Locally Dispersing Populations in Heterogeneous Dynamic Landscapes with Spatiotemporal Correlations. I. Block Disturbance

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Abstract

Locally dispersing populations are generally favorably affected by increasing the scale of habitat heterogeneity because they can exploit contiguous patches of suitable habitat. Increasing the spatial scale of landscape disturbances (such as by applying a pesticide to control an unwanted species) drives down population density because of reasons including dispersal-limited recolonization and the resulting increase in temporal variability. Here, we examine how population density changes as the spatial scale of landscape disturbance increases: does it increase due to increases in spatial correlations in landscape habitat type, or does it decrease due to the various spatial and temporal effects of larger-scale disturbances? We use simulations, mean field approximations, pair approximations, landscape-improved pair approximations (LIPA), and block probabilities to investigate a model of a locally dispersing species on a dynamic landscape with spatiotemporally structured heterogeneous habitat. Pesticide is applied at a given spatial scale, leaving habitat unsuitable for some time before dissipating and allowing the habitat to revert to a suitable state. We found that increasing the spatial scale of disturbances (while keeping the overall disturbance rate fixed) can increase population density, but generally only when landscape

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turnover is slow relative to population dynamics and when the population is somewhat close to its extinction threshold. Applying control measures at larger spatial scales may allow them to be more effective with the same overall treatment rate. The optimal spatial strategy for applying disturbances depends on both habitat availability as well as the turnover rate of the control measure being used. For the large-scale habitat dynamics in our model, it is possible to analytically calculate spatial correlations in habitat types over arbitrary scales. However, including exact habitat correlations at the triplet scale but approximating population correlations at that scale still neglects information needed to accurately predict simulation results, showing that larger-scale correlations in the population distribution have an important effect on dynamics.

Keywords: habitat disturbance, temporal variability, spatiotemporal structure, stochastic spatial simulation, dynamic habitat

1. Introduction

All methods of pest control have a spatial component to them, whether it be the distribution of the release of sterile insects within a given region (Rodríguez, 2015), or allocating removal efforts to patches according to qualities such as patch size or connectivity (Minor and Gardner, 2011). Other non-density dependent sources of mortality, such as lethal temperatures (Torgersen et al., 1999) or pesticide contamination in aquatic systems (Van den Brink et al., 2007) also include important spatial components. Control measures typically lead to spatially heterogeneous distributions of habitat quality which affect fecundity and/or mortality of the target species. The converse is also the case, where conservation of threatened or endangered species likewise has a spatial dynamic (Esler, 2000; Hanski, 2001; Silbernagel, 2003). Habitat loss (Coristine and Kerr, 2011), habitat disturbance (Elkin and Possingham, 2008), range restriction (Channell and Lomolino, 2000), refugia and dispersal corridors for connectivity (Visconti and Elkin, 2009; Cushman and Huettemann, 2010), reintroduction of a species to a locale (Carroll et al., 2003), and climate change

17 effects on geographic distribution (Kerr et al., 2015), all have foundations in the-
18 oretical spatial ecology. Spatiotemporal variability in habitat quality may arise
19 from several causes, including human activities (Munroe et al., 2002; Jacque-
20 myn et al., 2003; Cerda and Wright, 2004; Masaki, 2004; Linderman et al., 2006;
21 Carrière et al., 2012) or natural events such as the weather (Ringsby et al., 2002)
22 and forest gap formation (Kubo et al., 1996; Manrubia and Solé, 1997).

23 The expected impacts of heterogeneous habitat vary (Robinson et al., 1992;
24 Oborny, 1994). Movement and dispersal (colonization rate) and extinction rate
25 interact with and are often dependent upon patch quality, patch turnover rate,
26 and habitat fragmentation in affecting the success of a species (Naeem and Col-
27 well, 1991; Amarasekare and Possingham, 2001; Langellotto and Denno, 2001;
28 Fahrig, 2003; Radinger and Wolter, 2015). The spatial scale of correlations
29 in habitat quality relative to organism dispersal distances have been shown to
30 impact population success (Neuhauser, 1998; Lande et al., 1999; Schooley and
31 Branch, 2007). For instance, Liao et al. (2013) demonstrated that populations
32 restricted to local dispersal benefit from habitat clumping whereas those that
33 tend to be characterized by long distance dispersal are not affected by habitat
34 clumping. The same is true of spatial variability in control measures such
35 as when using pesticides to control unwanted species (González-Andujar and
36 Perry, 1995; Gontijo et al., 2013). Increased habitat heterogeneity may also
37 influence variability in population density, as seen in organisms such as desert
38 isopods (Shachak and Brand, 1991; Ye et al., 2014).

39 In heterogeneous landscapes, habitat association can allow a population to
40 exploit high-quality regions despite the presence of less-suitable habitat (Bolker,
41 2003; Franken and Hik, 2004; Elkin and Possingham, 2008; Hiebeler et al., 2013).
42 Both the location/connectivity and the quality of habitat patches influence the
43 success of resident or invading species (Ovaskainen and Hanski, 2003; Visconti
44 and Elkin, 2009; Liao et al., 2013). Regarding the geometry of heterogeneity,
45 intermediate sizes of high-quality patches have been found optimal in some pop-
46 ulation models (North and Ovaskainen, 2007). However, the dynamics of patch
47 quality and size are complex as Mortelliti et al. (2014) show how the landscape

48 structure surrounding fragmented high-quality patches can affect population dy-
49 namics. At a larger scale, variations in aspects of climate such as precipitation
50 affect community composition, and may drive the spatial distribution of species
51 diversity (Cleland et al., 2013).

52 The spatial scale of landscape structure, such as autocorrelations of habitat
53 heterogeneity and disturbances, play an important role for populations and
54 communities (Cohen and Levin, 1991; Topping and Sunderland, 1994; Roland
55 and Taylor, 1997; Smith and Gilpin, 1997; Kie et al., 2002; Ripa and Ives,
56 2003; Pike et al., 2004; Roy et al., 2004; Seabloom et al., 2005; Turner, 2010;
57 Limberger and Wickham, 2012). In particular, the relative scales of disturbance
58 and dispersal are important (Brown and Kodric-Brown, 1977; McCarthy and
59 Lindenmayer, 2000; Johst et al., 2002; Liao et al., 2015), as are the spatial
60 scales of disturbances versus fixed environmental heterogeneities (Kallimanis
61 et al., 2005; Hiebeler and Morin, 2007). The way in which spatial heterogeneity
62 changes over time may help inform management strategies as well (Munguia
63 et al., 2011).

64 When studying the interactions of temporal and spatial variability, both
65 habitat connectivity and quality of patches have been shown to have smaller
66 influences on patch occupancy in landscapes with dynamic habitat, rather than
67 static habitat distributions (Hodgson et al., 2009). Temporal and spatial vari-
68 ability have also been shown to be inexorably linked (Shachak and Brand, 1991;
69 Harrison and Fahrig, 1995; Moloney and Levin, 1996; Fleishman et al., 2002;
70 Perry, 2002; Cole et al., 2014). One example of this is the basic fact that the tem-
71 poral scale of observations may affect the spatial variability observed (Hiebeler
72 and Michaud, 2012). In models with spatially correlated disturbances, Johst
73 and Drechsler (2003) show that increasing the spatial correlations usually has
74 a negative effect on population density, in part due to the increase in tempo-
75 ral variability within a given region. The effects of dynamic habitat in spatial
76 population models has been explored in a variety of ways (Iwasa, 1991; Mat-
77 lack and Monde, 2004; Matlack, 2005; Loehle, 2007; Matlack and Leu, 2007).
78 Model results tend to agree in that the timescale of habitat dynamics rela-

79 tive to population dynamics is an essential parameter in determining whether
80 a population persists or goes extinct, even more so than the spatial scale of
81 landscape structure or dynamics (Fahrig, 1992; Keymer et al., 2000; Verheyen
82 et al., 2004; DeWoody et al., 2005). Spatiotemporal variability can also drive
83 the evolution of key parameters such as dispersal (McPeck and Holt, 1992; Roff,
84 1994), and have effects which are visible in population distributions many years
85 later (Lindborg and Eriksson, 2004).

