Locally Dispersing Populations in Heterogeneous Dynamic Landscapes with Spatiotemporal Correlations.

II. Habitat Driven by Voter Dynamics

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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.

Keywords: habitat loss and fragmentation, cellular automata voter model, dynamic habitat, spatiotemporal structure, stochastic spatial simulation

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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).

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

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

46 **2. The Model**

47 We use a single-species patch occupancy model based on a continuous-time
48 Poisson process on a discrete lattice where every site has z neighbors. Our
49 study used a rectangular lattice with $z = 4$. Each site in the lattice is in one
50 of three states: empty with suitable habitat (state 0), empty with unsuitable
51 habitat (state 1), or occupied with suitable habitat (state 2). The habitat is
52 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 .

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

81 overestimate of expected population density for our model), with a lower bound
 82 of 10% of sites initially occupied. Simulations were run until equilibrium was
 83 reached, using the same stopping criteria as Hiebeler et al. (submitted).

84 We explored four neighborhood combinations for landscape and population
 85 dynamics:

86 **Case 1GhGp:** global habitat dynamics, global population dispersal

87 **Case 2LhGp:** local habitat dynamics, global population dispersal

88 **Case 3GhLp:** global habitat dynamics, local population dispersal

89 **Case 4LhLp:** local habitat dynamics, local population dispersal

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

91 3. Mathematical approximations

92 Let $P[i]$ represent the proportion of sites in state i , with $i \in \{0, 1, 2\}$. Define
 93 $p_s = P[0] + P[2]$ as the proportion of sites containing suitable habitat; our
 94 assumption that the habitat distribution is at equilibrium implies that p_s is
 95 fixed over time. Note that $P[0] + P[1] + P[2] = 1$, giving $P[1] = 1 - p_s$ and
 96 $P[0] = p_s - P[2]$. We will summarize the state of the population via $\rho := P[2]/p_s$,
 97 the proportion of suitable sites that are occupied.

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

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

102 The assumption that the habitat distribution is at equilibrium implies that the
 103 amount of unsuitable habitat $P[1]$ is fixed and that the spatial distribution

Figure 1: Images of landscapes with the four different neighborhood combinations. Empty suitable sites are colored white, unsuitable sites are black, and occupied suitable sites are gray. **Top left:** global population dispersal and habitat dynamics (case 1GhGp). **Top right:** global population dispersal, local habitat dynamics (case 2LhGp). **Bottom left:** local population dispersal, global habitat dynamics (case 3GhLp). **Bottom right:** local population dispersal and habitat dynamics (case 4LhLp). With global habitat dynamics (cases 1GhGp and 3GhLp), fecundity $\phi = 8$ was used. With local habitat dynamics (cases 2LhGp and 4LhLp), $\phi = 4$ was used. Mortality was $\mu = 1$ for all four cases.

	Symbol	Meaning
States	0	Empty suitable habitat
	1	Empty unsuitable habitat
	2	Occupied suitable habitat
Model parameters	ϕ	Per-capita reproduction rate
	μ	Per-capita mortality rate
	z	Number of neighbors of each site in the lattice
Probabilities	$P[i]$	Probability a randomly-chosen site is in state i
	$P[ij]$	Probability a randomly-chosen pair of adjacent sites are in states i, j
	$Q_{i j}$	$P[ij]/P[j]$, the probability that a randomly-chosen neighbor of a randomly chosen state- j site is in state i
	p_s	$P[0] + P[2]$, the proportion of sites with suitable habitat
	ρ	$P[2]/p_s$, the proportion of suitable sites occupied
Model cases	1GhGp	Global habitat dynamics, global population dispersal
	2LhGp	Local habitat dynamics, global population dispersal
	3GhLp	Global habitat dynamics, local population dispersal
	4LhLp	Local habitat dynamics, local population dispersal

Table 1: Symbols used in the differential equation model, and the four cases of the model studied here.

