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Local Explanations of Landscape Patterns: Can Analytical Approaches Approximate Simulation Models of Spatial Processes?

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ABSTRACT

Research over the last 100 years has demonstrated the importance of space for ecological processes. Given this importance, it may seem natural to start investigations into broad-scale ecological processes with a comprehensive, broad-scale spatial map. Here we argue that it may sometimes be possible to answer important questions about spatial processes using crude spatial information obtained when a comprehensive map is not available. To present our argument, we first develop a simple simulation model for a perennial plant reproducing and dying on a landscape with different arrangements of suitable and unsuitable sites. We then develop a simple, analytical approximation to predict the fraction of suitable sites that are occupied by the simulated plants. The analytical approximation summarizes the spatial map by using a single parameter that gives the probability that a site adjacent to a suitable site is suitable. Comparing the predictions of both approaches highlights three points: (a) The role of the spatial environment in ecological processes may play out at the local scale. Therefore, studying the local-scale processes may provide insights into landscape patterns. (b) The predictions from the analytical approximation fail noticeably when suitable sites are rare and are distributed randomly (rather than clumped) on the map. In these situations, patches of interconnected suitable sites are very small, and populations within small patches may go extinct via demographic stochasticity. This illustrates how analytical approximations can be used to identify cases when local-scale spatial processes are not sufficient to understand the ecological consequences of space. (c) For many natural systems, constructing the appropriate environmental map needed to study ecological processes is difficult or impossible. However, summary characteristics such as those employed by the analytical approximation may be estimated directly in nature. Therefore, even in the absence of an explicitly spatial broad-scale map, it may be possible to study spatial processes by understanding which local-scale characteristics of space are important.

Key words: landscape ecology; spatial approximations; metapopulation dynamics; simulation modeling.

INTRODUCTION

Today there are two distinct ecological approaches to studying the response of organisms to spatial patterns: a landscape ecology approach and a population ecology approach. Although it is difficult to enumerate exactly how these approaches differ, we have little doubt that most studies on spatial processes would be unanimously categorized as one approach or the other by ecologists working in the field. The stereotypical starting point for landscape ecology studies is an explicit map. Owing to the complexities of real maps, landscape ecology models are usually computer simulations (Dunning and others 1995). Furthermore, many landscape ecol-

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ogy studies address management issues for specific plants or animals [for example, see Lamberson and others (1992), Pulliam and others (1992), Liu (1993), Lamberson and others (1994), Turner and others (1994), and Moen and others (1997)]. The need for quantitative predictions about the consequences of different management strategies further promotes the use of computer simulations that produce detailed output (Turner and others 1995). In short, a landscape ecology approach to studying the response of organisms to spatial patterns is characterized by complex models of organisms acting on a real (or at least realistically complex) map.

In contrast, the stereotypical theoretical study using a population ecology approach does not start with an explicit spatial map, but instead emphasizes how interactions within and among populations can generate spatial patterns and how these patterns influence the outcome of interactions; the product of the study is a map (Comins and others 1992; Durrett and Levin 1994a, 1994b; Halley and others 1994; Molofsky 1994; Keeling and Rand 1995; Wallinga 1995). For example, one of the important concepts from theoretical population ecology is *diffusive instability* (Edelstein-Keshet 1986; Murray 1989). In the absence of any environmental heterogeneity, a predator-prey system in which the predator has a higher movement rate than the prey can generate fixed spatial patterns with peaks and troughs in both predator and prey densities. In search of general properties of species interacting on a spatial plane, population ecology models often forego any pretense of detailed realism, and although simulation models are often used, the models are rarely cast in terms of specific ecological systems. The goal of most studies taking the population ecology approach is exploring the general consequences of spatial patterns for species interactions, rather than the effects of spatial environmental patterns on the spatial distribution of organisms or a particular management problem.

These gross caricatures of landscape and population ecology approaches to spatial processes are clearly simplifications that have many counterexamples. However, these caricatures help to summarize the "cultures" of landscape and population ecology. The contrasts between landscape and population ecology cultures bring out an obvious question of what can be learned by fusing landscape and population ecology approaches to space. Landscape ecology relies on simulation models that incorporate explicit spatial maps. Population ecology relies on analytical models that attempt to capture general properties of populations interacting in space. Can the analytical tools of population ecology help with the system-specific, detail-rich problems of landscape ecology that demand quantitative predictions?

Our objective in this article is to lay some initial groundwork to answer these questions. The ecological motivation for this work is understanding the implications of land-cover change on the spatiotemporal dynamics of herbs in mesic cove forests of the southern Appalachian Mountains. Many of the native herbs are long-lived perennials with poor dispersal capabilities. Due to topographic relief and past/present human land use, the region is characterized by substantial spatial heterogeneity in suitable habitat for these native herbs. Our particular question is whether it might be possible to quantify the fraction of suitable sites that are occupied by perennial plant populations, given information about the colonization and extinction rates of local plant populations and a few summary statistics of the spatial distribution of suitable sites, but without knowing the exact location of suitable sites on a spatial map. This type of problem is common in ecology. Some crude spatial information is known about the distribution of suitable habitat, obtained for example from sampling a series of transects. Yet a comprehensive map of the distribution of suitable habitat is not available, because the only way of assessing the suitability of habitat is through ground reconnaissance. The question we address is if and when relatively crude spatial information can be used to model the abundance of a species in a heterogeneous landscape.

We begin by developing a simple simulation model for the population dynamics of a perennial plant on an explicit map made up of suitable and unsuitable sites. We use the simulation model to produce simulated *datasets*, and then test the ability of an analytical approximation to predict the average fraction of occupied sites on the simulated landscape. The analytical approximation works by capturing the effects of space by using two local-scale variables. First, the map of suitable/unsuitable sites is summarized by a parameter that gives the probability that a site adjacent to a suitable site is also suitable. As suitable sites become more clumped, the plants are better able to spread from occupied sites into suitable, unoccupied sites. Second, the clustering of plants among the suitable sites is summarized by the probability that a suitable site adjacent to an occupied site is also occupied. Clustering of plants among suitable sites lowers the effective colonization rate of plants into unoccupied suitable sites, because propagules are more likely to land in already occupied sites.

Our test of the analytical approximation is whether it can describe the population dynamics produced by the simulation model. The simulation model itself is a very simple portrayal of plant population dynamics. We have intentionally made the simulation model simple in order to highlight the role of explicit spatial structure. For both simulation model and analytical approximation, we assume that both the colonization rate of plants from occupied sites into unoccupied suitable sites and the extinction rates of plant populations from sites are known. Thus, the only difference between the simulation model and the analytical approximation is whether or not explicit spatial structure is included. Of course, to apply either more realistic simulation models or more realistic analytical approximations to real plant systems, large amounts of data are needed on the dispersal distances and establishment rates of plant propagules, and the extinction rates of local populations. We ask the more restricted question of how much information is needed on the explicit spatial arrangement of suitable habitat for predicting changes in the average proportion of suitable habitat that is occupied by plant populations.

METHODS

Explicitly Spatial Simulation Model

The simulation model starts with a map of suitable and unsuitable sites arranged on a 100×100 grid. The plant population is modeled in terms of which suitable sites are occupied by plants. Thus, rather than keep track of the number of plants in each suitable site, the suitable sites are scored simply as being either occupied or unoccupied. An occupied suitable site has an annual probability e of becoming unoccupied due to the death of all plants in the site. Unoccupied sites can be colonized by propagules dispersing from any of the eight adjacent sites that are occupied. For simplicity, we assume that dispersal rates of propagules from occupied sites along diagonals in the grid are equal to those in the vertical and horizontal directions. Each occupied site produces propagules that on average disperse to m of the adjacent sites per year ($m \leq 8$), and thus the numbers of propagules dispersing from a site depends only on the site being occupied, not on the number of plants in the site. We will refer to m as the colonization rate of the plants. Finally, we assume that it takes a year (one time step) for a newly established plant population to produce propagules. Therefore, an occupied site cannot become unoccupied and then be recolonized and produce propagules in the same time step.

The simulation model was run using 20 maps, 10 of which were obtained from a land-cover map derived from 1991 Thematic Mapper imagery (P. Bolstad and H. Pape personal communication). The maps used here were 100×100-grid cell subsections (10.9 km^2) from within the French Broad River Basin, North Carolina. Deciduous forest comprised the suitable sites, and the other land-cover types were reclassified as unsuitable. The remaining 10 maps were generating by distributing suitable sites randomly on a 100×100 grid, varying the fraction of suitable sites from 0.1 to 1.0 in steps of 0.1. Figure 1 depicts the 10 real maps and the random maps with 0.1 and 0.5 suitable sites.

To characterize these maps, we calculated two parameters. The parameter $q(1)$ is the probability that a given site is suitable, and $q(1|1)$ is the probability that a site adjacent to a suitable site is suitable. In this notation, "1" symbolizes that a site is suitable, and "|" indicates a conditional probability. The quantity $q(1|1)$ is a measure of "contagion" used in landscape ecology (O'Neill and others 1988). Table 1 lists these and other parameters used throughout the article. To calculate $q(1|1)$, we counted the number of suitable sites adjacent to each suitable site over the entire map and divided by 8. For sites at the margins of the map, we assumed that the sites outside the map are unsuitable. For all of the real maps, $q(1|1)$ is considerably larger than $q(1)$, showing that suitable sites are strongly clumped (Figure 1). For random maps, $q(1)$ and $q(1|1)$ are roughly equal, differing only because the maps contain a finite number of sites.