86 Here we use a model to explore the effects of spatial and temporal correla-
87 tions in habitat quality on a locally dispersing population in a dynamic heteroge-
88 neous landscape. The model includes disturbance events which simultaneously
89 affect a specified number of contiguous sites, representing control measures (such
90 as a pesticide) applied at a given spatial scale. The primary question we ad-
91 dress with this model is: as the spatial scale of disturbance events increases,
92 does population density increase due to the resulting increase in spatial correla-
93 tions in landscape habitat type (Hiebeler, 2000), or decrease due to the various
94 spatial and temporal effects of larger-scale disturbances (Hiebeler, 2005)? We
95 also investigate how the answer to this question depends on the relative time
96 scales of landscape and population processes.

97 **2. The Model**

98 Our model is a spatially discrete continuous-time patch-occupancy Poisson
99 process model on a rectangular lattice with heterogeneous habitat. The habitat
100 type of each site may be either suitable or unsuitable. Suitable sites may either
101 be empty or occupied by the species of interest; unsuitable sites cannot be occu-
102 pied. Each site may therefore be in one of three states: empty suitable habitat,
103 (empty) unsuitable habitat, or occupied suitable habitat. In our previous similar
104 lattice population models on spatially structured heterogeneous landscapes, the
105 habitat distribution was fixed (Hiebeler, 2000, 2004; Hiebeler and Morin, 2007).
106 Here, the habitat types of sites change over time, as follows. Disturbance events
107 at a given spatial scale cause suitable sites to become unsuitable, representing

108 actions such as the application of pesticide, other control measures, or natural
 109 events such as gap formation. During such an event, a randomly-chosen $b \times b$
 110 block of sites is simultaneously disturbed, with all suitable sites within the block
 111 becoming unsuitable. Any occupied suitable sites that are disturbed in this way
 112 also become empty as they instantaneously transition to the unsuitable state.
 113 These block disturbances occur at a given location at rate r_{su}/b^2 , giving a per-
 114 site disturbance rate of r_{su} for suitable sites to become unsuitable, regardless
 115 of the disturbance size b . Note that the time until a particular suitable site
 116 is disturbed follows an exponential distribution with a mean of $1/r_{su}$; this can
 117 be thought of as the expected lifetime of a site (Keymer et al., 2000). These
 118 block disturbances are like those studied in previous models (Hiebeler, 2005;
 119 Hiebeler and Morin, 2007), except that in the previous models, a disturbed site
 120 was in principle immediately able to be recolonized, i.e., disturbances had no
 121 direct long-term effects (although it generally took some time for a population
 122 using only local dispersal to recolonize the center of a large region which had
 123 recently been disturbed). In the model used here, each unsuitable site recovers,
 124 becoming suitable again, independently at rate r_{us} as the habitat recovers (e.g.,
 125 the pesticide dissipates into the environment independent of patch quality, a
 126 reasonable assumption due to the dominant role in degradation played by ubiq-
 127 uitous microorganisms (Fenner et al., 2013)). Similar assumptions of correlated
 128 disturbances with independent recovery were used in a model of metapopulation
 129 persistence by Wilcox et al. (2006). The average time for a disturbed site to
 130 become suitable and a candidate for recolonization is therefore $1/r_{us}$. Together,
 131 the parameters r_{us} and r_{su} specify the temporal autocorrelation of habitat type
 132 within any given site. The size of the disturbances, given by parameter b , de-
 133 termines the spatial autocorrelation of habitat types among adjacent sites at
 134 any given time, as derived further below. In addition to the mortality of the
 135 species of interest in occupied sites due to the transition of occupied suitable
 136 habitat to unsuitable habitat, occupied sites also become empty (suitable) sites
 137 due to intrinsic mortality of the species of interest, which occurs at rate μ per
 138 site. Each occupied site in the lattice produces offspring at rate ϕ . When an

139 occupied site produces offspring, one of the four neighboring sites is chosen at
 140 random as the target location for its offspring. If the target site is empty and
 141 suitable, it is immediately colonized, becoming occupied. This model has similar
 142 basic features as that explored by Keymer et al. (2000) and Kun et al. (2009),
 143 with the key difference that their models only allowed suitable sites to become
 144 unsuitable independently, i.e., their models assumed $b = 1$.

145 When implemented via stochastic simulations, 300×300 lattices were used,
 146 with wraparound boundary conditions. The simulation was first run with only
 147 landscape dynamics and no population present, until the landscape was deter-
 148 mined to be at equilibrium. Then, a proportion ρ_0 of the suitable sites were
 149 chosen at random to be initially occupied, and the full simulation continued.
 150 We used $\rho_0 = 1 - \mu/\phi$, the equilibrium for a population with global dispersal
 151 at rate ϕ and mortality at rate μ with no unsuitable habitat, as an overesti-
 152 mate of the expected equilibrium population density in this model. If the above
 153 expression yielded a value of ρ_0 less than 0.1, we began with 10% of the sites
 154 occupied, to avoid fluctuation to extinction due to small initial population size.
 155 Simulations were run until equilibrium was reached, with the determination of
 156 equilibrium following the ideas of Caswell and Etter (1993), as follows. Every
 157 $90,000 = 300^2$ events is considered as one time step. All simulations are run
 158 for at least 300 time steps (assuming the population does not go extinct). After
 159 that, the population density is recorded after every time step. A linear regres-
 160 sion is fitted to the last 100 recorded values (via least squares regression); if the
 161 slope of the fitted line has magnitude less than 0.001, the system is considered
 162 to be at equilibrium.

163 Figure 1 shows snapshots of four landscapes with two different proportions
 164 of suitable habitat and two different block sizes, demonstrating the types of
 165 landscapes included in this model. Figure 2 shows the population on landscapes
 166 with the same parameters as the top images in Figure 1.

Figure 1: Snapshots of landscapes with four different parameter combinations. White sites are suitable, while black sites are unsuitable. The two landscapes on the top have $r_{su} = 0.5$ and $r_{us} = 1$, giving proportion $p^*[s] = 2/3$ of sites suitable. The two landscapes on the bottom have $r_{su} = 1$ and $r_{us} = 0.5$, giving proportion $p^*[s] = 1/3$ of sites suitable. The two landscapes on the left have disturbance block size $b = 2$, while the two landscapes on the right have disturbance size $b = 6$, leading to more spatial clustering of habitat types. Landscapes shown here are 100×100 for visual clarity, though 300×300 landscapes were used for actual simulations.

Figure 2: The population on landscapes with $\phi = 5$, $\mu = 1$, $r_{su} = 0.5$, and $r_{us} = 1$ (giving $p^*[s] = 2/3$), with disturbance sizes of $b = 2$ (left) and $b = 6$ (right). White sites are suitable and empty, gray sites are occupied, and black sites are unsuitable.