104 of unsuitable habitat as characterized by $P[11]$ is also fixed. The fact that
 105 $\sum_{j \in \{0,1,2\}} P[j1] = P[1]$ (with $P[1] = 1 - p_s$ fixed) eliminates another probability:

$$\begin{aligned} P[12] &= P[1] - P[01] - P[11] \\ &= 1 - p_s - P[01] - P[11] \end{aligned} \tag{1}$$

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

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

108 This allows us to work with only the three pair probabilities $P[00]$, $P[01]$,
 109 and $P[02]$, and recover the others as needed. However, we instead opt to use
 110 $P[2]$, $P[00]$, and $P[01]$, and then use the fact that $\sum_{j \in \{0,1,2\}} P[j0] = P[0] =$
 111 $p_s - P[2]$ to recover

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

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

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

119 by assuming that the states of non-adjacent sites are independent when condi-
 120 tioned on the known state of a common neighbor they share.

For the distribution of suitable and unsuitable habitat, we assumed proportion $p_s = 0.5$ of sites were suitable in our study. Exploration of the model with other values of p_s gave similar qualitative results. With global habitat dynamics, $Q_{1|1} = P[1] = 0.5$ as well, due to the lack of spatial correlations. With local habitat dynamics, analysis of the voter model on a rectangular lattice gives a clustering coefficient of $Q_{1|1} \approx (2P[1] + 1)/3 = 2/3$ when estimated using pair approximation (Hiebeler, 2007). We then use this to compute

$$P[11] = P[1]Q_{1|1}. \quad (4)$$

Measurements from simulations of the habitat distribution with local dynamics and with $p_s = 0.5$ indicate $Q_{1|1} \approx 0.8079$, which will also be used with our differential equation models, and compared with the above approximated value of $2/3$. Note that the above values of $Q_{1|1}$ are referring only to clustering of habitat types, and do not include any information about the population.

For case 1GhGp (global habitat dynamics and population dispersal), we can write a differential equation for the proportion of sites that are suitable and occupied:

$$\begin{aligned} \frac{dP[2]}{dt} &= \phi P[2]P[0] - (\mu + r_{s \rightarrow u})P[2] \\ &= \phi P[2](p_s - P[2]) - (\mu + P[1])P[2] \end{aligned}$$

where $r_{s \rightarrow u}$ is the rate at which suitable sites become unsuitable. With habitat dynamics using a global neighborhood, this rate is simply $P[1]$, the proportion of habitat that is unsuitable. The above ODE has the nontrivial equilibrium $P^*[2] = p_s - (\mu + P[1])/\phi$, which gives

$$\rho^* = 1 - \frac{\mu + P[1]}{p_s \phi} \quad (5)$$

which is biologically meaningful as long as $\phi p_s \geq \mu + P[1]$, i.e., the effective reproduction rate (filtering out offspring that land on unsuitable sites) is greater

than the total death rate due to both intrinsic mortality and the transition of
suitable habitat to unsuitable habitat.

For case 2LhGp (local habitat dynamics, global population dispersal), the
ODE for the proportion of suitable occupied sites is

$$\begin{aligned}\frac{dP[2]}{dt} &= \phi P[2]P[0] - P[2](\mu + Q_{1|2}) \\ &= \phi P[2](p_s - P[2]) - P[2]\mu - P[12].\end{aligned}$$

ODEs for $P[00]$ and $P[01]$ (derived in Appendix A for this case as well as cases
3GhLp and 4LhLp) are

$$\begin{aligned}\frac{dP[00]}{dt} &= 2P[01]\left(\frac{z-1}{z}(Q_{0|10} + Q_{2|10}) + \frac{1}{z}\right) + 2P[02]\mu \\ &\quad - 2P[00]\left(\frac{z-1}{z}Q_{1|00} + P[2]\phi\right) \\ \frac{dP[01]}{dt} &= \frac{z-1}{z}(P[00]Q_{1|00} + P[02]Q_{1|20} + P[11](Q_{0|11} + Q_{2|11})) + P[12]\mu \\ &\quad - P[01]\left(\frac{z-1}{z}(Q_{0|10} + Q_{2|10} + Q_{1|01}) + P[2]\phi + \frac{1}{2}\right).\end{aligned}$$

For case 3GhLp (global habitat dynamics, local population dispersal), the
three ODEs are

$$\begin{aligned}\frac{dP[2]}{dt} &= P[0]Q_{2|0}\phi - P[2](\mu + P[1]) \\ \frac{dP[00]}{dt} &= 2P[01](P[0] + P[2]) + 2P[02]\mu - 2P[00]\left(P[1] + \frac{z-1}{z}Q_{2|00}\phi\right) \\ \frac{dP[01]}{dt} &= (P[00] + P[02])P[1] + P[11](P[0] + P[2]) + P[12]\mu \\ &\quad - P[01]\left(P[0] + P[1] + P[2] + \frac{z-1}{z}Q_{2|01}\phi\right).\end{aligned}$$

