Interspecific Variation in Critical Patch Size and Gap-Crossing Ability as Determinants of Geographic Range Size Distributions

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ABSTRACT: How biological processes such as reproduction and dispersal relate to the size of species' geographic ranges constitutes a major challenge in spatial ecology and biogeography. Here we develop a spatially explicit theoretical framework that links fundamental population-level ecological traits (e.g., rates of dispersal and population growth or decay) with landscape heterogeneity to derive estimates of species' geographic range sizes and, further, distributions of geographic range sizes across species. Although local (patch-scale) population dynamics in this model are completely deterministic, we consider a fragmented landscape of patches and gaps in which the spatial heterogeneity is itself stochastic. This stochastic spatial structure, which juxtaposes landscape-level patch and gap characteristics against population-level critical patch sizes and maximum gap-crossing abilities, determines how far a novel species can spread from its evolutionary origin. Given reasonable assumptions about landscape structure and about the distribution of critical patch sizes and critical gap lengths among species, we obtain distributions of geographic range sizes that are qualitatively similar to those routinely found in nature (e.g., many species with small geographic ranges). Collectively, our results suggest that both interspecific differences in population-level traits and the landscapes through which species spread help determine patterns of occupancy and geographic extent.

Keywords: critical patch size, gap-crossing ability, geographic range size, range expansion, spatial heterogeneity.

Introduction

Interactions among habitat availability, biological processes, and physical factors determine the size of species' geographic ranges and the location of species' geographic range boundaries. Empirical data on geographic range sizes make clear that environmental thresholds (e.g., Cabrera 1996), gradients (e.g., Virgos and Casanovas 1999), and

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spatially varying physical processes (e.g., Gaylord and Gaines 2000) can all act as determinants of species' boundaries. Of these issues, environmental gradients have received the most attention from theoreticians, often in conjunction with studies of the spatial dynamics of evolutionary clines (Barton and Bengtsson 1986; Pialek and Barton 1997).

In contrast, the effects of discontinuous spatial variation (i.e., patchy landscapes) on species' boundaries have received relatively less attention. Nonetheless, some pertinent results about range limits in discontinuous landscapes are available. For example, metapopulation dynamics acting across an environmental gradient may enforce a species' range limit (Carter and Prince 1981, 1987; Holt et al. 2005). Likewise, a partial dispersal barrier may prevent competitive exclusion and facilitate stable parapatric boundaries (Goldberg and Lande 2007). In a discretized landscape, species' range limits can emerge even in the absence of clear environmental gradients via the mechanism of "invasion pinning" (Keitt et al. 2001), in which Allee dynamics, coupled with fine-scale patchiness, limit the spatial advance of a spreading species. In an important step toward unification, Holt et al. (2005) proposed that a small set of demographic mechanisms related to spatial variation in population dynamic parameters (e.g., birth, death, and dispersal rates) may collectively determine the spatial position of species' range boundaries under many conditions.

Overall, the issue of species' boundaries can be viewed from two complementary perspectives: (1) what processes initially limit the spatial expansion of a novel species (Webb and Gaston 2000; Keitt et al. 2001) and (2) what processes govern the long-term size and occupancy of a species' geographic range (Gaston 2003). Building on ideas of Keitt et al. (2001), we adopt the "initial expansion" perspective on geographic range dynamics to explore how landscape heterogeneity influences species range bound-

aries. However, unlike Keitt et al. (2001), who assumed the environment to be homogeneous or to have a directional gradient in quality, we assume here that the environment is heterogeneous, with the heterogeneity itself being stochastic. As a result, our efforts converge on a "landscape ecology of species spread," as outlined by With (2002).

Because the initial expansion perspective on species' boundaries shares its theoretical foundations with models of invasion dynamics (Shigesada and Kawasaki 1997), results from invasion theory are highly relevant here. A common theme in theoretical investigations of invasion dynamics is to quantify the speed of the invasion, that is, the rate at which spatial spread occurs. For example, using reaction-diffusion (RD) models, Shigesada et al. (1986) demonstrated how habitat heterogeneity (characterized as an alternating sequence of good and bad habitat patches of fixed sizes) could slow the progress of a traveling wave of invasion. Dewhirst and Lutscher (2009) have analyzed a similar spatial setup for cases of discrete-time integro-difference equations, obtaining an estimate of the fragmentation threshold necessary for an invasion to propagate (i.e., the minimum percentage of good habitat that allows population spread; see also With 2002). Several other studies have examined aspects of invasion dynamics in situations with spatial variation in population growth but not dispersal ability (Van Kirk and Lewis 1997; Botsford et al. 2001; Kawasaki and Shigesada 2007).