167 2.1. Mathematical approximations

168 To represent the state of the system, let the singlet probability $P[i]$ be the
 169 probability that a randomly-chosen site is in state i , with the states labeled as:
 170 $0 =$ empty suitable, $1 =$ unsuitable, and $2 =$ occupied suitable. The doublet
 171 probability $P[ij]$ then represents the probability that a pair of randomly-chosen
 172 adjacent sites are in states i and j , respectively. Triplet probabilities $P[ijk]$ and
 173 2×2 block probabilities $P \begin{bmatrix} i & j \\ k & l \end{bmatrix}$ will similarly be used. The probabilities
 174 of all state configurations must sum to one at all block scales:

$$\sum_j P[j] = 1, \quad \sum_{i,j} P[ij] = 1, \quad \sum_{i,j,k} P[ijk] = 1, \quad \sum_{i,j,k,l} P \begin{bmatrix} i & j \\ k & l \end{bmatrix} = 1. \quad (1)$$

175 Marginal (singlet) probabilities can be recovered from double probabilities by
 176 summing; similarly, doublet probabilities can be obtained from triplets:

$$P[i] = \sum_j P[ij], \quad P[ij] = \sum_k P[ijk] = \sum_k P[kij]. \quad (2)$$

Partial block probabilities may also be obtained from full blocks:

$$P \begin{bmatrix} \cdot & j \\ k & l \end{bmatrix} = \sum_i P \begin{bmatrix} i & j \\ k & l \end{bmatrix}, \quad (3)$$

where the dot in the top-left position indicates that we are not specifying the state of that site. We assume rotational and reflectional symmetry, $P[ij] = P[ji]$, $P[ijk] = P[kji]$, $P \begin{bmatrix} i & j \\ k & l \end{bmatrix} = P \begin{bmatrix} k & i \\ l & j \end{bmatrix} = P \begin{bmatrix} j & i \\ l & k \end{bmatrix}$, etc.

We will need conditional probabilities of the neighbors of sites being in various states. The quantity $Q_{i|j} = P[ij]/P[j]$ represents the conditional probability that, if we first randomly choose a site in state j , then a randomly-chosen neighbor of that site is in state i . Similarly, $Q_{i|jk} = P[ijk]/P[jk]$ represents the probability that, if we randomly choose a triplet of adjacent sites with the second and third sites in states j and k , respectively, then the first site is in state i .

We sometimes describe probabilities involving only the landscape configuration. To distinguish them from probabilities describing the full system, we use lowercase p to refer to these probabilities. The proportions of suitable (state = 0 or 2) and unsuitable (state = 1) sites are $p[s] = 1 - P[1]$ and $p[u] = P[1]$, respectively, and similarly we use doublet probabilities $p[ss]$, $p[su]$, and so on. We use lowercase q for conditional probabilities involving neighbors, such as $q_{s|s} = p[ss]/p[s]$ giving the probability that a particular neighbor of a randomly-chosen suitable site is also suitable.

We can also relate landscape-only probabilities to probabilities from the full model including the population, by considering whether suitable sites are empty or occupied. In particular, two relations that will be used when deriving our ODEs are

$$p[su] = p[s](1 - q_{s|s}) = P[01] + P[21] \quad (4)$$

$$\begin{aligned} p[ss] &= p[s]q_{s|s} = P[00] + P[02] + P[20] + P[22] \\ &= P[00] + 2P[02] + P[22]. \end{aligned} \quad (5)$$

200 The proportion of suitable sites that are occupied will be written as $\rho =$
 201 $P[2]/p[s]$. Another quantity that will arise in the subsequent analysis is θ ,
 202 defined as the probability that when one site in a doublet is disturbed, the
 203 other site is simultaneously affected by the disturbance. Following Hiebeler
 204 (2005), this quantity may be related to the disturbance block size b via the
 205 expression $\theta = 1 - 1/b$, derived by summing over all locations a disturbance
 206 event could be aimed at which would affect both sites in the pair. The rate at
 207 which disturbance events affect one or both sites in a doublet can similarly be
 208 derived as $r_{su}(2 - \theta)$.

209 *2.2. Landscape dynamics*

210 To simplify analysis, we assume that population dynamics take place after
 211 the landscape has reached a dynamic equilibrium, i.e., the amount $p[s]$ and
 212 spatial clustering $q_{s|s}$ of suitable and unsuitable sites have reached steady-state
 213 values, even as sites continue to transition between suitable and unsuitable
 214 habitat states.

215 Note that for the dynamics of habitat types in the landscape, none of the
 216 transitions between suitable and unsuitable habitat depend on the habitat types
 217 of neighboring sites. That is, a site may change its habitat type at any time,
 218 regardless of the states of its neighbors. Because of this, spatial correlations of
 219 habitat types do not grow over arbitrarily large distances in the lattice, as they
 220 do in the population occupancy status of sites in models with localized disper-
 221 sal (Levin and Durrett, 1996). As a result, no moment-closure approximations
 222 are needed when writing ODEs to describe landscape dynamics.

223 Equations for landscape dynamics are given in Appendix A.1. From Equations (A.2) and (A.4), the proportions of sites with suitable and unsuitable habitat, as well as the clustering of suitable sites at equilibrium, can be expressed

$$p^*[s] = \frac{r_{us}}{r_{us} + r_{su}} \quad (6)$$

$$p^*[u] = \frac{r_{su}}{r_{us} + r_{su}} \quad (7)$$

$$q_{s|s}^* = \frac{p^*[ss]}{p^*[s]} = \frac{r_{us}}{r_{us} + r_{su}(1 - \theta/2)}. \quad (8)$$

Because $0 \leq \theta \leq 1$, the clustering satisfies $q_{s|s}^* \geq p^*[s]$, with equality if and only if $r_{us} = 0$ (a degenerate case where unsuitable sites never recover to suitable status) or $\theta = 0$ (corresponding to $b = 1$, where suitable sites are disturbed and become unsuitable individually, i.e. multiple sites are never simultaneously disturbed, and so no spatial correlations in habitat types develop over time). As $\theta \rightarrow 1$, i.e. disturbances occur at larger and larger spatial scales (but less and less frequently to control the per-site disturbance rate), then $q_{s|s}^* \rightarrow r_{us}/(r_{us} + r_{su}/2) = 2/(1 + 1/p^*[s])$. This establishes the following bounds on clustering of suitable sites at equilibrium:

$$p^*[s] \leq q_{s|s}^* \leq \frac{2}{1 + 1/p^*[s]}.$$

Finally, note that given a particular disturbance rate r_{su} , Equation (6) may be solved for

$$r_{us} = \frac{r_{su}p^*[s]}{1 - p^*[s]}, \quad (9)$$

giving the recovery rate needed to achieve a specified level of habitat availability.

2.3. Singlet equations

A system of ordinary differential equations for $P[0]$, $P[1]$, and $P[2]$ may be written to describe the proportions of sites in various states in the full population model. By the assumption of landscape equilibrium, $P[1] = p^*[u]$ is fixed at the value given by Equation (7), and because $P[0] = 1 - P[2] - p^*[u]$ by Equation (1), in fact we only need a single ODE to characterize the system:

$$\frac{dP[2]}{dt} = P[0]\phi Q_{2|0} - P[2](\mu + r_{su}). \quad (10)$$

245 We then use the mean-field approximation that the states of all sites are in-
 246 dependent/uncorrelated, i.e. $Q_{i|j} = P[i]$, to approximate $Q_{2|0}$ by $P[2]$ in the
 247 above ODE. This closed system then has equilibrium

$$P^*[2] = p^*[s] - \frac{\mu + r_{su}}{\phi},$$

248 with $p^*[s]$ given by Equation (6). The equilibrium proportion of suitable sites
 249 that are occupied is $\rho^* = P^*[2]/p^*[s] = 1 - (\mu + r_{su})/(\phi p^*[s])$. This result agrees
 250 with the standard form of mean-field results for population models (e.g., Keymer
 251 et al., 2000; Hiebeler and Morin, 2007), i.e., the proportion of all sites occupied
 252 is the proportion of suitable sites less the total disturbance rate divided by the
 253 reproduction rate (with the reproduction rate modified to filter out offspring
 254 that land on unsuitable sites).

