (Molofsky et al., 1999; Molofsky and Bever, 2002), as well as the emergence of large-scale patterns from small-scale interactions and decisions in social systems (Schelling, 2006). They are also a variation of the stepping stone models used in population biology and genetics (Kimura and Weiss, 1964; Weiss and Kimura, 1965; Renshaw, 1991). Here we use the voter model to simulate the spread of two variations such as neutral alleles, or equal competitors, that make up an important part of the substrate for the species of interest. It could also represent the spread of ideas about human land use decisions, for example the application of pesticides, herbicides, or fertilizers in residential plots.

2. The model

We use a single-species patch occupancy model based on a continuous-time Poisson process on a discrete lattice where every site has z neighbors. Our study used a rectangular lattice with $z=4$. Each site in the lattice is in one of three states: empty with suitable habitat (state 0), empty with unsuitable habitat (state 1), or occupied with suitable habitat (state 2). The habitat is dynamic, with transitions between suitable and unsuitable habitat following a cellular automaton voter or contagion model. Habitat dynamics and population dynamics were both explored using local and global neighborhoods.

Without loss of generality, we rescale the time units in the model so that each occupied site in the lattice updates its habitat state at rate 1 in the sense of a Poisson process, with times between updates following an exponential distribution with a mean of 1. When a site updates its habitat, it copies the habitat state of one of its neighbors, chosen at random with equal probability for all neighbors. With the local neighborhood, the site to be copied is chosen from among the four adjacent sites in the lattice. With the global neighborhood, the site to be copied is chosen from among all sites in the lattice. If the habitat of an occupied suitable site changes to unsuitable, the site also becomes empty, i.e., the population is removed.

Each occupied site in the lattice reproduces at rate ϕ (with times between reproduction events following an exponential distribution with mean $1/\phi$). When reproduction occurs, a target site is chosen from among one of the neighbors. Again, the four nearest neighbors are used with local dispersal, and all sites in the lattice are used with global dispersal. If the chosen target site is empty and suitable, it immediately becomes colonized; otherwise, the offspring is wasted. Finally, each occupied site becomes empty at mortality rate μ. See Table 1 for a list of symbols used in this study.

Stochastic simulations were performed on a 300 × 300 lattice with wraparound boundary conditions. Throughout our study, we assume that the habitat distribution has reached a dynamic equilibrium, with the proportion and spatial correlations of suitable and unsuitable sites not changing other than due to stochastic fluctuations. When performing simulations, we first run each simulation until the habitat distribution has reached equilibrium We then introduce the population, setting proportion ρ_0 of suitable sites (chosen at random) as occupied. We used $\rho_0 = \max(1-\mu/\phi, 0.1)$; this is the equilibrium density for a globally dispersing population with only suitable habitat (which serves as an overestimate of expected population density for our model), with a lower bound of 10% of sites initially occupied. Simulations were run until equilibrium was reached, using the same stopping criteria as Hiebeler et al. (2016).

We explored four neighborhood combinations for landscape and population dynamics:

Case 1 GhGp:	global habitat dynamics, global population dispersal.
Case 2 LhGp:	local habitat dynamics, global population dispersal.
Case 3 GhLp:	global habitat dynamics, local population dispersal.
Case 4 LhLp:	local habitat dynamics, local population dispersal.

Fig. 1 displays images of 100 × 100 lattices corresponding to the four cases.

3. Mathematical approximations

Let $P[i]$ represent the proportion of sites in state i, with $i \in \{0, 1, 2\}$. Define $p_s = P[0] + P[2]$ as the proportion of sites containing suitable habitat; our assumption that the habitat distribution is at equilibrium implies that p_s is fixed over time. Note that $P[0] + P[1] + P[2] = 1$, giving $P[1] = 1 - p_s$ and $P[0] = p_s - P[2]$. We will summarize the state of the population via $\rho := P[2]/p_s$, the proportion of suitable sites that are occupied.

Similarly, let $P[ij]$ represent the proportion of pairs of adjacent sites where the first site is in state i and the second site is in state j. With three states per site, there are nine such pair probabilities. We assume rotational symmetry, eliminating three probabilities:

$$P[10] = P[01], \quad P[20] = P[02], \quad P[21] = P[12].$$

The assumption that the habitat distribution is at equilibrium implies that the amount of unsuitable habitat $P[1]$ is fixed and that the spatial distribution of unsuitable habitat as characterized by $P[11]$ is also fixed. The fact that $\sum_{j\in\{0,1,2\}} P[j1] = P[1]$ (with $P[1] = 1 - p_s$ fixed) eliminates another probability:

$$P[12] = P[1] - P[01] - P[11] = 1 - p_s - P[01] - P[11] \tag{1}$$

Finally, the constraint that all nine probabilities must sum to one eliminates one more:

$$\begin{aligned} P[22] &= 1 - P[00] - P[11] - 2P[01] - 2P[02] - 2P[12] \\ &= 2p_s - 1 + P[11] - P[00] - 2P[02]. \end{aligned}$$

This allows us to work with only the three pair probabilities $P[00]$, $P[01]$, and $P[02]$, and recover the others as needed. However, we instead opt to use $P[2]$, $P[00]$, and $P[01]$, and then use the fact that $\sum_{j\in\{0,1,2\}} P[j0] = P[0] = p_s - P[2]$ to recover

$$P[02] = p_s - P[2] - P[00] - P[01]. \tag{2}$$

We will also need conditional probabilities describing neighborhood configurations. We let $Q_{i|j} = P[ij]/P[j]$ be the probability that if we randomly choose a site in state j, then a randomly chosen neighbor of that site is in state i. Similarly, $Q_{i|jk}$ represents the probability that for a randomly chosen pair of adjacent sites in states j and k, a randomly chosen neighbor of the state-j site (distinct from its known neighbor in state k) is in state i. We use ordinary pair approximation to replace

$$Q_{i|jk} \approx Q_{i|j} = P[ij]/P[j], \tag{3}$$