We calculated $q(1)$ and $q(1|1)$ for each map using every site on the map. It is possible, however, to estimate $q(1)$ and $q(1|1)$ by sampling only a small proportion of sites. To illustrate this, for each of the maps in Figure 1, we randomly selected 100 of the 10,000 sites, and $q(1)$ was estimated as the proportion of the sampled sites that are suitable. For each of the suitable sites, we randomly selected one of the eight adjacent sites to determine whether it was suitable. This produced an estimate of $q(1|1)$. Actual and estimated values of $q(1)$ and $q(1|1)$ are listed in Table 2. These results show that sampling less than 2% of the sites (100 randomly selected sites and, for those sites being suitable, one additional adjacent site) produce reasonably good estimates of $q(1)$ and $q(1|1)$. This is important because the analytical approximation summarizes all of the spatial structure of the maps by using only the values of $q(1)$ and $q(1|1)$. Therefore, the analytical approximation can be applied even if only a small proportion of the

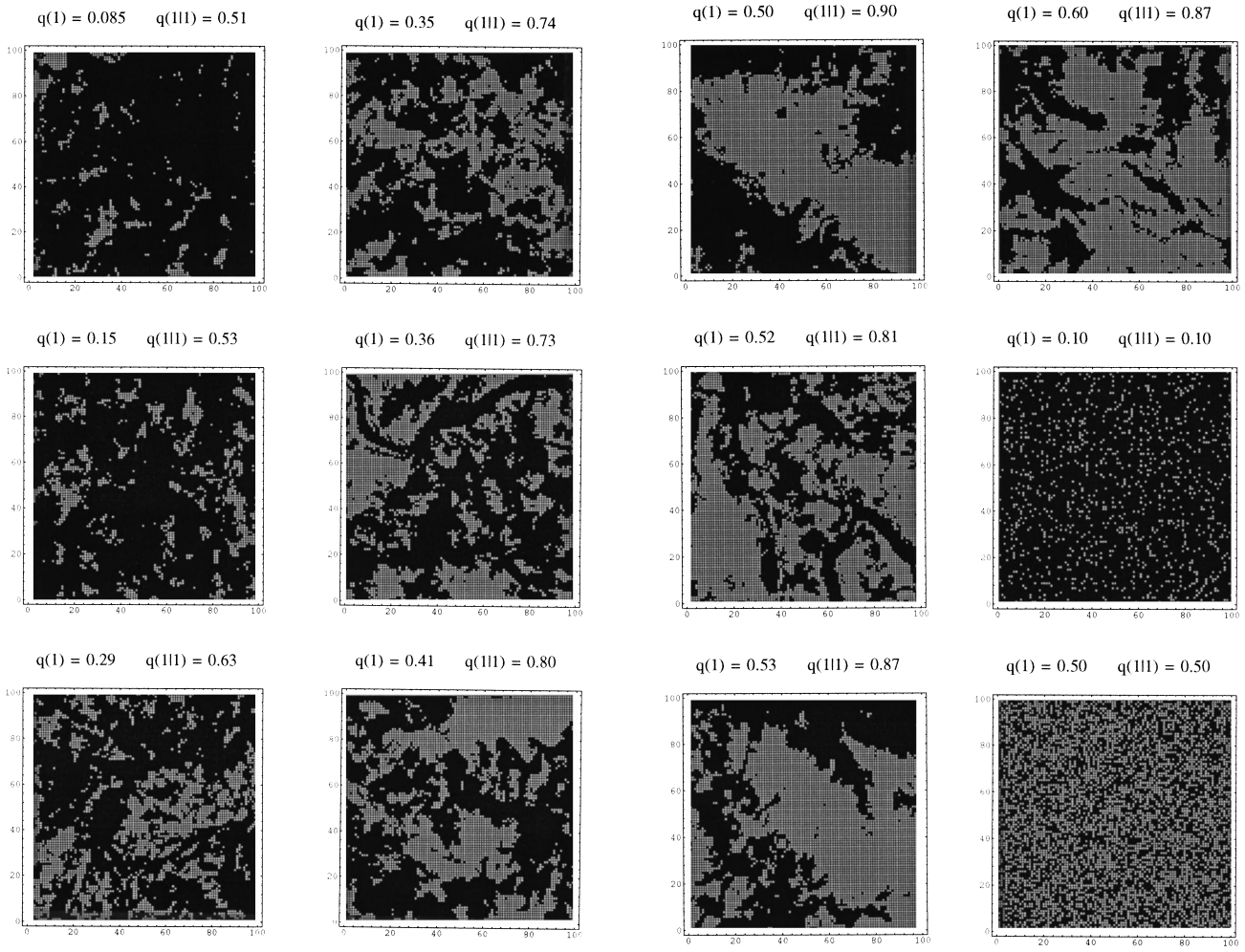

Figure 1. The 10 real maps and two random maps used in the simulations. Suitable sites are shown in white. For each map values are given of $q(1)$, the fraction of sites that are suitable, and $q(1|1)$, the probability that a site adjacent to a suitable site is suitable. The two random maps have $q(1) = q(1|1) = 0.10$ and 0.50.

landscape has been sampled, with more precise estimates of $q(1)$ and $q(1|1)$ possible when more of the landscape is sampled. Although the procedure we used here selects sites at random, other more systematic sampling protocols, such as linear transect sampling, can be used to estimate $q(1)$ and $q(1|1)$. For the analysis that follows, we use the actual rather than estimated values of $q(1)$ and $q(1|1)$, so the comparison between the simulation model and the analytical approximation is not complicated by the variability associated with estimating $q(1)$ and $q(1|1)$ from a subset of sites.

At the start of the simulations, we populated each map by randomly distributing plants among suitable sites. For each iteration, occupied sites became unoccupied with probability e. For each unoccupied suitable site, the number of adjacent occupied sites c was calculated. Since each occupied site on average produces propagules that disperse to m of the eight surrounding sites, the probability that a site receives a propagule from a given adjacent occupied site is $m/8$. The probability it does not receive a propagule from that site is $(1 - m/8)$, and if there are c adjacent occupied sites, the probability of not receiving a propagule is $(1 - m/8)^c$. Therefore, in each iteration of the model, unoccupied sites became occupied with probability $[1 - (1 - m/8)^c]$. Updates of the state of suitable sites (occupied or unoccupied) were made simultaneously for all sites on the map. Finally, at each time step, the probability that a suitable site was occupied, $p(1)$, and the probability that a suitable site adjacent to an occupied site was occupied, $p(1|1)$, were calculated using all sites in the 100×100-grid maps.

Technically speaking, the simulation model has no steady state. Because there is a finite number of suitable sites in each map, and because the extinction of plant populations from sites is random, the simulations will all eventually lead to the extinction of all plant populations from the landscape. How-

Table 1. Model Parameters and Their Definitions

Parameter	Definition
e	Plant population extinction rate: probability that an occupied site becomes unoccupied during a time step
m	Plant colonization rate: number of propagules produced per occupied site that can potentially establish in adjacent suitable unoccupied sites during a time step
c	Number of occupied suitable sites adjacent to a given suitable unoccupied site
$q(1)$	Probability that a site is suitable
$q(1\|1)$	Probability that a site adjacent to a suitable site is suitable
$q^*(1\|\text{occupied})$	Probability that a site adjacent to an occupied suitable site is suitable at the steady-state occupancy of plants among sites
$p(1)$	Probability that a suitable site is occupied in the simulation model
$p(1\|1)$	Clustering of plants among suitable sites: probability that a suitable site adjacent to a suitable occupied site is occupied in the simulation model
$p(1\|0)$	Probability that a suitable site adjacent to a suitable unoccupied site is occupied
p_m	Steady-steady fraction of suitable sites that are occupied approximated under the assumption that there is no clustering of plant populations among suitable sites (Eq. 5)
$\hat{p}(1)$	Approximation (Eq. 6) for the probability that a suitable site is occupied
$\hat{p}(1\|1)$	Approximation (Eq. 6) for the probability that a suitable site adjacent to a suitable occupied site is occupied

ever, this will take a tremendously long time. For all practical purposes, the simulated populations reached a quasi-steady state with no directional trends after 20 iterations. Therefore, we iterated the simulation model 40 times and averaged over iterations 21–40 to give quasi-steady state values of $p(1)$ and $p(1|1)$. We denote these values of $p(1)$ and $p(1|1)$ as $p^*(1)$ and $p^*(1|1)$, respectively.

First Analytical Approximation

The analytical approximation of the plant population dynamics is based on describing the spatial processes by using two local-scale characteristics. First, the distribution of suitable sites on the map is summarized by the probability that a site adjacent to a suitable site is suitable, $q(1|1)$. Second, the clustering of plants among neighboring suitable sites is summarized by the probability that a suitable site adjacent to an occupied suitable site is occupied, $p(1|1)$. Whereas $q(1|1)$ is a parameter that is calculated from a map and is input into the model, $p(1|1)$ is a variable that changes dynamically and is a component of the output of the model. To disentangle these two spatial characteristics, we first develop an approximation that accounts for only the distribution of suitable sites on the map, $q(1|1)$. In the next section, we develop an approximation that adds the effect of plant clustering among suitable sites, $p(1|1)$.