255 2.4. Doublet equations

256 Next, we include additional information about spatial correlations by study-
 257 ing ODEs for doublet probabilities $P[ij]$.

258 The following self-contained set of ODEs for the population dynamics on the
 259 landscape follow from Equations (A.10)–(A.12), derived in Appendix A.2 using
 260 ordinary pair approximation:

$$\begin{aligned} \frac{dP[00]}{dt} = & 2p^*[s]r_{us} - 2P[2]r_{us} + 2P[02](\mu - r_{us}) \\ & - P[00] \left(\frac{2(z-1)P[02]\phi}{zP[0]} + r_{su}(2-\theta) + 2r_{us} \right) \end{aligned} \quad (11)$$

$$\begin{aligned} \frac{dP[01]}{dt} = & P[00]r_{su}(1-\theta) + (1+p^*[s](q_{s|s}^* - 2))r_{us} + P[02](1-\theta)r_{su} \\ & + (p^*[s](1 - q_{s|s}^*) - P[01])\mu \\ & - P[01] \left(r_{us} + r_{su} + \frac{z-1}{z}\phi \frac{P[02]}{P[0]} \right) \end{aligned} \quad (12)$$

$$\begin{aligned} \frac{dP[02]}{dt} = & P[00] \left(\frac{(z-1)P[02]\phi}{zP[0]} + r_{us} - \mu \right) + P[2]r_{us} + p^*[s]q_{s|s}^*(\mu - r_{us}) \\ & - P[02] \left(\frac{(z-1)P[02]\phi}{zP[0]} + \frac{\phi}{z} + r_{su}(2-\theta) - r_{us} + 3\mu \right) \end{aligned} \quad (13)$$

261 with $p^*[s]$ and $q_{s|s}^*$ given by Equations (6) and (8).

262 2.5. Landscape-improved doublet equations

263 Additional information about the spatial structure could be included in the
 264 model by using triplet equations for $P[ijk]$ with $i, j, k \in \{0, 1, 2\}$. However, the
 265 number of state variables would be $27 = 3^3$, though some reduction would be
 266 possible by the assumptions of symmetry and of the landscape being at equilib-
 267 rium. Instead, we use another approach we refer to as landscape-improved pair
 268 approximation (LIPA). The LIPA incorporates known information about the
 269 structure of habitat at larger (triplet) scales while still using pair approxima-
 270 tion for the population structure, as a straightforward generalization of improved
 271 mean-field approximations previously used (Hiebeler, 2007; Hiebeler and Morin,
 272 2007).

273 The ODEs, derived in Section Appendix A.3, are:

$$\begin{aligned} \frac{dP[00]}{dt} = & 2P[01]r_{us} + 2P[02]\mu \\ & - P[00] \left(r_{su}(2 - \theta) + 2\frac{z-1}{z}\phi \frac{(p^*[ss] - p^*[uss])P[02]}{p^*[ss](P[00] + P[02])} \right) \end{aligned} \quad (14)$$

$$\begin{aligned} \frac{dP[01]}{dt} = & (P[00] + P[02])r_{su}(1 - \theta) + P[11]r_{us} + P[21]\mu \\ & - P[01] \left(r_{us} + r_{su} + \frac{z-1}{z}\phi \frac{p^*[uss]P[02]}{(p^*[s] - p^*[ss])(P[00] + P[02])} \right) \end{aligned} \quad (15)$$

$$\begin{aligned} \frac{dP[02]}{dt} = & \frac{z-1}{z}P[00]\phi \frac{(p^*[ss] - p^*[uss])P[02]}{p^*[ss](P[00] + P[02])} + P[12]r_{us} + P[22]\mu \\ & - P[02] \left(\mu + r_{su}(2 - \theta) + \frac{\phi}{z} + \frac{z-1}{z}\phi \frac{(p^*[ss] - p^*[uss])P[02]}{p^*[ss](P[00] + P[02])} \right) \end{aligned} \quad (16)$$

274 with $p^*[s]$, $p^*[ss]$, $p^*[uss]$ given by Equations (6), (A.4), and (A.9), respectively.

275 2.6. Block equations

276 Finally, we also explored the behavior of the model by considering the rates
 277 of change of all possible configurations of 2×2 blocks of sites. There are $3^4 = 81$
 278 probabilities in total, although assumptions of symmetry and of the landscape
 279 being at equilibrium again reduce this. There are too many equations to include
 280 here explicitly; a derivation of the process used to derive the equations is given
 281 in Section Appendix A.4. A moment-closure approximation similar to that used

in pair approximation was again used to study this system, where the states of non-adjacent sites were assumed to be conditionally independent, if the state of an intermediate common neighbor was known.

3. Results

We first performed two parameter sweeps as the size of disturbances increased from 1×1 disturbances (i.e., sites independently disturbed) up to 10×10 disturbances. Figure 3 shows how ρ^* , the proportion of suitable sites occupied at equilibrium, varies as the disturbance size b increases. Both parameter sweeps were done with $r_{su} = r_{us}$, resulting in 50% of the sites in the landscape being suitable, and with $\phi = 10$ and $\mu = 1 - r_{su}$, giving a total disturbance rate (from both intrinsic mortality and habitat disturbance) of $\mu + r_{su} = 1$ per occupied site. The left half of the figure had very slow landscape dynamics ($r_{su} = 0.02$), while the right half had faster landscape dynamics ($r_{su} = 1$). When landscape turnover is very slow relative to population dynamics (dispersal and population growth), increasing the spatial scale of disturbance blocks can increase population density, due to the large contiguous regions of suitable habitat that exist with larger disturbances, which the locally dispersing population can then more easily exploit. Eventually, however, with large enough disturbances, the spatial and temporal correlations that arise drive the equilibrium population density back down again. When landscape turnover is more rapid, no initial increase in population density is seen as the size of disturbance events increases.

To determine whether the behavior seen in Figure 3 depended on the amount of suitable habitat, we performed a triple parameter sweep. The values of landscape parameters r_{su} and r_{us} were independently varied from 0.02 to 1 with 50 uniformly-spaced values. For each combination of values, the disturbance size b was varied from 1 to 10. For simulation results, 10 independent replicate simulations were performed for each parameter combination (giving a total of 2.5×10^5 simulations), and the values of $\rho^* = P^*[2]/p^*[s]$ were averaged among the 10 replicates. The value of b that maximized ρ^* for each pair of values r_{su} ,

Figure 3: The proportion of suitable sites occupied, $\rho = P[2]/p[s]$, is shown as the size b of disturbance blocks b varies from 1 to 10. Both landscapes have 50% suitable habitat, with $r_{su} = r_{us}$. Left: $r_{su} = 0.02$ (slower landscape dynamics). Right: $r_{su} = 1$ (faster landscape dynamics). Simulation results are the average of 10 replicate simulations for each value of b ; error bars are not shown because the largest sample standard deviation for the value of ρ observed among the replicate simulations for any particular value of b was only roughly 0.02.