However, unlike most previous investigations of spatial spread, we focus here not on quantifying the rate of spread but instead on the maximum distance covered by a species that is expanding its range in a heterogeneous landscape. As we discuss below, we eschew the traveling-wave formalism that is standard in theoretical studies of invasion dynamics in favor of the critical patch size perspective on ecological dynamics in patchy systems (Skellam 1951; Kierstead and Slobodkin 1953; Cantrell et al. 2001). In what follows, we introduce a modeling approach that combines basic life-history traits with information on the patchiness of a landscape to estimate the size of a particular species' geographic range. Our efforts speak directly to the problem of nonequilibrial geographic range dynamics, including effects of landscape heterogeneity and Allee effects, a set of topics that has been identified as a major challenge in spatial ecology and biogeography (Holt et al. 2005)

We then extend the analysis to illustrate how one can obtain a multispecies distribution of geographic range sizes for a particular landscape. As such, our modeling efforts provide a novel route linking population biological traits to geographic range size distributions via the initial expansion perspective on geographic ranges. Consequently, our analysis complements but contrasts with models such as those of Gaston and He (2002) that focus on stochastic variations in range size occurring after the initial phase of spreading.

Empirical syntheses suggest that within major taxa (i.e., groups of species [such as waterfowl or pine trees] that, by virtue of shared evolutionary heritage, exhibit a diverse but not extreme range of life-history traits), geographic range sizes are strongly right (positively) skewed. In histograms of geographic range size for major taxa, the left-most category is typically the modal category (Brown et al. 1996; Gaston 2003). Consequently, as a final step we identify some conditions under which particular distributions of life-history traits will yield geographic range size distributions like those commonly observed in nature.

Model Setup

We seek to understand how ecological attributes of a species, specifically the minimum patch size needed for population persistence and the maximum gap length across which dispersal is possible, interact with landscape heterogeneity to determine how far that species can be expected to spread from its area of evolutionary origin and thus how big a geographic range that species is likely to attain. In this scenario, species expected to spread only short distances would likely be "endemics," whereas species expected to spread great distances would likely attain large geographic ranges.

Our modeling approach envisions a landscape as a one-dimensional environment consisting of alternating patches and gaps whose sizes are drawn from some specified distribution. This is a more generalized perspective than that used in previous studies of spatial spread in heterogeneous landscapes; those studies treated habitat heterogeneity as alternating pairs of good- and bad-quality patches of fixed size (Shigesada et al. 1986; Van Kirk and Lewis 1997; Botsford et al. 2001; Berestycki et al. 2005; Kawasaki and Shigesada 2007; Dewhirst and Lutscher 2009).

Given a set of biological parameters such as dispersal rates and birth or death rates, we derive a distribution for the distance that a species with those parameters could spread. How far, specifically, such a species could spread would depend on the particular landscape (and starting point). Finally, by considering the population parameters for different species as being drawn from some distribution, we derive a distribution for the frequency of species' geographic ranges along the axis from endemic to widespread. Our approach allows us to link expected range size of a species to parameters describing that species' dispersal and demography. We make this link by using simple RD models to obtain characteristics of minimum patch size and maximum gap length that we can then feed into the landscape model and thus predict the distance that the species can spread in any given landscape realization. The

combined RD-landscape model can be parameterized using distributions of species' life-history traits together with information about the spatial heterogeneity of a landscape.

Our model development hinges on several foundational concepts in spatial ecology. First, we require that there exists a "minimum patch size" needed for population persistence. This concept is a standard one in theoretical ecology, going back to Skellam (1951) and Kierstead and Slobodkin (1953), and a wide variety of empirical studies document the importance of patch size for population persistence (Groom 1998; Hanski 1998). Second, we require that the connectivity between two habitat patches depends on the size of the gap between those patches. Urban and Keitt (2001) clearly describe how dispersal between patches can depend on gap length. Third, we require that the founding population of a species in a habitat patch reach some minimum density to successfully colonize that patch. This idea, which corresponds to a kind of Allee effect, has been observed in a variety of empirical systems (Veit and Lewis 1996; Johnson et al. 2006; Tobin et al. 2007) and has been built into spatially explicit models for island colonization (Cantrell et al. 1996) and for the establishment of geographic range boundaries via invasion pinning (Keitt et al. 2001).

Analysis

To characterize minimum patch size we will use a simple RD model (Skellam 1951; Kierstead and Slobodkin 1953). If a population inhabits a patch of length L (distance), disperses through it with diffusion rate D (distance^2 time^{-1}), increases with local intrinsic growth rate r (time^{-1}), and has local carrying capacity K, then the population density u within the patch satisfies the relation

$$\frac{\partial u}{\partial t} = D\frac{\partial u^2}{\partial x^2} + ru\left(1 - \frac{u}{K}\right),$$ (1)

for $0 < x < L$. If individuals that reach the boundary of the patch always exit the patch, then equation (1) is augmented with the boundary condition

$$u(0, t) = u(L, t) = 0.$$ (2)

Solutions of equations (1) and (2) decay toward 0 if $r - D\pi^2/L^2 < 0$ and grow toward a unique positive density if $r - D\pi^2/L^2 > 0$ (Cantrell and Cosner 2003). Thus, for population persistence we must have

$$L > L^* = \pi\sqrt{\frac{D}{r}},$$ (3)

where L^* is the minimum patch size needed for successful persistence of the population.