The analytical approximation tracks the plant population using $\hat{p}(1)$, the estimated probability that a suitable site is occupied. [The hat $\hat{}$ notation is used to identify $\hat{p}(1)$ as the value of $p(1)$ estimated by the approximation.] Letting $\Delta\hat{p}(1)$ denote the change in $\hat{p}(1)$ each time step, the first approximation is

$$\Delta\hat{p}(1) = -e\hat{p}(1) + \left[1 - \left(1 - \frac{mq(1|1)\hat{p}(1)}{8}\right)^8\right](1 - \hat{p}(1)) \quad (1)$$

The first term in the approximation accounts for occupied sites becoming unoccupied. Since e is the extinction rate of plant populations from sites, the expected change in the fraction of occupied suitable sites in a time step is $-e\hat{p}(1)$. The second term in Eq. 1 accounts for colonization of plant populations into the fraction of suitable sites that are unoccupied. To explain this term, suppose that a suitable site is surrounded by c occupied sites. Then the probability that the site becomes occupied is $1 - (1 - m/8)^c$]. If $b(c)$ denotes the probability that a suitable unoccupied site has c adjacent occupied sites, the expecta-

Table 2. Estimates of $q(1)$ and $q(1|1)$ by Using 100 Randomly Selected Sites on the 100 × 100-Grid Maps[a]

$q(1)$			$q(1\|1)$		
Actual	Estimate	95% Confidence Interval	Actual	Estimate	95% Confidence Interval
Real maps			Real maps		
0.084	0.080	(0.037, 0.166)	0.514	0.500	(0.323, 0.677)
0.146	0.110	(0.061, 0.209)	0.532	0.636	(0.491, 0.781)
0.292	0.290	(0.218, 0.433)	0.63	0.586	(0.495, 0.678)
0.348	0.350	(0.275, 0.501)	0.737	0.771	(0.700, 0.842)
0.358	0.380	(0.303, 0.533)	0.728	0.737	(0.665, 0.808)
0.413	0.430	(0.352, 0.587)	0.799	0.814	(0.755, 0.873)
0.496	0.540	(0.461, 0.698)	0.896	0.944	(0.913, 0.976)
0.524	0.450	(0.371, 0.607)	0.813	0.733	(0.667, 0.799)
0.528	0.480	(0.401, 0.638)	0.873	0.875	(0.827, 0.923)
0.6	0.650	(0.575, 0.801)	0.871	0.892	(0.854, 0.931)
Random maps			Random maps		
0.103	0.150	(0.094, 0.263)	0.102	0.200	(0.097, 0.303)
0.489	0.530	(0.451, 0.688)	0.487	0.528	(0.460, 0.597)

[a]*For each map, 100 sites were selected by using a random number generator. If a site was suitable, an adjacent site was randomly selected to determine whether it was suitable. Confidence intervals were calculated assuming that the estimates of* q*(1)* and q*(1|1) are binomially distributed.*

tion that a suitable unoccupied site becomes occupied is

$$\sum_{c=0}^{8}\left[1-\left(1-\frac{m}{8}\right)^{c}\right]b(c) = 1-\sum_{c=0}^{8}\left(1-\frac{m}{8}\right)^{c}b(c) \quad (2)$$

If we assume that the probability of a given adjacent site being occupied is independent of the probability of another adjacent site being occupied, then $b(c)$ is a $B[n; p]$ binomial distribution with $n = 8$ and p estimated as described below.

The probability that a suitable site adjacent to an unoccupied suitable site is occupied depends on the probability that the adjacent site is suitable and the probability that it is occupied given it is suitable. For the approximation, we assume that $q(1|1)$ is the probability that a site adjacent to a suitable unoccupied site is suitable. Note that this is only approximately true, since $q(1|1)$ gives the probability that a site adjacent to a suitable site is suitable. For the approximation, we need the probability that a site adjacent to an *unoccupied* suitable site is suitable. Further, we assume that $\hat{p}(1)$ is the probability that a suitable site adjacent to an unoccupied suitable site is occupied. Again this is only approximately true, since $\hat{p}(1)$ is the probability that a suitable site is occupied without the conditional requirement that this site is adjacent to an unoccupied suitable site. With these two assumptions, the expected probability that a site adjacent to an unoccupied suitable site is occupied equals $q(1|1)\hat{p}(1)$. Therefore, the mean of the distribution $b(c)$ is $8q(1|1)\hat{p}(1)$. The generating function $G(z)$ for a $B[8; q(1|1)\hat{p}(1)]$ binomial distribution is (Larsen and Marx 1981)

$$G(z) = \sum_{c=0}^{8} z^{c}b(c) = [1 + q(1|1)\hat{p}(1)(z - 1)]^{8} \quad (3)$$

Letting $z = (1 - m/8)$, the probability that an unoccupied suitable site becomes occupied (Eq. 2) is

$$1-\sum_{c=0}^{8}\left(1-\frac{m}{8}\right)^{c}b(c) = 1-\left(1-\frac{mq(1|1)\hat{p}(1)}{8}\right)^{8} \quad (4)$$

Since the fraction of suitable sites that is unoccupied is $[1 - \hat{p}(1)]$, the second term in Eq. 1 approximates the increase in the expected fraction of occupied suitable sites at each time step due to colonization from adjacent sites.

Equation 1 can be used directly to estimate the expected fraction of occupied suitable sites at steady state, when $\Delta\hat{p}(1) = 0$. Letting p_m denote the approximate steady state value of $\hat{p}(1)$,

$$ep_m = \left[1-\left(1-\frac{mq(1|1)p_m}{8}\right)^{8}\right](1 - p_m) \quad (5)$$

Throughout the analysis of the simulation model, we use e, $q(1|1)$, and p_m as input variables and calculate m from Eq. 5. We have chosen to input p_m rather than m because the relationship between m and steady-state plant abundance in the simulation model, $p^*(1)$, is highly nonlinear, so using p_m rather than m makes the analysis more clear. We have used "m" to subscript p_m to emphasize that the selected value of p_m [along with e and $q(1|1)$] determines the colonization rate m. In addition, at the start of each simulation run, we populated the map by letting the probability that a suitable site is occupied be p_m. As shown below, p_m gives a rough estimate of the steady-state plant abundance in the simulation model, so starting with this rough estimate reduces the number of iterations of the simulation model before steady state is achieved.

Second Analytical Approximation Including Plant Clustering

The approximation given in Eq. 1 accounts only for the clumping of suitable sites on the map. To account for the clustering of plants among suitable sites, we derive equations not only for the probability that a suitable site is occupied, $\hat{p}(1)$, but also for $\hat{p}(1|0)$, the probability that a suitable site adjacent to an unoccupied suitable site is occupied. The approximation is

$$\Delta\hat{p}(1) = -e\hat{p}(1) + (1 - \hat{p}(1))\left[1 - \left(1 - \frac{mq(1|1)\hat{p}(1|0)}{8}\right)^8\right] \quad (6a)$$

$$\Delta\hat{p}(1|0) = -e\hat{p}(1|0) + (1 - \hat{p}(1|0)) \cdot \left[1 - \left(1 - \frac{mq(1|1)\hat{p}(1|0)}{8}\right)^7\right] \quad (6b)$$

Although more complex than Eq. 1, Eq. 6 is derived by using a very similar set of assumptions. This type of approximation has been used in a number of other ecological contexts (Matsuda and others 1992; Harada and others 1995; Keeling and Rand 1995; Van Baalen personal communication.

In Eq. 1, we approximated the probability that a suitable site adjacent to an unoccupied suitable site is occupied as $\hat{p}(1)$. However, if plant populations are clustered among suitable sites, this assumption will overestimate the true probability, because unoccupied suitable sites are more likely to be adjacent to other unoccupied suitable sites than expected if plants were distributed randomly. Therefore, rather than use $\hat{p}(1)$ as an estimate of the probability that a suitable site adjacent to an unoccupied suitable site is occupied, in Eq. 6a we explicitly approximate $\hat{p}(1|0)$. In other respects, Eq. 6a is the same as Eq. 1.

The change in $\hat{p}(1|0)$ each time step, Eq. 6b, is approximated in a similar manner as $\hat{p}(1)$. The fact that $\hat{p}(1|0)$ is now a conditional probability depending on the site being adjacent to an unoccupied suitable site does not change the general form of the equation. To explain the modifications in Eq. 6b, it is easiest to consider two suitable sites: site A, which is unoccupied; and site B, which is adjacent to site A and is also unoccupied. The number of propagules that could colonize site B depends on the number of sites surrounding site B that are occupied. We know that only seven of the eight sites surrounding site B could potentially be occupied, because the eighth site, site A, is unoccupied. The probability that any of the seven sites is occupied, $\hat{p}(1|0, 0)$, is conditioned on the information that both A and B are unoccupied. However, for the approximation we assume that $\hat{p}(1|0, 0) = \hat{p}(1|0)$, the probability that any suitable site adjacent to an unoccupied site is occupied. Alternatively, to approximate $\hat{p}(1|0, 0)$, we could have added another equation for $\hat{p}(1|0, 0)$ in the same manner as Eq. 6b; however, stopping at this second-order approximation proves to be sufficient to capture the population dynamics exhibited by the simulation model. Under these assumptions, the expected probability that site B becomes occupied is

$$1 - \sum_{c=0}^{7}\left(1 - \frac{m}{8}\right)^c b(c|0) = 1 - \left(1 - \frac{mq(1|1)\hat{p}(1|0)}{8}\right)^7 \quad (7)$$

where $b(c|0)$ is a $B[7; q(1|1)\hat{p}(1|0)]$ binomial distribution. This leads directly to Eq. 6b.