311 r_{us} was recorded (the value 0 was used if the population went extinct for all
 312 values of b). The results are shown in the heat maps in Figure 4. Along a line
 313 of constant slope m from the origin, $r_{su} = mr_{us}$, giving a constant proportion
 314 $p^*[s] = 1/(1 + m)$ of suitable habitat. As one travels away from the origin on
 315 such a line, the turnover rate of habitat increases, driving population density
 316 down until it eventually goes extinct. Simulation results in Figure 4 show that
 317 in general, population density is maximized with larger block sizes when the
 318 amount of suitable habitat available has decreased nearly to the critical value
 319 at which the population goes extinct. None of the mathematical approximations
 320 accurately predict the simulation results, though as more detailed spatial infor-
 321 mation is included in the approximations (from pair approximation to LIPA
 322 to block probabilities), the results begin to come closer to matching simulation
 323 results. This suggests that the correlation structure in the landscape at larger
 324 spatial scales that arises from the interactions of local dispersal and landscape
 325 structure is still playing an important role in the dynamics, and that includ-
 326 ing exact correlations in habitat type at the triplet scale together with pair
 327 approximation of population correlations at that scale is still not sufficient to
 328 accurately predict the behavior of the model. Note that for cases where the
 329 population density was maximized for a block size of 10, additional exploration
 330 of the model suggests that population density does not begin to decrease even
 331 up to $b = 20$. Results are presented with a maximum value of $b = 10$ here for
 332 more clarity in the color bar figure legends.

333 Figure 5 shows a similar parameter sweep, but with r_{su} and r_{us} varying
 334 between 0.02 and 4 (again with 50 uniformly-spaced values). At this sampling
 335 resolution of the parameters, the image showing simulation results did not en-
 336 counter values of r_{us} and r_{su} for which population density was maximized with
 337 $b = 10$, even though such cases were seen in Figure 4. However, the band of
 338 parameter values for which this happens is too narrow to be seen in Figure 5.
 339 Note that the color scale for the simulation results in Figure 5 was adjusted for
 340 clarity.

341 In our model, decreasing the amount of suitable habitat without changing the

Figure 4: Heat maps showing the block size b that maximizes population density (ρ^*), as a function of landscape parameters r_{us} and r_{su} which vary between 0 and 1. Results are shown for simulations, as well as the various approximations used here.

Figure 5: Heat maps showing the block size b that maximizes population density (ρ^*), with landscape parameters r_{us} and r_{su} now varying between 0 and 4. Note that simulation results have a different color scale to make results more clearly visible, as the largest block size b which maximized population density for all parameters shown here was $b = 5$.

342 average lifetime of a patch ($1/r_{su}$) or the total mortality of occupied sites (the
 343 sum of intrinsic mortality μ and disturbance rate r_{su}) corresponds to moving
 344 horizontally to the left across either Figure 4 or 5. Increasing the turnover rate
 345 of habitat, while maintaining the same amount of suitable habitat, corresponds
 346 to moving along a line of fixed slope away from the origin. As can be seen in
 347 those two figures, which change will have the largest effect, such as leading the
 348 system to extinction most easily, depends on where one begins in the parameter
 349 space. Species close to the extinction threshold (near the top-left border of
 350 the non-black region in the figures) can likely tolerate a greater increase in
 351 habitat turnover (moving out along a line from the origin) than a corresponding
 352 reduction of suitable habitat (moving to the left) before moving into the black
 353 extinction region of the parameter space. For species far from the extinction
 354 threshold (farther lower right in the figures), the opposite can be true.

355 4. Discussion

356 In agreement with Keymer et al. (2000), we found that a population may go
 357 extinct if either there is insufficient suitable habitat available (far up in Figure 5,
 358 with large r_{su} relative to r_{us}), or if the habitat turnover rate is too rapid rela-
 359 tive to population demographic rates (far out from the origin along a line with
 360 fixed slope in Figure 5). The specific cause of extinction will depend upon the
 361 population dynamics / life history strategy of the species. Our findings suggest
 362 that an r -strategist species is more likely to be adversely affected by insufficient
 363 suitable habitat, whereas a K -strategist is more likely to be negatively affected
 364 by a high turnover rate (under the assumption of only local dispersal). Johst
 365 et al. (2002) found the same results, but also showed that in a dynamic land-
 366 scape, the most important factor that affects long-term population persistence
 367 is the ability of individuals to disperse long-distance.

368 In addition, we have investigated the spatial scale of disturbances, and the
 369 resulting effects on correlations in habitat type and clustering of occupied sites,
 370 as another factor affecting survival of the species of interest. The effects of the

371 disturbance size b vary with both the amount of suitable habitat and turnover
372 rate (or patch lifetime, in the terms of Keymer et al. (2000)).

373 The ultimate goal of taking advantage of spatial structure in control mea-
374 sures (such as pesticides) of invasive species is to find a way to make those
375 control measures more effective. That is, can certain ways of spatially and
376 temporally allocating treatments allow one to reduce the density of an invasive
377 species more greatly, for a given amount of effort?

378 The results seen in this model indicate that when the population is far from
379 its critical point, i.e., when the invasive species is thriving, increasing the spa-
380 tial scale of control measures may be more effective. This involves applying the
381 pesticide at the same total rate, but in less frequent but larger-scale patterns.
382 In that case, the direct effects of larger disturbances on the population outweigh
383 the more highly clustered distribution of suitable habitat that arises, since pop-
384 ulation density is maximized with smaller disturbance sizes. Liao et al. (2013),
385 while not investigating the size of a block disturbance, did find that random
386 habitat degradation or disturbance posed a more serious threat to species per-
387 sistence than clustered habitat degradation. However, as a pest population is
388 pushed more closely to its critical extinction point, smaller spatial scale dis-
389 turbances are more effective at reducing population density. In this case, the
390 benefits of the increased clustering of suitable habitat outweigh the direct effects
391 of large-scale disturbances on the population, since population density is max-
392 imized with larger disturbance sizes. Increasing the rate of pesticide temporal
393 frequency would be a better strategy in that case, in order to further reduce
394 population density. Our findings suggest that “area-wide” management of in-
395 vasive species (strategy of large regional block applications of insecticides) may
396 need to be rethought (Vreysen et al., 2007) and become more flexible depending
397 upon a dynamic understanding of the species critical extinction point.

398 Keymer et al. (2000) found that in ephemeral landscapes (i.e., those with
399 large values of r_{su}), changes in patch lifetime via the disturbance rate r_{su} had
400 a larger effect than changing the amount of suitable habitat, while in virtually
401 permanent environments (with small r_{su}), habitat availability played a larger

402 role. Their results were based in part upon mean-field approximations, and
 403 examining the rates of change $\partial\rho/\partial\bar{\tau}$ (where $\bar{\tau} = 1/r_{su}$) and $\partial\rho/\partial p^*[s]$ in our
 404 notation. Mean-field approximations are inadequate for studying our system due
 405 to its neglect of all spatial structure, and closed-form analytical solutions are not
 406 available for our more detailed approximations. Also, we chose to characterize
 407 our system via the landscape parameters r_{su} and r_{us} , rather than via what we
 408 consider a dependent variable $p^*[s]$. This difference can change quantitative
 409 results such as the magnitude of the change in population density with respect
 410 to model parameters mentioned above because of the nonlinear relation between
 411 $p^*[s]$ and r_{us} in Equations (6) and (9), which give $dp^*[s]/dr_{us} = (1-p^*[s])/(r_{us} +$
 412 $r_{su})$ and $dr_{us}/dp^*[s] = r_{su}/(1-p^*[s])^2$. However, our qualitative results are
 413 generally in agreement with those of Keymer et al. (2000), though with the
 414 additional complexity of the spatial scale of disturbances included.