Finally, for case 4LhLp (local habitat dynamics and population dispersal),

the ODEs are

$$\begin{aligned}
\frac{dP[2]}{dt} &= P[0]Q_{2|0}\phi - P[2](\mu + Q_{1|2}) \\
\frac{dP[00]}{dt} &= 2P[01]\left(\frac{z-1}{z}(Q_{0|10} + Q_{2|10}) + \frac{1}{z}\right) + 2P[02]\mu \\
&\quad - 2P[00]\frac{z-1}{z}(Q_{1|00} + Q_{2|00}\phi) \\
\frac{dP[01]}{dt} &= \frac{z-1}{z}(P[00]Q_{1|00} + P[02]Q_{1|20} + P[11](Q_{0|11} + Q_{2|11})) + P[12]\mu \\
&\quad - P[01]\left(\frac{2}{z} + \frac{z-1}{z}(Q_{0|10} + Q_{2|10} + Q_{1|01} + Q_{2|01}\phi)\right).
\end{aligned}$$

Equations (1), (2), (3), and (4) are then used to close each of the systems of ODEs, which are analyzed numerically.

4. Results

We first performed a parameter sweep varying ϕ between 1 and 20, with fixed $\mu = 1$. Figure 2 displays $\rho^* = P^*[2]/p_s$, the proportion of suitable sites occupied at equilibrium, as a function of ϕ . Consider case 1GhGp (global habitat dynamics and population dispersal) as the baseline case. Case 2LhGp, with local habitat dynamics, has a higher equilibrium population density, despite the fact that the population is dispersing globally. This is due to the fact that with local habitat dynamics, suitable sites tend to have more suitable sites nearby, and therefore become unsuitable at a lower rate. Specifically, with $P[1] = 0.5$ (half of the sites unsuitable), with global habitat dynamics, a suitable site becomes unsuitable at rate 0.5. With local habitat dynamics, a suitable site becomes unsuitable (and vice versa) at rate $Q_{1|0} \approx 1 - 0.8079 = 0.1921$ (as measured from simulations). Relative to case 2LhGp, case 4LhLp (with population dynamics now local as well) has an even slightly higher population density. Local population dynamics leads to more intraspecific competition for space due to local crowding, which typically decreases population density (Hiebeler, 2004). However, the higher chance of finding suitable habitat when reproducing locally

171 rather than globally is enough to overcome the population crowding. Finally,
 172 case 3GhLp (global habitat dynamics, local population dynamics) has both the
 173 lowest population density and largest variability, as the population suffers from
 174 both local crowding and rapid habitat turnover.

175 Figure 3 also displays the results of the parameter sweeps, but this time
 176 with predicted population density from the various ODE approximations. For
 177 local habitat dynamics, results using $Q_{1|1} = 2/3$ (from pair approximations)
 178 as well as $Q_{1|1} = 0.8079$ (from simulation measurements) were used; for global
 179 habitat dynamics, $Q_{1|1} = P[1] = 0.5$ was used. For case 1GhGp, with no spatial
 180 correlations, simulations and predictions were in agreement. No spatial approx-
 181 imations were needed in case 1GhGp, and the ODE matches simulations exactly
 182 in the limit of an infinite lattice. For case 2LhGp, using $Q_{1|1} = 2/3$ as obtained
 183 from pair approximations underestimates clustering of habitat and therefore
 184 underestimates population density; using the value $Q_{1|1} = 0.8079$ measured
 185 from simulations in the ODEs yields very good agreement. For case 3GhLp, the
 186 ODEs overestimate equilibrium population density, as is typically the case when
 187 using pair approximation with locally dispersing population models (Matsuda
 188 et al., 1992); the presence of spatially unstructured dynamic habitat does not
 189 change that behavior. Finally, for case 4LhLp, with only local interactions, the
 190 underestimation of habitat clustering $Q_{1|1} = 2/3$ leads to an underestimation
 191 of population density; using the more accurate value of habitat clustering then
 192 yields the typical overestimation of population density from pair approximation
 193 (due to underestimating the clustering of occupied sites).