Although we have focused this particular derivation of a species' critical patch size (i.e., diffusion-mediated loss across the patch boundary), we note that there are several alternative routes to a critical patch size that might be substituted for species that possess dispersal behaviors more sophisticated than simple diffusion. These mechanisms include (1) scenarios where there is within-patch habitat heterogeneity (Cantrell and Cosner 2001) or where a species tends to move toward or away from edges or up or down spatial gradients (Cantrell and Cosner 1991), (2) situations where the regrowth capacity of a species scales with patch size (Cantrell et al. 2005), and (3) cases where a species as a whole suffers from an Allee effect but individuals defend home ranges, placing limits on the number of individuals that can be packed into a given patch.

We use a model similar to equation (1) to describe the expected density of a population in a gap of matrix habitat between patches, but we also incorporate the idea that there is a minimum rate at which individuals must arrive at the next patch for colonization to succeed. The notion that propagule pressure influences colonization success is widely supported from both theoretical and empirical viewpoints (Lockwood et al. 2005; Drake and Lodge 2006). Suppose that a population inhabits an isolated patch at density K, disperses through the matrix outside the patch by diffusion at rate d, and experiences mortality in the matrix at rate s. The propagule density v in the matrix can then be described by

$$\frac{\partial v}{\partial t} = d\frac{\partial v^2}{\partial x^2} - sv,$$ (4)

with boundary condition

$$v(0, t) = K.$$ (5)

The unique bounded equilibrium of equations (4) and (5) is $v(x) = K\exp\left[-x(s/d)^{1/2}\right]$. We use m to indicate the minimum average propagule density needed for successful colonization of a new patch. As such, m can thus be thought of as a type of Allee threshold necessary for invasion success (Lewis and Kareiva 1993; Veit and Lewis 1996). If the new patch is at distance l from the original patch, successful colonization requires $K\exp\left[-l(s/d)^{1/2}\right] > m$, which can be rewritten as

$$l < l^* = \ln\left(\frac{K}{m}\right)\sqrt{\frac{d}{s}},$$ (6)

where l^* is the maximum gap length that the species can

be expected to cross successfully. A model similar to equations (4) and (5) was used by Cantrell et al. (1996) as part of a spatially explicit model for a species colonizing an island. The idea that the rate of successful colonization decreases exponentially with distance from a source, which we have adopted here, is a common assumption in ecological theory and is a mainstay of both island biogeography theory (MacArthur and Wilson 1967) and metapopulation theory (Hanski 1998).

To describe the landscape that a spreading species might encounter, we assume that the overall environment consists of an alternating series of patches and gaps whose lengths are drawn from distributions that reflect the large-scale structure of the landscape. Specifically, we assume that each realization of the landscape starts with a patch of length L_1, which is followed by a gap of length l_1, which is followed by a patch of length L_2, then a gap of length l_2, and so on, with patches and gaps alternating (fig. 1). We assume that the species we are considering will spread until it reaches a patch too small to support a population, that is, $L_n < L^*$, or a gap too large to cross, that is, $l_n > l^*$.

Note that as we develop it here, the full model does not allow a species to "jump over" (i.e., bypass) a nearby small patch and still colonize a sufficiently large patch downstream. However, we address this issue in the example cases, where we work with what amount to upper and lower bounds on a species' geographic range size. In cases 1 and 2, we consider the situation where there are no critical patch size effects and any patch can be effectively bypassed by a spreading species. In these upper-bound scenarios, we develop geographic range size distributions using an overestimate of each species' geographic range size. Later, in case 3, we consider a corresponding lower-bound scenario, in which a spreading species cannot jump

over a nearby small patch. We return to this important topic in "Discussion."

Assume that $(L_n)_{n \geq 1}$ and $(l_n)_{n \geq 1}$ are sequences of independent identically distributed random variables. We define

$$\tau_1 = \min\{n : L_n < L^*\},$$

$$\tau_2 = \min\{n : l_n > l^*\}, \tag{7}$$

$$\tau = \min\{\tau_1, \tau_2\}.$$

The distance that a species will spread in the positive direction from $x = 0$ is then $\Theta_1 = \sum_{j=1}^{\tau} (L_j + l_j)$. The initial geographic range of species i after it has spread across the landscape would then be $\Theta_i = \Theta_{i1} + \Theta_{i2}$, where Θ_2 is a second random variable, independent of Θ_1 but with the same distribution, representing spread in the negative direction. For any given parameter set describing the minimum patch size L_i^* and the maximum gap length l_i^* for species i, the geographic range size Θ_i will be a random variable with a distribution depending on the life-history parameters that determine the critical patch size and maximum gap length for species i.