415 Other studies of the effects of spatially correlated disturbances found that
 416 more highly-correlated disturbances tended to reduce population density or the
 417 effective speed at which a population spreads in a variety of cases (Johst and
 418 Drechsler, 2003; Brown et al., 2012). Liao et al. (2015) also found that increasing
 419 the spatial scale or correlation of disturbance lowered the population density of
 420 locally dispersing species under a variety of conditions such as varying intraspe-
 421 cific competition intensities and relative birth rates. Indeed, as seen in our
 422 Figure 3, population density does decrease with increased disturbance size more
 423 often than it increases, though sometimes by relatively minor amounts depend-
 424 ing on the relative timescales of landscape dynamics and population dynamics.
 425 This is also reflected in Figures 4 and 5 which show that population density is
 426 maximized for small block sizes over the majority of the landscape-dynamics
 427 parameter space. It is possible that had Johst and Drechsler (2003) explored
 428 their parameter space more thoroughly, they would also have seen an increase in
 429 population density as disturbances become more spatially correlated, particu-
 430 larly near the extinction threshold. In our model, the lasting effects on suitable
 431 habitat distribution resulting from disturbances also allows for larger-scale dis-
 432 turbances to increase population density, particularly when habitat turnover is

433 relatively slow compared with the population’s demographic rates.

434 In the model of Kun et al. (2009), which is similar to ours but with individual-
435 site disturbances ($b = 1$), they found that equilibrium population density was
436 maximized at an intermediate temporal disturbance rate (r_{su} in our notation),
437 as long as intrinsic mortality (μ in our notation) was not 0. This is because as
438 the disturbance rate r_{su} increases from a small initial value, there is initially a
439 direct effect on the population where more occupied sites become empty because
440 they are disturbed. However, when the disturbance rate becomes large enough,
441 it causes pathways to open up between patches of suitable habitat, allowing re-
442 colonization of small patches that have gone extinct. We see a similar effect with
443 the spatial scale of disturbances in our model. Further exploration of our model
444 indicates that when $\mu = 0$, increasing the scale b of disturbances drives equilib-
445 rium population density ρ^* down, but that when $\mu > 0$, increasing b initially
446 increases ρ^* (but then possibly subsequently decreasing ρ^* for large enough b ,
447 particularly for larger landscape turnover rates). In a model with large-scale
448 disturbances which do not have lingering effects on habitat type, Banitz et al.
449 (2008) found that intermediate disturbance rates maximize biodiversity. Re-
450 sults presented in their Figure 3 also indicate that for some disturbance rates,
451 biodiversity is maximized for intermediate spatial scales of disturbances (with
452 scale quantified by the number of clumps a given large-scale disturbance event
453 is broken into).

454 There are of course many other aspects of spatiotemporal variability that
455 may come into play in population and community dynamics. A model with more
456 complex disturbance dynamics showed that temporal autocorrelations among
457 disturbances had a larger influence than features such as spatial autocorrela-
458 tion or separate disturbances or the spatial scale of individual disturbances
459 (Moloney and Levin, 1996). The interactions between spatial and temporal
460 variability may impact competition between multiple species (Chesson, 1985),
461 while the spatial scale of fragmentation also impacts the amount of time (and
462 therefore the chances of success) for dispersing organisms to find new suitable
463 habitat (Doak et al., 1992). In general, the dispersal behavior of organisms is

464 another key factor in determining how the spatiotemporal structure of dynamic
 465 landscapes will be perceived by a given organism (Matlack and Monde, 2004).
 466 Including heterogeneity in habitat turnover rates across a landscape also affects
 467 the connectivity of patches of suitable habitat to an extent that population
 468 dynamics may be noticeably affected (Matlack and Leu, 2007).

469 In summary, our key findings are as follows:

- 470 1. When landscape turnover is very slow relative to population dynamics,
 471 increasing the spatial scale of disturbance blocks can increase population
 472 density.
- 473 2. However, with large enough disturbances, the spatial and temporal corre-
 474 lations that arise drive the equilibrium population density down.
- 475 3. When landscape turnover is more rapid, no initial increase in population
 476 density is seen as the size of disturbance events increases and subsequently
 477 population size continues to decrease.
- 478 4. In general, population density is maximized with larger block sizes when
 479 the amount of suitable habitat available has decreased nearly to the crit-
 480 ical value at which the population goes extinct. This suggests that the
 481 correlation structure in the landscape at large spatial scales that arises
 482 from the interactions of local dispersal and landscape structure is still
 483 playing an important role in the dynamics.
- 484 5. Species close to their extinction threshold tolerate a greater increase in
 485 habitat turnover than a corresponding reduction of suitable habitat before
 486 eventual extinction.
- 487 6. For species far from their extinction threshold, the opposite appears to be
 488 true. In this case, the direct effects of larger disturbances on the popula-
 489 tion outweigh the more highly clustered distribution of suitable habitat,
 490 and population density is maximized with smaller disturbance sizes.
- 491 7. However, as a pest population is pushed more closely to its critical extinc-
 492 tion point, smaller spatial scale disturbances are more effective at reducing
 493 population density. In this case, the benefits of the increased clustering

494 of suitable habitat outweigh the direct effects of large-scale disturbances
495 on the population, since population density is maximized with larger dis-
496 turbance sizes. Increasing the rate of pesticide temporal frequency would
497 be a better strategy in that case, in order to further reduce population
498 density.

499 Applied perspectives of our findings suggest spatial strategies for managing
500 dynamic habitat may be helpful not only for controlling invasive or unwanted
501 species, but also in protecting desired species in managed landscapes, by con-
502 sidering the spatial and temporal distribution of refugia (Topping and Sunder-
503 land, 1994). When controlling invasive species, we typically would like to apply
504 control measures, such as pesticides, infrequently for economic, ecological, or
505 environmental reasons (Terry and Gourley, 2010). However, decisions about
506 the optimal spatial scale for control measures should also be considered in con-
507 cert with decisions about the temporal scale. As seen here, such decisions may
508 need to be modified on the go, because the optimal strategy may vary as the
509 population being controlled approaches local extinction in the region of interest.
510 Our findings have great implications in pest management. The philosophy of
511 integrated pest management (IPM) has for a long time been based upon mak-
512 ing management decisions (usually implementation of pesticide applications) on
513 “real-time” pest densities (Pedigo and Rice, 2014). However, this has almost en-
514 tirely been within a framework of temporal pesticide frequency of applications
515 and not a more integrated synthesis of both temporal and spatial dynamics of
516 disturbance.

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783 **Appendix A. Derivation of ODEs**

784 *Appendix A.1. Landscape equations*

785 A differential equation for the proportion of suitable sites can be written:

$$\begin{aligned}
 \frac{dp[s]}{dt} &= p[u]r_{us} - p[s]r_{su} \\
 &= (1 - p[s])r_{us} - p[s]r_{su}.
 \end{aligned}
 \tag{A.1}$$

786 This has equilibrium

$$p^*[s] = \frac{r_{us}}{r_{su} + r_{us}}. \quad (\text{A.2})$$

787 When describing doublet probabilities for the landscape, there are four prob-
 788 abilities: $p[ss]$, $p[su]$, $p[us]$, and $p[uu]$. The symmetry assumption $p[su] = p[us]$
 789 and the fact that all four probabilities must sum to one reduces this to two inde-
 790 pendent probabilities. We could use $p[ss]$ and $p[su]$ to characterize the system.
 791 Instead, we use the relation $p[ss] + p[su] = p[s]$, and describe the system via $p[s]$
 792 and $p[ss]$.