To compare with the output from the simulation model, we iterated Eq. 6 40 times starting from p_m, and as a measure of the population abundance of plants, we averaged $\hat{p}(1)$ over the last 20 iterations to give $\hat{p}^*(1)$. Since $\hat{p}(1) = \hat{p}(1|0)\hat{p}(0) = \hat{p}(1|1)\hat{p}(1)$, $\hat{p}(1|1)$ can be computed as $\hat{p}(1|1) = \hat{p}(1|0)[1 - \hat{p}(1)]/\hat{p}(1)$. From this we calculated $\hat{p}(1|1)$ at each iteration and averaged over the last 20 iterations to give $\hat{p}^*(1|1)$.

Results

Assessing the Analytical Approximations

In the simulation model, plant population dynamics measured by the fraction of suitable sites occupied by plants $p(1)$, reached a quasi-steady state in which site occupancy fluctuated narrowly around an average value. Figure 2 shows typical output from the simulation model starting with the proportion of occupied suitable sites far from steady state. In addition to $p(1)$, we also graph $p(1|1)$, the probability that a suitable site adjacent to an occupied site is

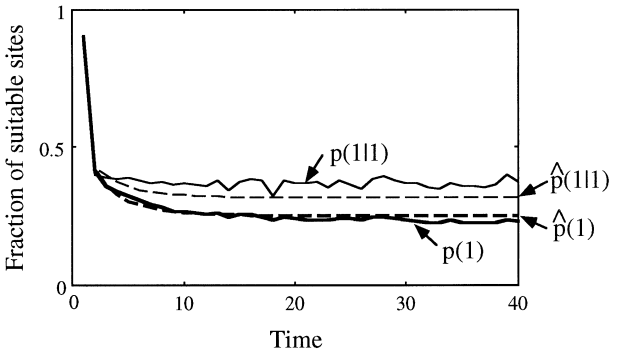

Figure 2. Plant population dynamics from the simulation model (solid lines) and the approximation given by Eq. 6 (dashed lines). The heavy lines give values of $p(1)$ and $\hat{p}(1)$, the simulated and approximated fraction of suitable sites occupied by plants. The light lines give values of $p(1|1)$ and $\hat{p}(1|1)$, the simulated and approximated probabilities that a suitable site adjacent to an occupied site is occupied.

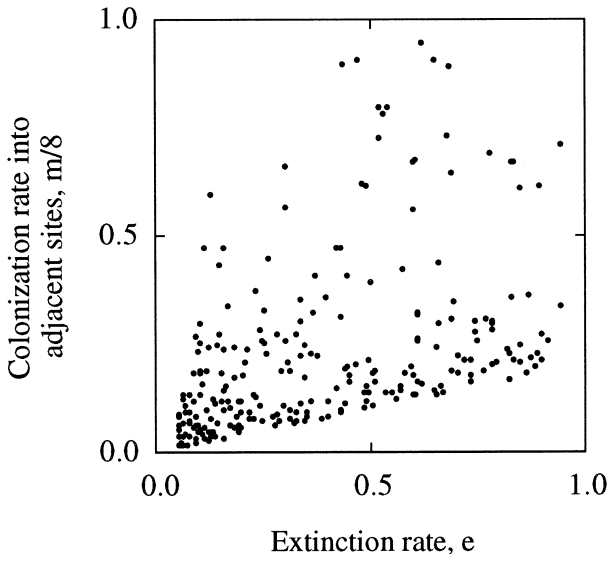

Figure 3. Combinations of values of extinction rates, e, and colonization rates, m, obtained from the procedure used to select parameter values for the simulation model. In the vertical axis, the colonization rate m is divided by 8 to give annual probability that propagules from an occupied site colonize a given adjacent site.

occupied. Since $p(1|1)$ is greater than $p(1)$, plant populations are clustered among suitable sites. The dashed lines give the corresponding analytical approximations $\hat{p}(1)$ and $\hat{p}(1|1)$ calculated from Eq. 6. The approximations of $p(1)$ and $p(1|1)$ match not only the steady state but also the dynamics of the plant population as it approaches steady state.

To investigate in detail the ability of the approximation to predict steady-state site occupancies given by the simulation model, we created 25 datasets for each of the 20 maps. To create a dataset for a particular map, we first selected p_m from a uniform distribution between 0.1 and 0.9. The maximum permissible value of e depends on the selected value of p_m (see the Appendix), so after selecting p_m we calculated the maximum value of e, $e_{\max}(p_m)$. We then selected e from a uniform distribution between 0.05 and $e_{\max}(p_m) - 0.05$.

Although we do not use the colonization rate m as an input parameter, it is nonetheless relevant to ask what are the values of m in the simulations. Figure 3 depicts combinations of e and m selected by the procedure just described. Since the value of m depends not only on e and p_m but also on $q(1|1)$, we used the value of $q(1|1) = 0.74$ to correspond to the real map with $q(1) = 0.35$ (Figure 1). As seen in Figure 3, most values of $m/8$ are less than 0.2, implying that the probability that an unoccupied suitable site is colonized by propagules from a given adjacent occupied site is less than 20% per year. No pairs of values of e and m occur in the lower right-hand corner of the figure, because when extinction rates are high, colonization rates must be above a minimum threshold for the entire plant population to persist in the landscape. Considering other maps, for particular values of e and p_m, m and $q(1|1)$ are inversely proportional (see the Appendix). Therefore, for maps with lower values of $q(1|1)$, colonization rates m must be proportionally greater to maintain the same fraction of occupied suitable sites at steady state.

For the simulated datasets, Figure 4 shows the steady state values of $p^*(1|1)$ versus $p^*(1)$ for the real and random maps. In each graph, data from the two maps of either type (real or random) with the lowest frequencies of suitable sites [$q(1) \leq 0.2$] are shown with solid dots, whereas the remainder of the maps are shown as open dots. Clustering of plant populations among suitable sites is the norm; $p^*(1|1) > p^*(1)$ for most combinations of e and p_m. This is especially true for maps with a relatively small fraction of suitable sites (shown by solid dots). In addition, clustering depends on the values of p_m and e. Table 3 gives a regression analysis for the clustering of plant populations among suitable sites, measured by $p^*(1|1) - p^*(1)$, versus p_m and e for the real and random maps. For both real and random maps, p_m and e had negative effects on clustering, with e acting directly on clustering for the random maps and acting in interaction with p_m for the real maps. Therefore, the plant populations became relatively more randomly (Poisson) distributed when colonization and extinction rates were high.

The approximation used to give p_m (Eq. 1) takes account of the clumped distribution of suitable sites

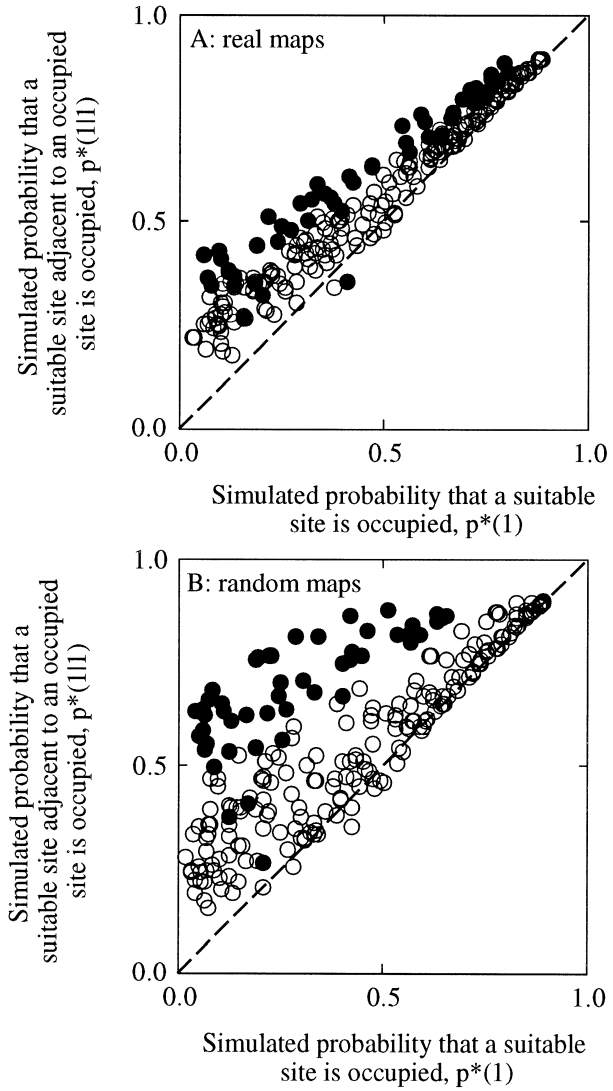

Figure 4. The clustering of plant populations in the simulated datasets. The steady-state probability that a suitable site adjacent to an occupied site is occupied, $p^*(1|1)$, is graphed against the steady-state fraction of occupied suitable sites, $p^*(1)$, for **A** 10 real and **B** 10 random maps. For real and random maps, the two maps with the lowest fractions of suitable sites [$q(1) \leq 0.2$] are shown with solid dots. Each dot represents a combination of values of p_m and e, and 25 combinations were run for each map. Values of p_m were selected from a uniform distribution between 0.1 and 0.9, and e was selected from a uniform distribution between 0.05 and $e_{\max}(p_m) - 0.05$ (see the Appendix).