194 Next, note that in population models on fixed landscapes, equilibrium den-
 195 sity is a function of the fecundity and mortality parameters ϕ and μ only through
 196 their ratio ϕ/μ . To explore how this result differs in our model due to the ad-
 197 ditional presence of dynamic habitat, we again performed a parameter sweep
 198 where ϕ varied between 1 and 20; however, we also let $\mu = \phi/10$ to keep a

Figure 2: The equilibrium proportion of suitable sites occupied, $\rho^* = P^*[2]/p_s$, is shown as fecundity ϕ varies from 1 to 20. Mortality was fixed at $\mu = 1$. The figure legend is ordered to match the relative positions of the curves in the figure.

Figure 3: Results as in Figure 2, but with ODE results included as well.

Figure 4: The proportion of suitable sites occupied, $\rho = P[2]/p_s$, is shown as fecundity ϕ varies from 1 to 20. Mortality was adjusted to keep a constant ratio $\phi/\mu = 10$.

199 fixed ratio $\phi/\mu = 10$. The results are shown in Figure 4. For large enough
200 ϕ , equilibrium density is essentially independent of the value of ϕ , as popula-
201 tion dynamics overwhelm habitat dynamics. However, as ϕ becomes smaller,
202 eventually habitat dynamics begin to dominate and decrease population density.

203 Finally, we performed a double parameter sweep with ϕ varying between 0
204 and 20 and μ varying between 0 and 10, with 40 values each. We measured
205 the equilibrium population density ρ^* from among five replicate simulations
206 for each parameter combination. For the $8000 = 40 \times 40 \times 5$ observations of

Case	β_0	β_1	β_2	R^2
1GhGp	0.9910437	1.0038078	0.5130016	0.993310
2LhGp	0.9856285	4.3238963	2.1829193	0.997674
3GhLp	1.0507575	0.9479394	0.2321650	0.976244
4LhLp	0.9787122	4.5287909	2.6741057	0.998141

Table 2: Results of fitting the model $\rho^* = \beta_0 - (\beta_1\mu + 0.5)/(\beta_2\phi)$ to simulation results as ϕ was varied between 0 and 20, and μ was varied between 0 and 10.

207 (ρ^*, ϕ, μ) in each of the four cases, we fit a nonlinear least-squares regression
 208 model $\rho^* = \beta_0 - (\beta_1\mu + 0.5)/(\beta_2\phi)$ to obtain a descriptive relation between
 209 equilibrium population density and the fecundity and mortality parameters;
 210 the results are shown in Table 2. The model fit fairly well in all four cases, with
 211 the results for case 1GhGp matching their expected values from Equation (5)
 212 of $\beta_1 = 1$ and $\beta_2 = 0.5$.

213 5. Discussion

214 With spatial population models of this type, one of the primary challenges
 215 is to determine why a given set of results emerge; that is, what are the salient
 216 properties of the system that affect quantities of interest, such as population
 217 density or clustering? By examining four different cases with our model, we have
 218 explored several types of spatial structure and dynamics that can play important
 219 roles in populations on landscapes with changing habitat distributions.

220 With static habitat heterogeneity and a globally dispersing population, the
 221 spatial arrangement of suitable and unsuitable habitat has no effect on equilib-
 222 rium population density due to the absence of spatial correlations in occupied
 223 sites (Hiebeler, 2004). In such a case, all suitable sites are equally likely to be
 224 occupied, regardless of the states of other sites in the neighborhood. If that

225 were still true with our model, the population density would be identical in
 226 cases 1GhGp and 2LhGp (global population dispersal, with global and local
 227 habitat dynamics respectively). However, with dynamic habitat, the spatial
 228 scale of habitat dynamics does influence the density of even a population with
 229 global dispersal, because it affects the effective turnover rate of habitat. With
 230 localized habitat dynamics, sites tend to be surrounded by sites with the same
 231 habitat type, and therefore change habitat type more slowly as compared to the
 232 case with global habitat dynamics. This slowdown in effective habitat turnover
 233 leads to an increase in population density, even with global population dispersal.
 234 Also, for a globally dispersing population on a static heterogeneous landscape,
 235 all suitable sites on the landscape are equally likely to be occupied, with no spa-
 236 tial correlations in patch occupancy among adjacent suitable sites. In our case
 237 2LhGp, however, even with global dispersal, there are still spatial correlations
 238 in patch occupancy among nearby suitable sites, due to the spatial dynamics
 239 (and resulting local spatial correlations) of habitat. Suitable sites near the edge
 240 of a patch are less likely to be occupied, because it is more likely that they were
 241 recently unsuitable.