793 A system of ordinary differential equations describing the landscape dynam-
 794 ics consists of Equation (A.1), along with:

$$\frac{dp[ss]}{dt} = 2p[su]r_{us} - 2p[ss]r_{su}(1 - \theta). \quad (\text{A.3})$$

795 The system may be closed by making the substitution $p[su] = p[s] - p[ss]$, which
 796 follows from Equation (2).

797 The equilibrium value of $p[ss]$ is

$$p^*[ss] = \frac{2r_{us}^2}{2r_{us}^2 + 4r_{us}r_{su} + 2r_{su}^2 - r_{su}^2\theta - r_{su}r_{us}\theta}. \quad (\text{A.4})$$

798 When describing triplet probabilities for the landscape, there are eight prob-
 799 abilities. Symmetry allows two to be eliminated ($p[uss] = p[ssu]$ and $p[uus] =$
 800 $p[suu]$); the probabilities summing to one allows elimination of another one.
 801 Equation (2) implies $p[sus] + p[suu] = p[ssu] + p[usu]$ (with both sums being
 802 equal to $p[su]$), allowing one more probability to be eliminated, bringing the

total needed to four. A system of four ODEs for landscape triplets is:

$$\begin{aligned} \frac{dp[uuu]}{dt} = & (2p[uus] + p[usu])r_{su} + \frac{2p[uss](b-1)r_{su}}{b} \\ & + \frac{1_{b>1}(p[sss] + p[sus])(b-2)r_{su}}{b} - 3p[uuu]r_{us} \end{aligned} \quad (\text{A.5})$$

$$\begin{aligned} \frac{dp[usu]}{dt} = & \frac{r_{su}}{b} \{1_{b>1}(p[sss] + 2p[sus]) + p[uss]\} + 1_{b=1}p[sus]r_{su} + p[uuu]r_{us} \\ & - p[usu](2r_{us} + r_{su}) \end{aligned} \quad (\text{A.6})$$

$$\frac{dp[usu]}{dt} = \frac{p[uss]2r_{su}}{b} + p[uuu]r_{us} - p[usu](2r_{us} + r_{su}) \quad (\text{A.7})$$

$$\frac{dp[uss]}{dt} = r_{us}(p[usu] + p[uus]) + \frac{p[sss]r_{su}}{b} - p[uss] \left(r_{us} + \frac{r_{su}(b+1)}{b} \right) \quad (\text{A.8})$$

The factor of $(b-1)/b$ in the second term of Equation (A.5) above comes from the fact that there are $(b-1)b$ locations that the upper-left corner of a $b \times b$ disturbance block could hit (each with rate r_{su}/b^2) that would cause a $[uss]$ triplet of sites to become a $[uuu]$ triplet. Similarly, the factor of $(b+1)/b$ in the last term of Equation (A.8) follows from the fact that there are $(b+1)b$ sites a disturbance block could hit which would cause the $[uss]$ triplet to change its state to either $[uuu]$, $[uus]$, or $[usu]$.

This could be further reduced to a system of two equations, if we assume that $p[s]$ and $p[ss]$ are already at their equilibrium values given by Equations (A.2) and (A.4), respectively. Note that the system of ODEs differs according to whether $b > 1$ or $b = 1$. Indicator functions are used to select terms according to the two cases, with $1_{b>1}$ being 1 or 0 according to whether b is or is not larger than one. When $b = 1$, at equilibrium, the landscape has no spatial correlations. However, during the transient dynamics before equilibrium, spatial correlations will exist if they were present initially; in that sense, the case where $b = 1$ is therefore different from a model assuming everything is well-mixed.

Equations (1) and (2) may be used to make substitutions to make Equations (A.5)–(A.8) self-contained. When $b > 1$, the system may be solved for the

822 following equilibrium:

$$\begin{aligned}
p^*[uuu] &= \frac{r_{su}((1+b)(2+b)r_{su}^2 + (b-4+3b^2)r_{su}r_{us} + 2(b-2)br_{us}^2)}{(r_{su} + r_{us})(r_{su} + br_{su} + 2br_{us})((2+b)r_{su} + 3br_{us})} \\
p^*[uus] &= \frac{(1+b)r_{su}r_{us}((2+b)r_{su} + br_{us})}{(r_{su} + r_{us})(r_{su} + br_{su} + 2br_{us})((2+b)r_{su} + 3br_{us})} \\
p^*[usu] &= \frac{r_{su}r_{us}((1+b)(2+b)^2r_{su}^2 + b(2+b)(1+3b)r_{su}r_{us} + 2(b-2)b^2r_{us}^2)}{(r_{su} + r_{us})(r_{su} + br_{su} + 2br_{us})((2+b)r_{su} + 2br_{us})((2+b)r_{su} + 3br_{us})} \\
p^*[uss] &= \frac{1}{(r_{su} + r_{us})(r_{su} + br_{su} + 2br_{us})} \\
&\quad \times \frac{2br_{su}r_{us}^2((2+b)^2r_{su} + b(5+2b)r_{us})}{((2+b)r_{su} + 2br_{us})((2+b)r_{su} + 3br_{us})}. \tag{A.9}
\end{aligned}$$

823 When $b = 1$, at equilibrium the system has no spatial correlations among adja-
824 cent sites, giving simply

$$p^*[uuu] = (p[u])^3, \quad p^*[uus] = p^*[usu] = (p[u])^2p[s], \quad p^*[uss] = p[u](p[s])^2.$$

825 Note that in this model, the transition rates for the configurations of habitat
826 types in any block of sites are fixed, and not dependent on the states of neigh-
827 boring sites or on the prevalence of habitat types in the landscape. Because
828 of that, the system of equations for the probabilities of habitat configurations
829 for blocks (of any size) of sites will be a linear system of ODEs. The equilib-
830 rium distribution of habitat types for any size blocks is therefore analytically
831 obtainable, in principle, as the solution to a system of linear equations.

832 *Appendix A.2. Doublet equations*

833 With three states per site, there are nine doublet probabilities $P[ij]$. How-
834 ever, one probability (say, $P[22]$) may be eliminated because all nine must sum
835 to one by Equation (1). Rotational symmetry allows the elimination of three
836 more probabilities via $P[ij] = P[ji]$ for $[ij] \in \{[01], [02], [12]\}$. The assump-
837 tion that the landscape is at dynamic equilibrium means that both $P[11]$ and
838 $P[1] = P[01] + P[11] + P[21]$ are fixed, allowing two more probabilities to be
839 eliminated. That leaves a total of three independent probabilities.

840 We choose to write ODEs for $P[00]$, $P[01]$, and $P[02]$:

$$\begin{aligned}\frac{dP[00]}{dt} &= 2P[01]r_{us} + 2P[02]\mu - P[00] \left(r_{su}(2 - \theta) + 2\frac{z-1}{z}\phi Q_{2|00} \right) \quad (\text{A.10}) \\ \frac{dP[01]}{dt} &= (P[00] + P[02])r_{su}(1 - \theta) + P[11]r_{us} + P[21]\mu \\ &\quad - P[01] \left(r_{us} + r_{su} + \frac{z-1}{z}\phi Q_{2|01} \right) \quad (\text{A.11})\end{aligned}$$

$$\begin{aligned}\frac{dP[02]}{dt} &= \frac{z-1}{z}P[00]\phi Q_{2|00} + P[12]r_{us} + P[22]\mu \\ &\quad - P[02] \left(\mu + r_{su}(2 - \theta) + \frac{\phi}{z} + \frac{z-1}{z}Q_{2|02} \right). \quad (\text{A.12})\end{aligned}$$

841 We use ordinary pair approximation, assuming conditional independence be-
842 tween the states of the first and third sites in a triplet when conditioned on
843 knowing the state of the second site, namely $Q_{i|jk} = P[i \cdot \cdot | \cdot jk] \approx P[i \cdot \cdot | \cdot j \cdot] =$
844 $Q_{i|j} = P[ij]/P[j]$. This is used to replace the quantities $Q_{2|00}$, $Q_{2|01}$, and $Q_{2|02}$
845 in the above ODEs.