on the maps but does not account for the clustering of plant populations among suitable sites. Figure 5 graphs the approximate steady-state occupancy p_m versus the simulated steady state $p^*(1)$ for the real and random maps. In most cases, $p_m > p^*(1)$, indicating that the simple approximation of Eq. 1 generally overestimates the steady-state occupancy

Table 3. Results of a Regression Analysis for the Clustering of Plant Populations Among Suitable Sites, $p*(1|1) - p*(1)$, Versus e, p_m, and the Interaction $e \times p_m$

Source	Coefficient	SS	*df*	*F*	*p*
Real maps ($R^2 = 0.94$)					
Map		0.028	9	9.46	$\ll 0.001$
e	0.012	0.000097	1	0.29	0.59
p_m	−0.38	0.11	1	335.8	$\ll 0.001$
$e \times p_m$	−0.32	0.012	1	34.9	$\ll 0.001$
Error		0.078	237		
Random maps ($R^2 = 0.93$)					
Map		3.42	9	207	$\ll 0.001$
e	−0.27	0.23	1	126	$\ll 0.001$
p_m	−0.44	0.93	1	508	$\ll 0.001$
$e \times p_m$	−0.080	0.0037	1	2.03	0.16
Error		0.63	237		

of suitable sites in the simulated datasets. As shown below, this overestimation is due to the clustering of plant populations among suitable sites. When plant populations are clustered, their propagules are more likely to disperse into sites that are already occupied. This has the effect of decreasing the effective colonization rate and consequently decreasing the fraction of occupied sites on the landscape.

The effect of plant population clustering can be seen by comparing the predictions of the steady state in the simulated datasets, $p^*(1)$, made by p_m with those made by $\hat{p}^*(1)$, the estimated steady state calculated from the approximation that accounts for plant population clustering (Eq. 6). Figure 6 depicts $\hat{p}^*(1)$ versus the simulated steady state $p^*(1)$ for real and random maps. The estimates given by $\hat{p}^*(1)$ are lower than those given by p_m, particularly for small values of $p^*(1)$ (compare Figures 5 and 6), illustrating quantitatively the effect of plant population clustering on steady states. For the real maps, $\hat{p}^*(1)$ gives a very good approximation of $p^*(1)$. The approximations are not as good for the random maps, particularly the randommaps with ≤20% suitable sites (shown as solid dots) in which $\hat{p}^*(1)$ consistently overestimates $p^*(1)$. For the real maps, Eq. 6 also gives a reasonable approximation of $p^*(1|1)$, the measure of plant population clustering in the simulated datasets, although it is less successful for the random maps (Figure 7). Generally, the approximation $\hat{p}^*(1|1)$ underestimates $p^*(1|1)$, implying that the approximation does not fully account for the clustering of plant populations among suitable sites.

The difference between the analytically approximated steady state, $\hat{p}^*(1)$, and the steady state of the

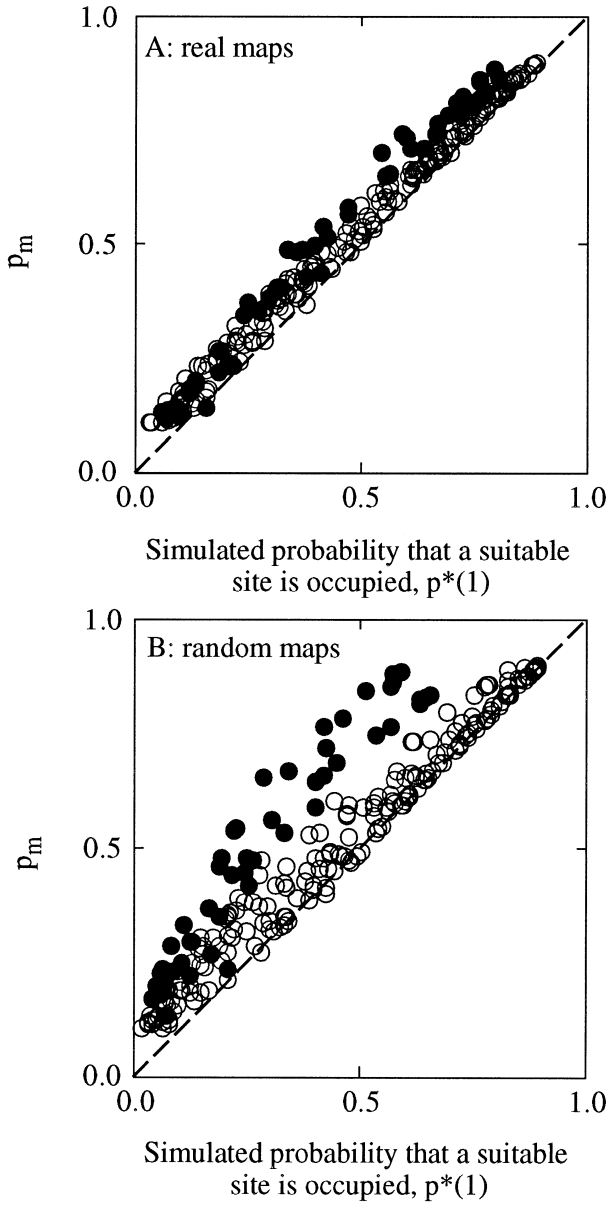

Figure 5. The steady-state fraction of suitable sites that are occupied approximated by using Eq. 1, p_m, versus the steady-state fraction calculated from the simulated datasets, $p^*(1)$, for **A** 10 real and **B** 10 random maps. For real and random maps, the two maps with the lowest fractions of suitable sites [$q(1) \leq 0.2$] are shown with solid dots. The data come from the same simulations used to give Figure 4.

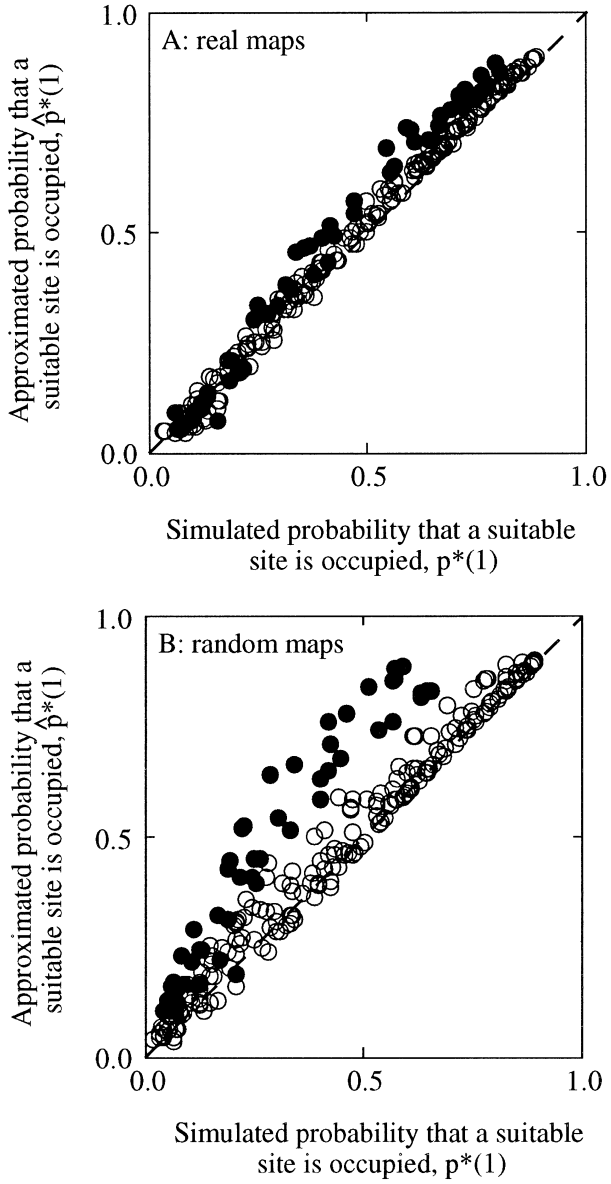

Figure 6. The steady-state fraction of suitable sites that are occupied approximated by using Eq. 6, $\hat{p}^*(1)$, versus the steady-state fraction calculated from the simulated datasets, $p^*(1)$, for **A** 10 real and **B** 10 random maps. For real and random maps, the two maps with the lowest fractions of suitable sites [$q(1) \leq 0.2$] are shown with solid dots. The data come from the same simulations used to give Figure 4.