In table 1 we recapitulate all of the key life-history parameters that together determine a species' critical patch size and maximum gap length, along with a qualitative summary of how an increase in the magnitude of a given life-history trait would affect a species' critical patch size, maximum gap length, and geographic range size. Note that all of the life-history parameters enter the calculations of critical patch size and maximum gap length (eqq. [3], [6]) in a sublinear fashion, such that a doubling (or halving) of the magnitude of a particular trait will translate into a less than linear increase or decrease in the patch size or gap length thresholds.
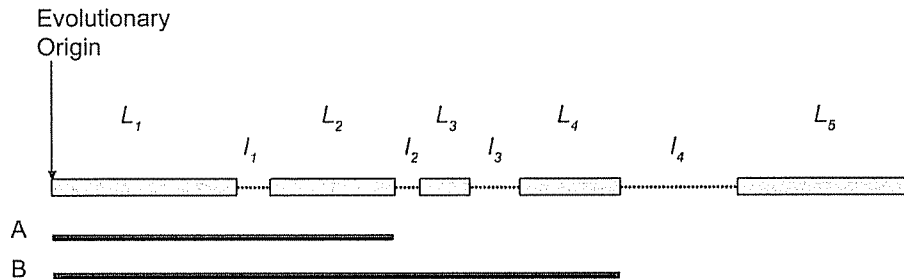

Figure 1: Schematic of the model setup for our analysis of geographic range size. Patch sizes and gap widths vary stochastically across the landscape. As it expands outward from its evolutionary origin, species A cannot persist on patch L_3 (minimum patch size $L_A^* > L_3$). In contrast, species B has a different suite of life-history traits and can persist on patch L_3 but cannot cross gap l_4 (maximum gap width $l_B^* < l_4$). Consequently, species A has a geographic range smaller than that of species B (*lines*).

Table 1: Key parameters linking life history to geographic range size

Parameter	Interpretation	Consequences of an increase in parameter value on CPS, MGL, and GRS
r	Population growth rate in habitat patches	Decreases CPS and increases GRS
D	Diffusion rate in habitat patches	Increases CPS and decreases GRS
s	Death rate in matrix gaps	Decreases MGL and decreases GRS
d	Diffusion rate in matrix gaps	Increases MGL and increases GRS
K	Carrying capacity (as a density) in patches	Increases MGL and increases GRS
m	Minimum propagule density at patch edge necessary for successful colonization	Decreases MGL and decreases GRS
$L^* = \pi\sqrt{D/r}$	Minimum patch size to support a population	Decreases GRS
$l^* = \ln(K/m)\sqrt{d/s}$	Maximum gap length across which colonization is possible	Increases GRS
E_0	Mean patch size in the landscape	Increases GRS
e_0	Mean gap length in the landscape	Decreases GRS
Θ_i	Geographic range size of species i	

Note: CPS = critical patch size; MGL = maximum gap length; GRS = geographic range size.

Next, we assume that the parameters describing minimum patch size and maximum gap length are distributed among a pool of species; thus, quantities such as the mean and variance of the range size ($E(\Theta_i)$ and $V(\Theta_i)$, respectively) will themselves be treated as random variables that differ among species. Given a distribution of dispersal and demographic parameters across a species pool, we can then, in principle, compute the probability $\Pr(a \leq E(\Theta_i) \leq b)$, which can be interpreted as giving a distribution of the probability that a species i drawn from the pool of candidates will be endemic, widespread, or in between. Table 1 summarizes all parameters involved in the development of this model.

A Brief Sketch of Model Analysis Necessary to Derive a Species' Geographic Range Size

The analysis and justification of the model presented above (eqq. [1]–[7]) depend on results from probability theory. We will sketch the results of the analysis in this section, leaving detailed derivations and justifications for appendix A in the online edition of the *American Naturalist*. We will denote the probability of an event e as $\Pr(e)$. The first key observation is that τ_1, τ_2, and τ in equation (7) are stopping times, so they can be treated as random variables. Let E and V denote the mean and variance, respectively. For independent random variables X and Y, $E(X + Y) = E(X) + E(Y)$ and $V(X + Y) = V(X) + V(Y)$. Thus, $E(\Theta) = E(\Theta_1 + \Theta_2) = 2E(\Theta_1)$ and $V(\Theta) = 2V(\Theta_1)$. If L denotes a random variable with the same distribution as the patch sizes in our model and l is a random variable with the same distribution as the gap lengths, then

$$E(\Theta) = 2[E(L) + E(l)]E(\tau), \qquad (8)$$

with

$$E(\tau_i) = \frac{1}{1 - \Pr(L \geq L_i^*)\Pr(l \leq l_i^*)}, \qquad (9)$$

where L_i^* and l_i^* are the minimum patch size (eq. [3]) and maximum gap length (eq. [6]) of species i, respectively. (This assumes that $\Pr(L \geq L_i^*)\Pr(l \leq l_i^*) < 1$; otherwise $E(\tau)$ is infinite.) Thus,

$$E(\Theta_i) = \frac{2[E(L) + E(l)]}{1 - \Pr(L \geq L_i^*)\Pr(l \leq l_i^*)}. \qquad (10)$$