242 Previous work by Matlack and Leu (2007) with dynamic landscapes found
 243 that segregating habitat turnover into fewer sites increased population density,
 244 compared with a case where habitat turnover was more widely distributed. In
 245 our model, when habitat dynamics are local, habitat turnover is also segregated
 246 into a smaller number of sites relative to the case of global habitat dynamics.
 247 Unlike the model of Matlack and Leu (2007), the set of particular sites capable
 248 of experiencing habitat turnover in our model with local habitat dynamics shifts
 249 over time as the distribution of habitat types evolves. That is, the segregation
 250 of disturbances is not done within fixed regions over time. But within any short
 251 interval of time, only sites near the boundary of suitable and unsuitable habitat
 252 experience turnover.

Pair approximation in spatial population models tends to underestimate
 the amount of local clustering, and therefore overestimate population density,
 though various techniques can be used to build improved approximations, de-
 pending on the geometry of the lattice (Sato et al., 1994; Hiebeler, 1997; van
 Baalen, 2000). However, a pair approximation model of case 2LhGp (local
 habitat, global population) leads to a predicted equilibrium population density
 ρ^* that underestimates the value as measured by simulations. We speculated
 that this was due to underestimation of the clustering of suitable habitat in
 the landscape. Replacing the pair approximated value $Q_{1|1} = 2/3$ by the value
 $Q_{1|1} = 0.8079$ measured from simulations confirmed this suspicion, as ODEs
 and simulations then agreed. When both types of interactions are local (case
 4LhLp), pair approximation again underestimates population density. In that
 case, the clustering of suitable habitat and of occupied sites are both being
 underestimated, with the former error having a larger effect on the predicted
 population density than the latter. This is again seen when habitat clustering
 is based on simulation measurements rather than pair approximation.

In the model explored here, either local or global population dispersal may
 be more beneficial (in terms of increasing equilibrium population density ρ^*),
 depending on the spatial scale of habitat dynamics and of the resulting spatial
 correlations in habitat type. This type of response to habitat structure has also
 been observed in models with fixed habitat (Hiebeler, 2000). When habitat
 types are clustered, local population dispersal allows the population to exploit
 suitable patches (case 4LhLp versus case 2LhGp); when habitat is not clustered,
 global dispersal allows the population to escape local crowding (case 1GhGp
 versus case 3GhLp). In addition to changing the likelihood of dispersal into
 poor habitat and increasing edge effects, the fragmentation of suitable habitat
 may also lead to increased demographic stochasticity (North and Ovaskainen,
 2007), although when the habitat fragmentation is dynamic, this effect is likely

281 to be reduced relative to a system with static or slowly-changing habitat. The
 282 change in the spatial distribution of organisms with respect to other individuals
 283 and with respect to the quality of nearby habitat can have both positive and
 284 negative effects on population density (North and Ovaskainen, 2007).

285 The presence of habitat dynamics with its own intrinsic timescale also re-
 286 moves the invariance of the model with respect to changes in fecundity and
 287 mortality rates ϕ and μ with fixed ratio ϕ/μ . Now, even when ϕ/μ is held
 288 constant, the relative rates of population dynamics versus habitat dynamics de-
 289 termines which type of dynamics will dominate the system. This phenomenon
 290 is also seen in a related model of populations on dynamic habitat where habitat
 291 dynamics are due to outside disturbances (Hiebeler et al., submitted).

292 In landscapes with static heterogeneous habitat, spatial clustering of habitat
 293 types can lead to the presence of isolated patches of suitable habitat surrounded
 294 by a matrix of unsuitable sites. Local dispersers cannot cross these barriers,
 295 leading to local extinction within patches. In systems with dynamic habitat,
 296 dynamic corridors can connect these otherwise separate patches, allowing the
 297 population to move from one patch to another (Wimberly, 2006; Kun et al.,
 298 2009), which can be more difficult on static landscapes, especially when suitable
 299 habitat is less frequent. The situation may be more complex with multi-species
 300 models, where dynamic corridors may affect species richness curves via increased
 301 persistence time, albeit with fewer species (Roy et al., 2004). The strength of
 302 fragmentation effects will also be strongly affected by the dispersal pattern of
 303 new offspring (Matlack and Leu, 2007).