simulated datasets, $p^*(1)$, depends both on the distribution of suitable sites on the map and on the parameters p_m and e. Comparing the mean squared difference between approximated and simulated steady states, $[\hat{p}^*(1) - p^*(1)]^2$, shows that approximations were worse for maps with fewer suitable sites, $q(1)$ (Figure 8A). When plotting $[\hat{p}^*(1) - p^*(1)]^2$ against $q(1)$, it appears as if the approximation works better for the real maps than for the random maps. Nonetheless, plotting $[\hat{p}^*(1) - p^*(1)]^2$ against $q(1|1)$ reveals that the clumping of suitable sites measured by $q(1|1)$ is a good predictor of the performance of the approximation for both real and random maps. For maps with low $q(1|1)$, the "perceived" availability of suitable sites is low, implying

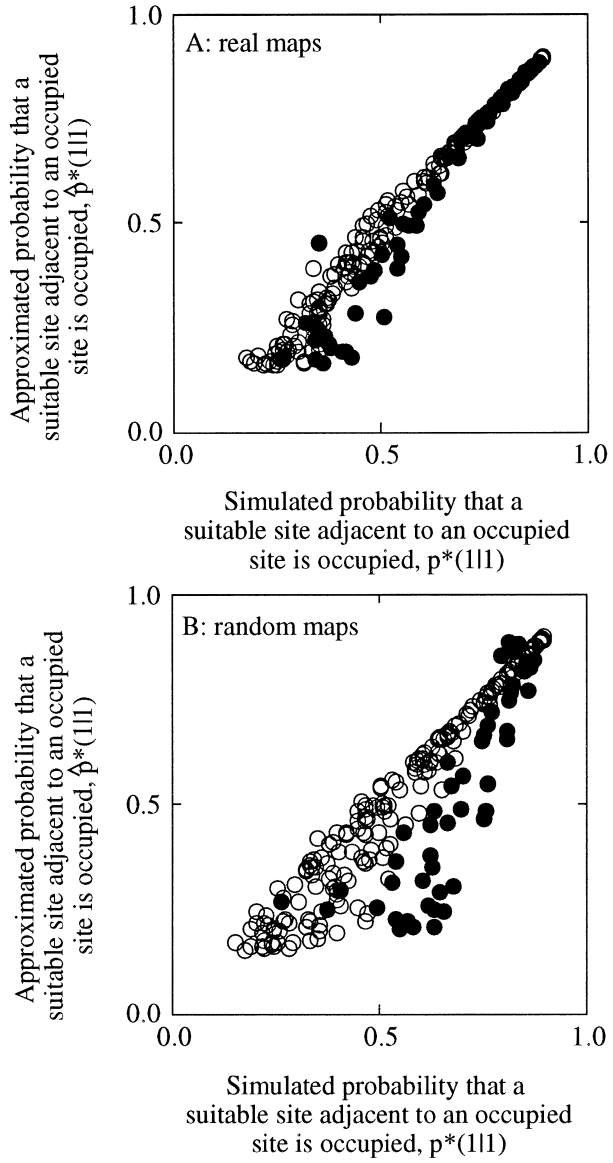

Figure 7. The approximated and simulated clustering of plant populations among suitable sites for **A** 10 real and **B** 10 random maps. The clustering of populations is given by $\hat{p}^*(1|1)$ and $p^*(1|1)$, the approximated and simulated probabilities that a suitable site adjacent to an occupied suitable site is suitable. For real and random maps, the two maps with the lowest fractions of suitable sites $[q(1) \leq 0.2]$ are shown with solid dots. The data come from the same simulations used to give Figure 4.

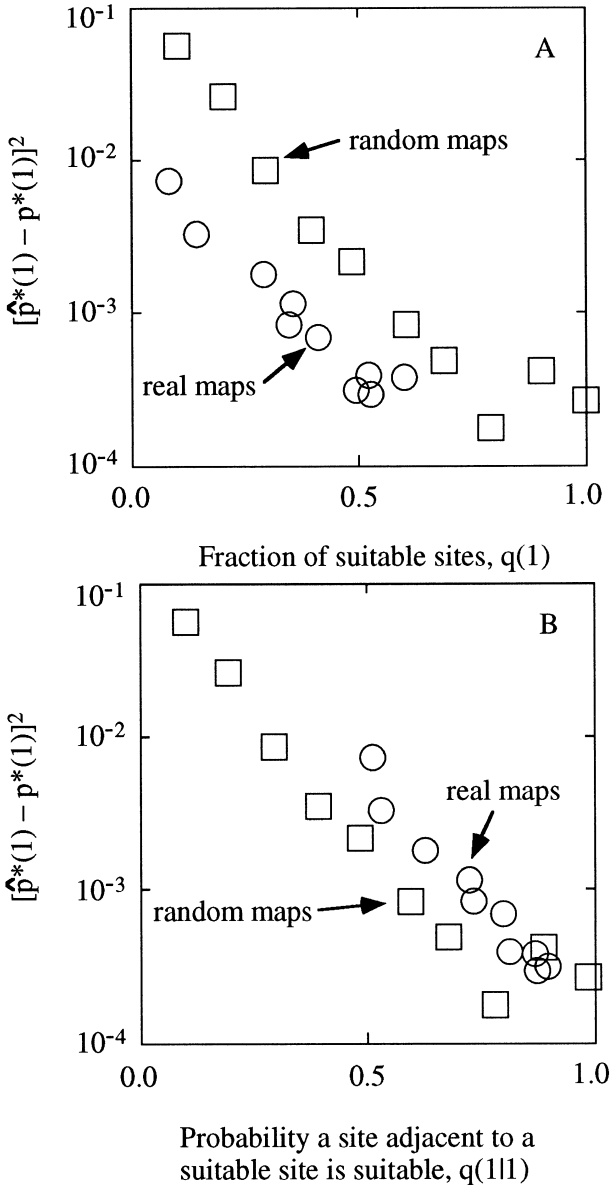

Figure 8. The mean squared difference between approximated and simulated fractions of occupied suitable sites, $[\hat{p}^*(1) - p^*(1)]^2$, versus **A** the fraction of suitable sites $q(1)$ and **B** the probability that a site adjacent to a suitable site is suitable, $q(1|1)$. Real maps are shown as circles, and random maps are shown as squares. The data come from the same simulations used to give Figure 4.

that low availability of suitable sites breaks down the assumptions made for the approximated steady state $\hat{p}^*(1)$.

In addition to differences among maps, the parameters p_m and e may influence the performance of the approximation. A regression analysis shows that the difference between the approximated steady state and the steady state in the simulated datasets, $\hat{p}^*(1) - p^*(1)$, depends only weakly on direct effects of p_m for both real and random maps (Table 4). For random maps, the effect of e is weakly negative, indicating that $\hat{p}^*(1)$ overestimates $p^*(1)$ to the greatest extent when extinction rates are low. For real maps, the effect of e is strongly negative, but there is also a strong positive interaction with p_m. Therefore, $\hat{p}^*(1)$ overestimates $p^*(1)$ when e and p_m are either both small or both large.

Table 4. Results of a Regression Analysis for the Difference Between the Approximated (Eq. 6) and Simulated Steady States, $\hat{p}^*(1) - p^*(1)$, Versus e, p_m, and the Interaction $e \times p_m$

Source	Coefficient	SS	*df*	*F*	*p*
Real maps ($R^2 = 0.70$)					
Map		0.066	9	19.9	$\ll 0.001$
e	−0.15	0.069	1	187	$\ll 0.001$
p_m	−0.033	0.0051	1	13.9	< 0.001
$e \times p_m$	0.26	0.043	1	115	$\ll 0.001$
Error		0.087	237		
Random maps ($R^2 = 0.77$)					
Map		1.03	9	67.4	$\ll 0.001$
e	−0.084	0.021	1	12.7	< 0.001
p_m	0.010	0.0005	1	0.31	0.58
$e \times p_m$	0.055	0.0018	1	1.04	0.31
Error		0.40	237		

Although the preceding discussion focused on identifying when the approximated steady state $\hat{p}^*(1)$ does not work well, for the real maps and the random maps with $q(1)$ greater than 20% $\hat{p}^*(1)$ gave good approximations to the steady states in the simulated datasets. Therefore, the spatial processes modeled explicitly in the simulation model can be approximated from the local interactions among adjacent sites. In the approximations, the spatial map is summarized by only one parameter, $q(1|1)$, and the clustering of plant populations is summarized by only $p(1|1)$ (Eq. 6). Cases in which the approximation $\hat{p}^*(1)$ does not perform well [when $q(1|1) \leq 20\%$] presumably occur because local processes are not sufficient to predict plant population dynamics. The possible broader-scale processes affecting population dynamics when $q(1|1) \leq 20\%$ are investigated in the next section.

When Local Explanations of Landscape Patterns Are Not Enough

For random maps with 20% or fewer suitable sites [or, equivalently, for any maps with $q(1|1) \leq 20\%$], the approximation $\hat{p}^*(1)$ predicted higher steady state site occupancies than occurred in the simulated datasets. When suitable sites are rare and randomly distributed, the sizes of patches of contiguous suitable sites become very small. Therefore, stochasticity may lead to extinction of all populations within the patch. Because this stochasticity is a product of the small number of suitable sites in small patches, we will refer to it as demographic stochasticity. If extinction from all sites occurs, repopulation of the patch is impossible due to the limited plant dispersal abilities that we assume in the simulation model. Therefore, small patches will become permanently depopulated. This phenomenon is not accounted for in the approximation, because the approximation was derived from local interactions among adjacent sites and is blind to the size of patches on a map.