Similarly, we have

$$V(\Theta_i) = 2\{[E(L) + E(l)]^2 V(\tau_i) + [V(L) + V(l)]E(\tau_i)\}, \qquad (11)$$

with

$$V(\tau_i) = \frac{\Pr(L \geq L_i^*)\Pr(l \leq l_i^*)}{[1 - \Pr(L \geq L_i^*)\Pr(l \leq l_i^*)]^2}. \qquad (12)$$

Using equations (8)–(12), we can compute the mean and variance of the geographic range size for species i, Θ_i, if we know L_i^*, l_i^*, and the landscape distributions of L and l.

Extending the Model to Multiple Species to Characterize Geographic Range Size Distributions

Equations (8)–(12) are general results that hold for a wide range of landscapes (defined by distributions of L and l) and for a wide range of species (whose critical patch size and gap-crossing ability are determined for species i by r_i and D_i in habitat patches, s_i and d_i in the matrix, and the

colonization constraints m_i/K_i). To explore the effects that particular assumptions about landscapes and species pools have on the distribution of geographic range size, we present three cases here. In each of these cases we make assumptions about the distributions of patch and gap lengths in the landscapes and the distributions of critical patch sizes and maximum gap lengths among species. Most commonly we assume that these landscape components and interspecific thresholds are distributed exponentially, and before proceeding, we provide some justification for these assumptions.

Situations in which patch sizes and/or gap lengths are approximately exponentially distributed appear repeatedly in the landscape ecology literature, both from remote sensing analyses of real landscapes and as a consequence of standard assumptions in landscapes generated for percolation theory and other spatial analyses. Examples of exponential distributions occurring in binary (patch, nonpatch) landscapes include the size of snowfields (Bahr and Meier 2000), the size of patches created by forest fires (Cumming 2001), analyses of forest patch (gap) structure in temperate (Keitt et al. 1997) and tropical (Lawton and Putz 1988) forests, and patch sizes and interpatch distances in one-dimensional planktonic landscapes (Curriel et al. 1998). Patch size distributions that are approximately exponential in form are to be expected in random landscape models with low to moderate percent habitat cover and a high degree of habitat fragmentation (R. Gardner, personal communication). In a detailed analysis of a southern California landscape classified into many patch types (San Bernardino Mountains), frequency is a monotonic and strongly declining function of patch size on an arithmetic axis (M. Neel, unpublished data). Distance to nearest neighboring patch (of the same patch classification) exhibits a similar shape.

Moving from landscapes to the distributions of interspecific traits, recent analyses yielding estimates of critical patch size for 474 resident bird species and 163 mammal species that live in native habitats in Costa Rica (Pereira et al. 2004; Pereira and Daily 2006) both indicate monotonic, steeply declining distributions of critical patch size across species, so our assumption here that critical patch sizes are distributed exponentially appears reasonable. Our assumptions about how maximum gap-crossing ability is distributed among species are arguably the most tenuous. In a compilation of data on gap-crossing ability for selected tropical species, Dale et al. (1994) reported many more species with small or intermediate maximum gap lengths than with large maximum gap lengths. Creegan and Osborne (2005) reported similar data for a suite of temperate birds. Numerous other studies have examined gap-crossing ability for individual taxa (e.g., Bakker and Van Vuren 2004; van der Ree et al. 2004; Castellón and Sieving

2006). However, we are not aware of a systematic assessment of the distribution of maximum gap length across many species, as has been done for critical patch size.

Case 1: Exponentially Distributed Gap Lengths

If gap lengths follow an exponential distribution with mean e_0, the probability density function for gap length is $l \sim (1/e_0) \exp(-x/e_0)$ and

$$\Pr(l \le l_i^*) = \int_0^{l_i^*} \left(\frac{1}{e_0}\right) \exp\left(\frac{-x}{e_0}\right) dx$$

$$= 1 - \exp\left(\frac{-l_i^*}{e_0}\right), \tag{13}$$

where l_i^* is the maximum gap length for species i. Let E_0 denote the mean patch size in the landscape. We next make the further assumption that all habitat patches are adequately large with probability 1. (Note that this assumption implies that all species' in-patch dispersal rates D_i are small enough and/or all species' reproductive rates r_i are large enough to avoid any critical patch size constraints on species' geographic range sizes; eq. [3]). With this assumption, equation (10) reduces to

$$E(\Theta_i) = 2(E_0 + e_0) \exp\left(\frac{l_i^*}{e_0}\right).$$

In formulating our models we assume that any species starts out by spreading into the initial patch and gap in either direction. Thus, the expected range size is always at least as large as the expected size of two patches plus two gaps, that is, $2(E_0 + e_0)$. Constraining a landscape threshold B such that $B \ge 2(E_0 + e_0)$, then

$$\Pr(E(\Theta_i) > B) = \Pr\left\{l_i^* > e_0 \ln\left[\frac{B}{2(E_0 + e_0)}\right]\right\}. \tag{14}$$