304 By rescaling time, the results in Figure 4 could also be interpreted as showing
 305 equilibrium population density ρ^* versus landscape turnover rate while keep-
 306 ing ϕ and μ fixed. This shows that ρ^* typically decreases monotonically as
 307 the landscape/habitat turnover rate increases. Previous work by Banitz et al.
 308 (2008) showed that under some circumstances, biodiversity is maximized at in-

309 termediate disturbance rates, when the disturbances are spatially correlated.
 310 However, in their model, a disturbed site was immediately able to be recolo-
 311 nized; there were no lasting effects of disturbance as in our model when a site
 312 turns unsuitable. Kun et al. (2009) explored a locally dispersing population on
 313 a landscape with spatially uncorrelated dynamic habitat type; their model cor-
 314 responds to our case 3GhLp. In their study, they found that as long as $\mu > 0$,
 315 equilibrium population density is maximized for an intermediate value of the
 316 landscape turnover/disturbance rate. However, the effect was very weak (with
 317 the change in ρ^* becoming nearly monotonic) as the amount of suitable habitat
 318 p_s increased. The curve corresponding to case 3GhLp in Figure 4 may indeed
 319 show that ρ^* is maximized for an intermediate value of ϕ . Differences in models
 320 details between this study (in continuous time) and that of Kun et al. (2009)
 321 (in discrete time) make it difficult to perform a direct comparison of results for
 322 given parameter values.

323 Many additional features could be added to the model explored here. For
 324 example, there could be two-way interactions between population and habi-
 325 tat, with populations affecting the dynamics of habitat fragments (del Castillo,
 326 2015). For example, plant consumption by herbivores changes the distribution
 327 of plants (suitable habitat); it may even be possible for the quality of plants
 328 to evolve over time (de Mazancourt and Loreau, 2000). Dispersal distance
 329 could be made a function of local habitat suitability, as population dispersal
 330 has been shown to have interactive effects with habitat suitability and fragmen-
 331 tation (Radinger and Wolter, 2015). Directed dispersal toward more favorable
 332 habitat would allow the population to exploit spatial structure in habitat suit-
 333 ability even more strongly (Cantrell et al., 2006). Spatial scales in natural and
 334 human-driven systems of course does not follow a clear black-and-white distinc-
 335 tion with local and global spatial scales, but instead involves interactions over
 336 a variety of intermediate scales. This model and related ones show that the

relative spatial and temporal scales of population and environmental processes as well as disturbances (such as control measures) all come into play when trying to control the outbreak of invasive or undesirable species (Hiebeler, 2005; Hiebeler and Morin, 2007; Hiebeler et al., submitted). The spatial scale of measurements may affect observed population dynamics, including the amount of variability observed (Lundberg et al., 2000).

Underlying/intrinsic habitat dynamics such as those explored here may be due to natural processes such as forest gap formation (Kubo et al., 1996), where new gaps form far from other gaps (“global transitions”) due to individual tree mortality or wind events, or adjacent to other gaps (“local transitions”) due to the change in environmental conditions within an existing gap. They may also arise due to human influences, such as management of forest stands, where again transitions may be global, due to policy or advice at a regional scale, or local, due to the influence of nearby landowners (Huff et al., 2015). When using pesticides to control invasive species, the spatial and temporal scale of population dispersal and intrinsic habitat dynamics may interact to guide management strategies, including the spatial extent of disturbance events acting as control measured (Hiebeler et al., submitted).

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515 **Appendix A. Derivation of ODEs**

516 The general ODE for $P[00]$ in all of the cases is as follows:

517

$$\begin{aligned} \frac{dP[00]}{dt} = & P[01]r_{[01] \rightarrow [00]} + P[10]r_{[10] \rightarrow [00]} + P[02]r_{[02] \rightarrow [00]} + P[02]r_{[20] \rightarrow [00]} \\ & - P[00] (r_{[00] \rightarrow [01]} + r_{[00] \rightarrow [10]} + r_{[00] \rightarrow [02]} + r_{[00] \rightarrow [20]}) \end{aligned}$$

518 where $r_{[ij] \rightarrow [k\ell]}$ gives the rate at which a pair of sites in states $[ij]$ transitions
519 to the state pair $[k\ell]$. For all cases, $r_{[02] \rightarrow [00]} = r_{[20] \rightarrow [00]} = \mu$ due to intrinsic
520 mortality.