To demonstrate the effect of patch size on the persistence of plant populations within a patch, Figure 9A shows the fraction of patches that contain at least one occupied site following 40 time steps. Values for p_m and e were selected from the range of values used for the random map with 10% suitable sites [$q(1) = 0.1$]. Therefore, the patches used to produce Figure 9A could be viewed as separate patches in the simulation model for the 10% suitable randommap. For patches containing a given number of contiguous suitable sites, the sites were distributed either in a clumped fashion (making as close to a square as possible) or in a straight line to give low connectedness among suitable sites. As shown in Figure 9A, only roughly 25% and 50% of the patches of sizes 2 and 3, respectively, contained occupied sites after 40 time steps. Even large patches with 8 or more suitable sites were not immune to extinction. Moreover, patches that had suitable sites clumped together tended to have plant populations that persisted more frequently than linear patches of suitable sites.

The importance of extinctions from entire patches of contiguous suitable sites depends on the frequency of small patches on the map. Figure 9B shows the fraction of the total number of suitable sites on a map contained within patches of sizes in the ranges 2–4 (dashed lines) and 2–8 (solid lines). We excluded patches with only a single site, because the approximation cannot account for patches of size 1; the approximation allows for none of the sites surrounding a suitable site to be suitable. However, the approximation assumes that if there is an adjacent suitable site, then there is a chance that this site will be occupied. This cannot be the case if the site is in a patch with no occupied sites. In the random map with 10% suitable sites, 50% of the suitable sites lie in patches of sizes 2–4, and 60% lie in patches of sizes 2–8. Thus, patches on average are very small, and the risk of extinction of populations from many of the patches due to demographic stochasticity is high.

The preceding argument implicates demographic stochasticity and small patch sizes in the breakdown of the approximated steady-state fraction of occupied suitable sites, $\hat{p}^*(1)$. To provide concrete evidence for how the approximation breaks down, we

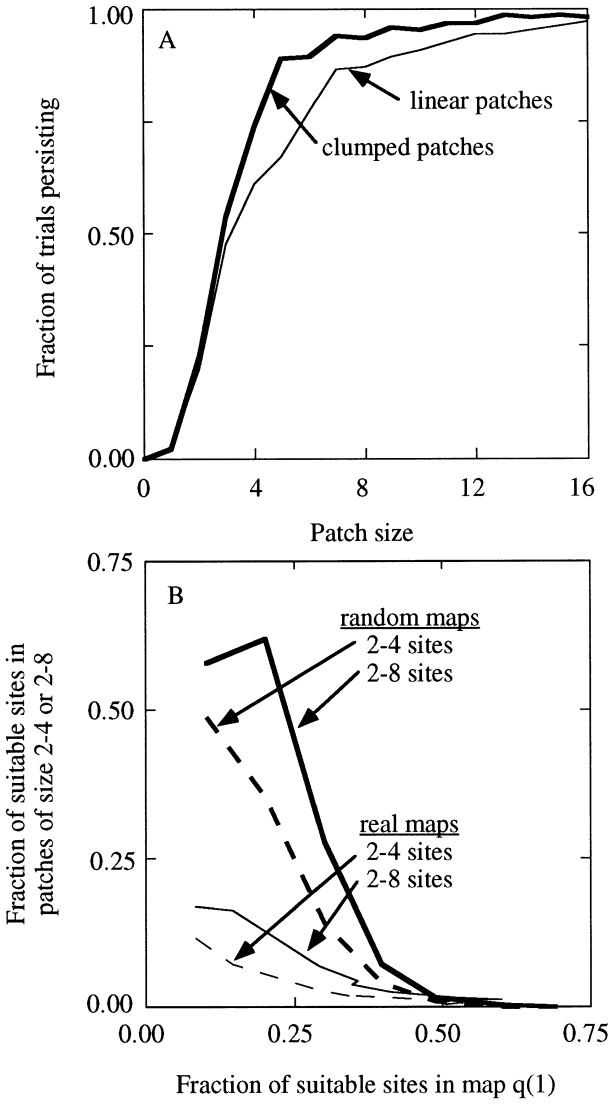

Figure 9. A The fraction of patches remaining occupied after 40 simulation iterations, versus the size of the patch. The heavy line corresponds to patches having suitable sites arranged in squares or near squares, and the light line corresponds to patches having suitable sites arranged in a straight line. For each patch size and type, 500 combinations of p_m and e were selected from the same range of values used for the random map with 10% suitable sites. B The fraction of suitable sites in patches of sizes 2–4 (dashed lines) and 2–8 (solid lines) for the real maps (light lines) and random maps (heavy lines) used for simulations, versus the fraction of suitable sites on the map, $q(1)$. The random maps with $q(1) > 0.7$ had no patches of sizes 2–8 and therefore are excluded.

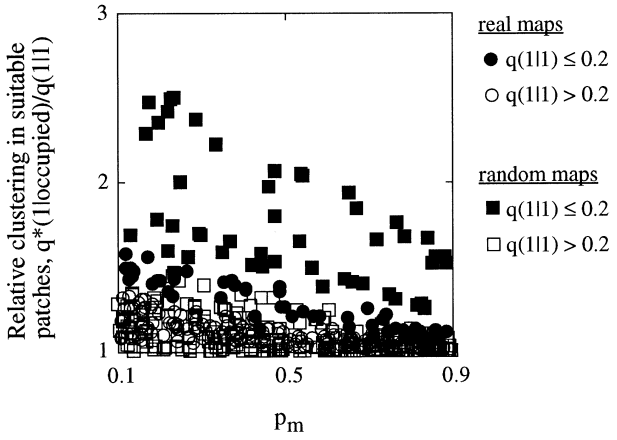

Figure 10. The clustering of plant populations in areas with high suitable site abundance, $q^*(1|\text{occupied})/q(1|1)$, versus the approximated fraction of occupied suitable sites from Eq. 5, p_m, for real (circles) and random (squares) maps. The two real and two random maps having the lowest fractions of suitable sites [$q(1) = 0.2$] are shown as solid circles and squares. The data come from the same simulations used to give Figure 4.

need to look at which assumptions in the equations used to calculate $\hat{p}^*(1)$ do not hold. When all populations go extinct within small patches, plant populations are confined to the remaining patches. To measure this effect, we used $q(1|\text{occupied})$, the probability that a site adjacent to an occupied suitable site is suitable. If $q(1|\text{occupied})$ is greater than $q(1|1)$, then the plants occur in areas with a relatively high abundance of suitable sites. In other words, occupied sites tend to be clustered in clumps of suitable sites. Note that to derive the approximation $\hat{p}^*(1)$, we assumed that $q(1|\text{occupied})$ equals $q(1|1)$. Therefore, if $q(1|\text{occupied})$ is much greater than $q(1|1)$, the approximation will break down.

For the simulations with the 20 real and random maps discussed previously, we calculated $q(1|\text{occupied})$ at each time step and averaged over the last 20 time steps to give $q^*(1|\text{occupied})$. Figure 10 shows the ratio $q^*(1|\text{occupied})/q(1|1)$ for all of the maps. Although $q^*(1|\text{occupied})/q(1|1)$ was always greater than 1, it was sizably greater than 1 only for the random maps with 10% and 20% suitable sites (solid squares). Furthermore, the clustering of plant populations into areas with high abundance of suitable sites was associated with the breakdown of the approximation $\hat{p}^*(1)$ (Table 5). The ratio $q^*(1|\text{occupied})/q(1|1)$ and p_m together explained 88% of the variance in the difference $\hat{p}^*(1) - p^*(1)$. The large positive interaction term $q^*(1|\text{occupied})/q(1|1) \times p_m$ indicates that the approximation $\hat{p}^*(1)$ overestimates the simulated value $p^*(1)$ to the greatest extent when both $q^*(1|\text{occupied})/q(1|1)$ and p_m are large. This corresponds to the case when plant populations are clustered into larger patches and when the plant colonization rate, m, is high relative to the extinction rate, e. Thus, although there is the potential for high site occupancy owing

Table 5. Results of a Regression Analysis for the Difference Between the Approximated (Eq. 6) and Simulated Steady States, $\hat{p}^*(1) - p^*(1)$, Versus $q^*(1\,|\,\text{occupied})/q(1|1)$, p_m, and the Interaction $q^*(1|\text{occupied})/q(1|1) \times p_m$

Real maps ($R^2 = 0.88$) Source	Coefficient	SE	*df*	T	*p*
Constant	−0.1080	0.0031	1	−2.6	<0.02
p_m	0.79	0.052	1	4.2	≪0.001
$q*(1\|\text{occupied})/q(1\|1)$	−0.10	0.0089	1	−11	≪0.001
$q*(1\|\text{occupied})/q(1\|1) \times p_m$	0.77	0.020	1	38	≪0.001
Error			496		

to the high colonization rates [thereby leading to high predicted values $\hat{p}^*(1)$], this potential cannot be reached because of the loss of plant populations from small patches.