We now move from considering the landscape to focusing on the species pool. Equations (8)–(12) and hence equations (13) and (14) should now be interpreted as giving the conditional expectation and variance of Θ_i given L_i^* and l_i^*. With that interpretation we will retain our previous notation. If we assume that the critical gap lengths l_i^* are exponentially distributed among species with mean e^*, then equation (14) can be rewritten as

$$\Pr(E(\Theta_i) > B) = \exp\left\{\frac{-e_0}{e^*}\ln\left[\frac{B}{2(E_0 + e_0)}\right]\right\}$$

$$= \left[\frac{B}{2(E_0 + e_0)}\right]^{-e_0/e^*}. \quad (15)$$

Provided $B \geq 2(E_0 + e_0)$, the full multispecies distribution of geographic range sizes can be obtained from equation (15) and has the probability density function

$$\frac{d[\Pr(E(\Theta_i) < B)]}{dB} = \left(\frac{e_0}{e^*}\right)[2(E_0 + e_0)]^{e_0/e^*} B^{-(1+e_0/e^*)}, \quad (16)$$

which is a Pareto distribution (Johnson et al. 1994). The function in equation (16) declines monotonically such that, in a histogram, the leftmost category would be the modal category, a pattern that agrees with empirical observations on geographic range size distributions (Brown et al. 1996; Gaston 2003). Initially equation (16) declines faster than exponential, but the function has a heavy tail compared with an exponential distribution that (eventually) becomes apparent for large range sizes. The ratio e_0/e^*, which appears three times in the probability density function of range size given in equation (16), relates e_0, the mean gap length in the landscape, to e^*, the mean critical gap length among species, and is a crucial factor that affects both the shape of the geographic range size distribution and its spatial scale. In figure 2, we show how a mere fourfold change in this key ratio may shift the shape of the geographic range size distribution from a scenario where almost all species are very narrowly distributed (<50 range size units) to one in which fully 20% of species in the pool are geographically widespread (>200 range size units). Note that because this case does not allow for any constraints on geographic range size due to critical patch size, from the perspective of the underlying life-history traits themselves, the key determinants of these range size distributions are the ratio of in-matrix diffusion rate to in-matrix mortality rate (d/s) and the ratio of carrying capacity to colonization threshold (K/m; table 1; eq. [6]).

Case 2: An Alternative Distribution for Gap Lengths

Suppose instead that gap length l has the distribution

$$\alpha\left(\frac{\alpha-1}{\alpha}\right)^{\alpha} e_0^{\alpha} x^{-1-\alpha} \quad \text{on} \quad \left[e_0\frac{\alpha-1}{\alpha}, \infty\right) \quad (17)$$

for $\alpha > 1$. Expression (17) is a Pareto distribution with mean e_0 and shape parameter α (Johnson et al. 1994).
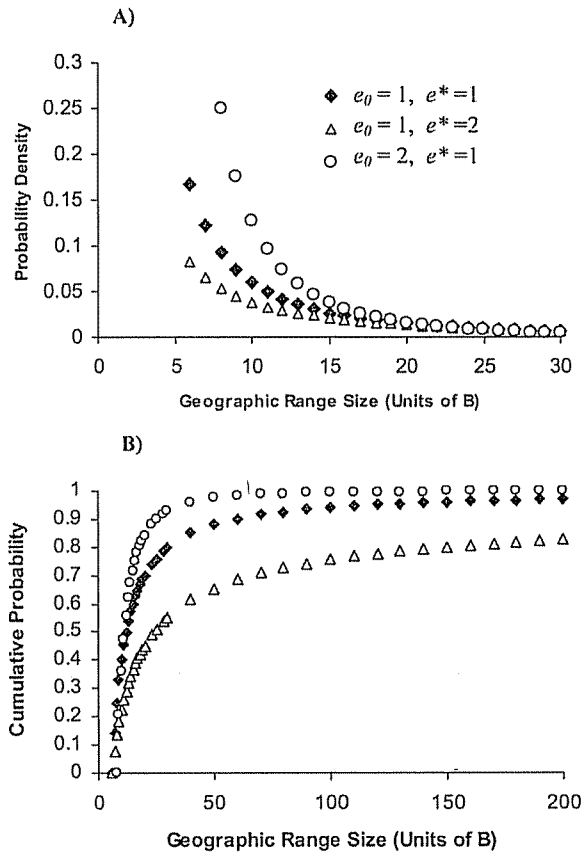