521 For cases 1GhGp and 3GhLp with global habitat dynamics,

$$r_{[01] \rightarrow [00]} = r_{[10] \rightarrow [00]} = p_s = P[0] + P[2] \quad (\text{A.1})$$

522 as unsuitable becomes suitable at a rate equal to the proportion of suitable
523 habitat in the entire landscape. For cases 2LhGp and 4LhLp with local habitat
524 dynamics,

$$r_{[01] \rightarrow [00]} = r_{[10] \rightarrow [00]} = \frac{z-1}{z} Q_{s|10} + \frac{1}{z} \quad (\text{A.2})$$

525 where the first term give the rate of the type-1 site in the pair turning suitable
 526 due to one of the $z - 1$ neighbors outside of the pair being suitable (with $Q_{s|10} =$
 527 $Q_{0|10} + Q_{2|10}$) and the second term gives the rate of the type-1 site turning
 528 suitable due to its known suitable neighbor within the pair.

529 Similarly, for cases 1GhGp and 3GhLp,

$$r_{[00] \rightarrow [01]} = r_{[00] \rightarrow [10]} = P[1], \quad (\text{A.3})$$

530 while for cases 2LhGp and 4LhLp,

$$r_{[00] \rightarrow [01]} = r_{[00] \rightarrow [10]} = \frac{z-1}{z} Q_{1|00} \quad (\text{A.4})$$

531 where in the latter expression, there is no $1/z$ term because there is no unsuitable
 532 site in the pair to turn the other site unsuitable.

533 Finally, for cases 1GhGp and 2LhGp with global population dispersal,

$$r_{[00] \rightarrow [02]} = r_{00 \rightarrow [20]} = P[2]\phi.$$

534 For cases 3GhLp and 4LhLp with local population dispersal,

$$r_{[00] \rightarrow [02]} = r_{00 \rightarrow [20]} = \frac{z-1}{z} Q_{2|00}\phi$$

535 due to colonization by one of the $z - 1$ neighbors outside of the pair.

536 The general ODE for $P[01]$ is

537

$$\begin{aligned} \frac{dP[01]}{dt} = & P[00]r_{[00] \rightarrow [01]} + P[02]r_{[02] \rightarrow [01]} + P[11]r_{[11] \rightarrow [01]} + P[21]r_{[21] \rightarrow [01]} \\ & - P[01] \left(r_{[01] \rightarrow [00]} + r_{[01] \rightarrow [11]} + r_{[01] \rightarrow [21]} \right). \end{aligned}$$

538 As with the ODE for $P[00]$, for all cases, $r_{[21] \rightarrow [01]} = \mu$ due to intrinsic mortality.

539 The rates $r_{[00] \rightarrow [01]}$ and $r_{[01] \rightarrow [00]}$ are the same as in Equations (A.1)–(A.4)
 540 above.

541 For cases 1GhGp and 3GhLp,

$$r_{[02] \rightarrow [01]} = P[1].$$

542 For cases 2LhGp and 4LhLp,

$$r_{[02] \rightarrow [01]} = \frac{z-1}{z} Q_{1|20}.$$

543 For cases 1GhGp and 3GhLp,

$$r_{[11] \rightarrow [01]} = p_s = P[0] + P[2].$$

544 For cases 2LhGp and 4LhLp,

$$r_{[11] \rightarrow [01]} = \frac{z-1}{z} Q_{s|11} = \frac{z-1}{z} (Q_{0|11} + Q_{2|11}).$$

545 For cases 1GhGp and 3GhLp,

$$r_{[01] \rightarrow [11]} = P[1].$$

546 For cases 2LhGp and 4LhLp,

$$r_{[01] \rightarrow [11]} = \frac{z-1}{z} Q_{1|01} + \frac{1}{z}$$

547 where the last term is the rate at which the known unsuitable site in the pair
 548 causes the known suitable site to become unsuitable.

549 Finally, for cases 1GhGp and 2LhGp,

$$r_{[01] \rightarrow [21]} = P[2]\phi.$$

550 For cases 3GhLp and 4LhLp,

$$r_{[01] \rightarrow [21]} = \frac{z-1}{z} Q_{2|01}\phi.$$