Discussion

When faced with an ecological problem acted out on a complex landscape, it might seem essential to start with a complex map showing spatially explicit detail over a broad area. We argue that this is not always the case, and that it may be possible to answer some questions by analyzing the local-scale consequences of landscape processes without incorporating all of the complexity of the landscape. If local-scale processes dominate the dynamics of a population, then analytical approximations based on these processes can represent landscape-scale dynamics. To substantiate our argument, we derived an approximation to predict the average fraction of suitable sites that are occupied by plant populations in a simulation model. The simulation model was explicitly spatial, starting with maps of suitable and unsuitable sites on a landscape. Our approximation summarized the spatial processes in the simulation model by using two parameters: $q(1|1)$, the probability that a site adjacent to a suitable site is suitable, and $p(1|1)$, the probability that a suitable site adjacent to an occupied site is occupied. Comparing the approximation with the simulation model showed that these two parameters were often sufficient to characterize the effects of both the distribution of suitable habitat on the spatial map and the clustering of plant populations among suitable sites. Only in the extreme case of sparsely suitable random maps did the analytical approximation perform poorly.

The success of the simple approximation to summarize patterns produced by an explicitly spatial simulation model highlights the fact that some spatial effects on population processes can be understood by looking at the local scale. The clumping of suitable sites acts to increase effective colonization rates into unoccupied sites by surrounding unoccupied suitable sites with suitable sites that potentially contain plants. Conversely, the clustering of plant populations among suitable sites decreases the effective colonization rate, because propagules from occupied sites are more likely to be wasted in adjacent occupied sites. These two phenomena can be quantified by looking only at adjacent sites, independently from the more complex structure of a map.

When the approximation breaks down—when the probability is 20% or less that a site adjacent to a suitable site is also suitable—local effects of spatial structure are not sufficient to predict population dynamics. The breakdown occurs because plant populations within small patches of contiguous suitable sites may all go extinct, and when this occurs the patch cannot be repopulated. Thus, the approximation has identified a spatial process operating on a *regional* scale. The importance of this 20% threshold in the proportion of suitable habitat in random maps has been previously demonstrated by Andren (1994). By analyzing random 100 × 100 maps produced in the same manner as our random maps, he also noted that, below 20% habitat suitability, the landscape becomes fractured into many small patches. Moreover, Andren reviewed studies on the density and species richness of birds and mammals in landscapes composed of suitable and unsuitable habitats. For studies in which the proportion of suitable habitat made up more than 30% of the landscape, the results of the studies were consistent with the "random sample" hypothesis; either the density of individual species or the number of different species were no different than one would expect if individuals were randomly dispersed among suitable sites. However, when the fraction of suitable habitat was less than 30%, and particularly when it was less than 20%, many studies found that species density or species richness declined more rapidly with patch size than predicted by the random sample hypothesis, presumably because the landscape was fractured into relatively small, isolated patches. Although these findings are consistent with our own, we should point out that the fraction of suitable habitat in a landscape is poten-

tially a poor predictor of patch size when suitable habitat is not randomly distributed. For example, our real map with the lowest proportion of suitable habitat [$q(1) = 0.085$] nonetheless had large patches of suitable habitat (Figure 1) owing to the strong clumping of suitable sites [$q(1|1) = 0.51$]. Thus, as a single estimator for the effect of patchiness on the abundance of species in a landscape, $q(1|1)$ is better than simply the proportion of suitable habitat, $q(1)$.

Previous theoretical studies using spatial simulation models have demonstrated effects of abundance and spatial arrangement of suitable sites on ecological processes (Turner and others 1989; Hassell and others 1993; With and Crist 1995; Pearson and others 1996; With and others 1997). Simple models of disturbance dynamics similar to our simulation model have demonstrated the influence of habitat connectivity thresholds on processes controlling the extent of area affected by disturbance (Turner and others 1989). In these models, disturbance (for example, fire) was simulated on random maps containing varying fractions of susceptible sites by using two simple parameters: the frequency of initiation of disturbance events, *f*, and the probability of spread to an adjacent suitable site, *i*. When suitable sites occupied a fraction of the landscape above a threshold of connectivity, the number of sites affected by disturbance was controlled by both *f* and *i*. However, when suitable sites occupied a fraction of the landscape below the threshold of connectivity, the number of sites affected by the disturbance was controlled primarily of *f*, because the disturbance was unable to spread across gaps of unsusceptible sites. As in our simulation model, the disturbance eventually became extinguished in small isolated patches and required new initiations within patches of susceptible habitat. An approximation of this disturbance dynamic using an analytical model based on epidemiology theory performed well when susceptible sites were connected, but failed when patches of susceptible sites were disconnected; this failure coincided with cases in which low connectivity among sites inhibited the disturbance from becoming endemic on the landscape (O'Neill and others 1992). Our approximation also failed in cases when patches of suitable habitat were small, thereby causing fragmentation of suitable sites and the increased importance of stochastic events—the simultaneous extinciton of all plant populations in a patch.

One could question our argument about the need for explicit spatial maps on the grounds that we have stacked the deck in favor of the analytical approximation by comparing it with a simulation model in which dispersal occurs only into adjacent suitable sites; the approximation is successful at capturing local-scale effects of dispersal because dispersal occurs only at the local scale in the simulation model. However, increasing the dispersal distance has two effects that work in favor of the approximation. First, increasing dispersal distances reduces the clustering of occupied sites, because propagules disperse farther from their source population. Although the approximation accounts for the clustering of occupied sites, the approximation is not precise (Figure 7), and the less clustering, the better the performance of the approximation is likely to be (A. R. Ives unpublished). Second, increasing the dispersal distance overcomes the problem arising from small patches that are produced in the random maps with 20% or fewer suitable sites. If dispersal distance is increased, then small patches in which all sites are unoccupied can be repopulated by long-range dispersal, and the problem of demographic stochasticity will not be as severe. Despite these effects working in favor of approximating spatial processes without an explicit spatial map, increasing the dispersal range of propagules will make approximating the spatial processes more complicated. Although it is possible to extend our analytical approximations to include dispersal to larger neighborhoods of surrounding sites, this will not account for dispersal of propagules tapering off with increasing distance between sites. Clearly, our work is only a first step, and new types of approximations are being developed that can be applied to this situation (C. Neuhauser personal communication).

One could also question our argument on the grounds that the simulation model is based on a very simple description of plant ecology, categorizing habitat as either suitable or unsuitable, and scoring sites based only on the presence/absence of plant populations. Nonetheless, our argument is not based on the realism of the simulation model, but instead on the ability of the analytical model to approximate the simulation model by summarizing the local-scale consequences of landscape patterns. The spatially explicit map is the only thing that separates the simulation model and the analytical approximation. Our goal has been to demonstrate the potential of analytical approximations. Whether this potential can be realized in natural systems depends on the specific questions being asked, the degree of precision required for an answer, and the particular system being studied.

Finally, one should ask what the benefits are of using an analytical approximation. There are two.

First, an analytical approximation can reveal how spatial patterns influence population dynamics. For example, our analyses explicitly revealed how the clumping of suitable sites increased the effective colonization rate by plants, and how the clustering of occupied sites decreased the effective colonization rate. Thus, analytical approximations can give insights into spatial processes, particularly when used in conjunction with simulation models. Second, analytical approximations raise the possibility of analyzing real systems in which spatial processes are important, yet no complete map of the landscape exists. For example, the abundance and clumping of suitable habitat can be assessed by direct sampling of an area, as we illustrated by estimating $q(1)$ and $q(1|1)$ by sampling less than 2% of the sites on our maps (Table 2). This approach might be particularly useful when the suitability of sites can only be assessed from ground surveys rather than through remote sensing. By focusing on the local-scale consequences of landscape patterns, it may be easier to investigate how landscape patterns influence the abundance and distribution of species for which local-scale processes predominate.

This work grew out of a friendly challenge between landscape and population ecologists: is it possible to capture explicit spatial processes by using simple approximations of local interactions? The answer, at least for simple models of plant population dynamics, is yes, provided (a) that the patches of suitable sites are not so small that repopulation of patches—a landscape rather than local process—becomes important, and (b) that one is interested in average abundance across a landscape rather than abundance at a specific location. It remains a challenge to define the conditions that best suit or limit application of these different approaches to the same type of problems (Fahrig 1991). We believe that landscape and population ecologists should be more active in pursuing this challenge collaboratively; they ask many of the same questions, and combining scientific cultural backgrounds is likely to produce interesting answers.

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Appendix Permissible Values of e Given p_m

For a given value of p_m, the value of e is constrained to guarantee that m is less than 8. The value of m cannot be greater than 8, because m is defined as the number of sites adjacent to an occupied site that are colonized by propagules. From Eq. 5, the value of m can be calculated from p_m and e as

$$m = 8\left[1-\left(1-\frac{ep_m}{1-p_m}\right)^{1/8}\right]\Big/ p_m q(1|1) \qquad \text{(A1)}$$

For m to remain less than 8, the maximum value of e is

$$e_{\max}(p_m) = [1 - (1 - p_m q(1|1))^8](1 - p_m)/p_m \qquad \text{(A2)}$$

In addition, e must be less than 1, so $e_{\max}(p_m)$ was given a maximum value of 1.