A)

B)

Figure 2: Geographic range size distribution derived from case 1 (eqq. [15], [16]). Three parameter combinations are plotted that examine how range size distribution depends on the ratio between the mean gap length of the landscape (e_0) and the mean critical gap length among species (e^*). These combinations are (1) $e_0/e^* = 1$ (*diamonds*), (2) $e_0/e^* = 0.5$ (*triangles*), and (3) $e_0/e^* = 2$ (*circles*). In combination 2, where $e_0 < e^*$, fully 20% of species in the pool are geographically widespread (>200 range size units), whereas in combination 3, where $e_0 > e^*$, almost all species are very narrowly distributed (<50 range size units). In all cases, $E_0 = 2$. Combinations 1 and 2 equal 0 below $B = 6$; combination 3 equals 0 below $B = 8$.

Pareto distributions have been used as models for the size distributions of lakes (Downing et al. 2006) and other natural features (Vidondo et al. 1997), so this is at least a plausible choice for a distribution of gap or patch sizes. Then,

$$\Pr(l \leq l^*) = \int_{e_0[(\alpha-1)/\alpha]}^{l^*} \alpha\left(\frac{\alpha-1}{\alpha}\right)^{\alpha} e_0^{\alpha} x^{-1-\alpha} dx$$

$$= 1 - \left(\frac{\alpha-1}{\alpha}\right)^{\alpha} \frac{e_0^{\alpha}}{(l^*)^{\alpha}}. \quad (18)$$

Thus, using the same approach as in case 1,

$$\Pr\left(E(\Theta_i) > B\right) = \Pr\left(\frac{2(E_0 + e_0)(l^*)^\alpha}{\{[(\alpha - 1)/\alpha]e_0\}^\alpha} > B\right)$$

$$= \frac{1}{e^*}\exp\left\{\left(\frac{-1}{e^*}\right)\left[\left(\frac{\alpha - 1}{\alpha}\right)e_0\right]\left[\frac{B}{2(E_0 + e_0)}\right]^{1/\alpha}\right\}. \quad (19)$$

So

$$\Pr\left(E(\Theta_i) < B\right) =$$

$$1 - \frac{1}{e^*}\exp\left\{\left(\frac{-e_0}{e^*}\right)\left(\frac{\alpha - 1}{\alpha}\right)\left[\frac{1}{2(E_0 + e_0)}\right]^{1/\alpha}B^{1/\alpha}\right\}, \quad (20)$$

and by taking the derivative d/dB, we obtain the multispecies geographic range size distribution as

$$\frac{d[\Pr\left(E(\Theta_i) < B\right)]}{dB} = \frac{-1}{e^*}\left(\frac{-e_0}{e^*}\right)\left(\frac{\alpha - 1}{\alpha}\right)\left[\frac{1}{2(E_0 + e_0)}\right]^{1/\alpha}$$

$$\times \exp\left\{\left(\frac{-e_0}{e^*}\right)\left(\frac{\alpha - 1}{\alpha}\right)\left[\frac{1}{2(E_0 + e_0)}\right]^{1/\alpha}B^{1/\alpha}\right\}\left(\frac{1}{\alpha}\right)B^{-1+(1/\alpha)}. \quad (21)$$

Because $\alpha > 1$, equation (21) is not an exponential distribution, but if α is close to 1, then the resulting distribution of geographic range sizes is approximately exponential in form. As was the situation in case 1, the key ratio e_0/e^*, which relates the mean gap length in the landscape to the mean critical gap length among species, helps determine both the shape of the geographic range size distribution and its spatial scale. In figure 3, we again demonstrate how a fourfold change in this key ratio may shift the shape of geographic range size distribution. In this case, however, the same three parameter combinations all yield range size distributions with fairly heavy tails (i.e., a large proportion of widespread species), and moreover, the curves for the cumulative distribution functions actually cross. Note again that because this case does not allow for any constraints on geographic range size due to critical patch size, from the perspective of the underlying life-history traits themselves, the key determinants of these range size distributions are the ratios d/s and K/m (table 1; eq. [6]).
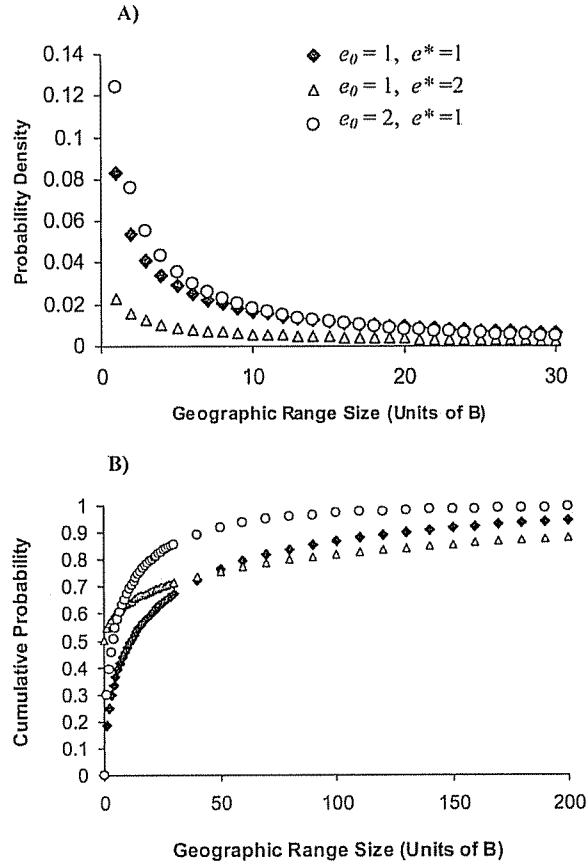