846 The quantities $P[12]$ and $P[22]$ that appear in Equations (A.10)–(A.12) may
847 be expressed in terms of known quantities by using Equations (4) and (5):

$$\begin{aligned}P[12] &= p^*[s](1 - q_{s|s}^*) - P[01] \\ P[22] &= p^*[s]q_{s|s}^* - P[00] - 2P[02].\end{aligned}$$

848 Making all of the above substitutions in Equations (A.10)–(A.12) yields the
849 system of Equations (11)–(13).

850 *Appendix A.3. Landscape-improved doublet equations*

851 Equations (A.10)–(A.12) include the quantities $Q_{2|00}$, $Q_{2|01}$, and $Q_{2|02}$, in-
852 volving conditional probabilities that the first site in a triplet is suitable and
853 occupied, given information about the states of the last two sites. Ordinary
854 pair approximation conditionally neglects correlations between the first and
855 third site, conditioned on knowing the state of the second. In the landscape-
856 improved pair approximation, we first compute the probability that the first site
857 in the triplet is suitable given the known habitat types of the last two, and then
858 compute the probability that the first site is occupied given that it's suitable

(and given the state of the second site). In this way, information about habitat structure at the triplet scale is included (and, as mentioned in Section Appendix A.1, no approximations are needed when computing these triplet probabilities); population clustering is still utilized at the doublet scale.

Mathematically, this approach consists of the following approximations:

$$\begin{aligned} Q_{2|00} &\approx q_{s|ss} Q_{2\cdot|s0} \\ Q_{2|01} &\approx q_{s|su} Q_{2\cdot|s0} \\ Q_{2|02} &\approx q_{s|ss} Q_{2\cdot|s0}. \end{aligned}$$

The common factor in all three expressions above can be written as

$$Q_{2\cdot|s0} = \frac{P[20]}{P[s0]} = \frac{P[20]}{P[00] + P[20]}.$$

The other quantities in the above expressions can be expressed as

$$\begin{aligned} q_{s|ss} &= \frac{p[sss]}{p[ss]} = \frac{p[ss] - p[uss]}{p[ss]} \\ q_{s|su} &= \frac{p[ssu]}{p[su]} = \frac{p[uss]}{p[s] - p[ss]} \end{aligned}$$

where $p[s]$, $p[ss]$, and $p[uss]$ may be substituted in from Equations (A.2), (A.4), and (A.9) at equilibrium.

Appendix A.4. Block equations

The rate of change of the probability for a general 2×2 block may be written as

$$\frac{dP}{dt} \begin{bmatrix} v & w \\ x & y \end{bmatrix} = \sum_{i,j,k,l \in \{0,1,2\}} P \begin{bmatrix} i & j \\ k & l \end{bmatrix} r \left(\begin{smallmatrix} i & j \\ k & l \end{smallmatrix} \rightarrow \begin{smallmatrix} v & w \\ x & y \end{smallmatrix} \right) - P \begin{bmatrix} v & w \\ x & y \end{bmatrix} \sum_{i,j,k,l \in \{0,1,2\}} r \left(\begin{smallmatrix} v & w \\ x & y \end{smallmatrix} \rightarrow \begin{smallmatrix} i & j \\ k & l \end{smallmatrix} \right)$$

where $r \left(\begin{smallmatrix} v & w \\ x & y \end{smallmatrix} \rightarrow \begin{smallmatrix} i & j \\ k & l \end{smallmatrix} \right)$ is the rate at which a $\begin{bmatrix} v & w \\ x & y \end{bmatrix}$ block transitions to a $\begin{bmatrix} i & j \\ k & l \end{bmatrix}$ block. We compute these transition rates according to how many sites are affected by the event causing the transition, as follows.

872 A single-site transition may be a death, disturbance, or birth, with rates of
 873 those three events given below:

$$\begin{aligned}
 r\left(\begin{smallmatrix} 2 & w \\ x & y \end{smallmatrix} \rightarrow \begin{smallmatrix} 0 & w \\ x & y \end{smallmatrix}\right) &= \mu \\
 r\left(\begin{smallmatrix} v & w \\ x & y \end{smallmatrix} \rightarrow \begin{smallmatrix} 1 & w \\ x & y \end{smallmatrix}\right) &= \frac{rsu}{b^2} \quad \text{where } v \neq 1 \\
 r\left(\begin{smallmatrix} 0 & w \\ x & y \end{smallmatrix} \rightarrow \begin{smallmatrix} 2 & w \\ x & y \end{smallmatrix}\right) &= \frac{\phi}{z} \left(1_{w=2} + 1_{x=2} + P \left[\begin{array}{c|cc} 2 & \cdot & \cdot & \cdot \\ \cdot & \cdot & 0 & w \\ \cdot & \cdot & x & y \end{array} \right] + P \left[\begin{array}{ccc|c} 2 & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & 0 \\ \cdot & \cdot & \cdot & x \end{array} \right] \right) \\
 &\approx \frac{\phi}{z} \left(1_{w=2} + 1_{x=2} + P \left[\begin{array}{c|cc} 2 & \cdot & \cdot \\ \cdot & \cdot & 0 \\ \cdot & \cdot & w \end{array} \right] + P \left[\begin{array}{c|cc} 2 & \cdot & \cdot \\ \cdot & \cdot & \cdot \\ \cdot & \cdot & x \end{array} \right] \right) \\
 &= \frac{\phi}{z} \left(1_{w=2} + 1_{x=2} + \frac{P \left[\begin{array}{c|c} 2 & \cdot \\ 0 & w \end{array} \right]}{P[0w]} + \frac{P \left[\begin{array}{cc} 2 & 0 \\ \cdot & x \end{array} \right]}{P[0x]} \right).
 \end{aligned} \tag{A.13}$$

874 During a birth event, the top-left corner may be colonized by one of its known
 875 neighbors in the block, if either of them are in state 2 (occupied), or by one
 876 of its two neighbors outside of the block. When approximating the probability
 877 that a particular one of those external neighbors is occupied, we again neglect
 878 correlations between non-adjacent sites in the lattice, conditioned on knowing
 879 the state of a site between them. The probabilities of the partial blocks above
 880 may be obtained by summation, as in Equation (3).

881 Note that in the disturbance transition given by Equation (A.13) above, we
 882 ignore disturbance events that hit multiple sites but only actually change the
 883 state of one site (for example, if a disturbance affects all four sites in the block,
 884 but $w = x = y = 1$, then those three sites do not change state). Events hitting
 885 multiple sites are counted below.

886 A two-site transition may only be a disturbance, since intrinsic mortality
 887 and birth only affect one site at a time. Two-site disturbances can only affect
 888 two adjacent sites in the block; they cannot affect two diagonally opposite sites

889 within the block. The rates of these events are:

$$r\left(\begin{smallmatrix} v & w \\ x & y \end{smallmatrix} \rightarrow \begin{smallmatrix} 1 & 1 \\ x & y \end{smallmatrix}\right) = \frac{r_{su}(b-1)}{b^2} \quad \text{where } v \neq 1 \text{ and/or } w \neq 1.$$

890 The above rate counts the fact that there are $b-1$ locations a disturbance block
891 could be focused at which would affect only the top two sites in the block.

892 No events can affect exactly three sites within a 2×2 block, because dis-
893 turbance events are square. Finally, a four-site transition may only be a distur-
894 bance, with the following rate:

$$r\left(\begin{smallmatrix} v & w \\ x & y \end{smallmatrix} \rightarrow \begin{smallmatrix} 1 & 1 \\ 1 & 1 \end{smallmatrix}\right) = \frac{r_{su}(b-1)^2}{b^2} \quad \text{where at least one of } v, w, x, y \neq 1,$$

895 again counting the number of locations a disturbance block could target which
896 would affect all four sites in the 2×2 block being considered.