Figure 3: Geographic range size distribution derived from case 2 (eqq. [20], [21]). Three parameter combinations are plotted that examine how range size distribution depends on the ratio between the mean gap length of the landscape (e_0) and the mean critical gap length among species (e^*). These combinations are (1) $e_0/e^* = 1$ (*diamonds*), (2) $e_0/e^* = 0.5$ (*triangles*), and (3) $e_0/e^* = 2$ (*circles*). In all cases, $E_0 = 2$ and $\alpha = 2$.

Case 3: Exponential Distributions for Patch Size and Gap Length in the Landscape and for Critical Patch Size and Critical Gap Length among Species

In the cases we have considered so far, we have assumed for simplicity that all patches are larger than the minimal size needed to support a population of the focal species, but it is natural to allow the possibility that some patches are too small to support populations. Suppose that the sizes of the patches as well as the lengths of the gaps are exponentially distributed. If patch sizes follow an exponential distribution with mean E_0, then $\Pr\left(L \geq L_i^*\right) = \exp\left(-L_i^*/E_0\right)$, where L_i^* is the minimum patch size for species i. Combining this with equation (13) yields

$$E(\Theta_i) = \frac{2(E_0 + e_0)}{1 - \exp(-L_i^*/E_0)[1 - \exp(-l_i^*/e_0)]}. \quad (22)$$

Note that $E(\Theta_i) \geq 2(E_0 + e_0)$. Continuing as in the earlier cases, the probability density function for the distribution of geographic range sizes is

$$\frac{d[\Pr(E(\Theta_i) < B)]}{dB} = \frac{2(E_0 + e_0)}{B^2}\left(\frac{e_0}{e^*}\right)\left(\frac{E_0}{E^*}\right)$$

$$\times \left[1 - \frac{2(E_0 + e_0)}{B}\right]^{(E_0/E^*)-1} \quad (23)$$

$$\times \int_0^{[2(E_0+e_0)]/B} (1 - w)^{-(E_0/E^*)}w^{(e_0/e^*)-1}dw$$

for $B \geq 2(E_0 + e_0)$ and 0 otherwise (app. B in the online edition of the *American Naturalist*). The integral in equation (23) cannot generally be evaluated in terms of elementary functions; however, for a range of parameter values, it can be expressed in terms of incomplete beta integrals (see app. B; Abramowitz and Stegun 1965), and for certain parameter values, it can be computed explicitly. For example, if $(E_0/E^*) = (e_0/e^*) = 1$, then the density function is given by

$$-\frac{2(E_0 + e_0)}{B^2}\ln\left[1 - \frac{2(E_0 + e_0)}{B}\right]$$

for $B \geq 2(E_0 + e_0)$ and is 0 otherwise. Since $\ln(1 - x) \approx -x$ when x is small, this density is approximately $4(E_0 + e_0)^2/B^3$ when B is large. Thus, in this situation, the distribution with density given by equation (23) is qualitatively similar to Pareto distributions for large B (i.e., the distribution would decline monotonically but have a heavy tail compared with an exponential distribution). The expression in equation (23) can be computed explicitly in other cases where E_0/E^* and e_0/e^* are integers, again leading to distributions with asymptotic behavior similar to Pareto distributions.

Note that because this case allows for constraints on geographic range size due to both critical patch size and maximum gap length, all six of the key life-history parameters (table 1) will influence the shape of the geographic range size distribution. In this case, the key life-history determinants of these range size distributions are (1) the ratio of in-patch diffusion to reproductive rate (D/r, which determines E^*), (2) the ratio of in-matrix diffusion rate to in-matrix mortality rate (d/s), and (3) the

ratio of carrying capacity to colonization threshold (K/m; table 1; eq. [6]).

Discussion

Using equations like those typically used to study invasion dynamics (e.g., Skellam 1951), we have developed an analytical framework that links fundamental population-level ecological traits with the distribution of geographic range sizes among species. This is admittedly a large conceptual gulf to bridge with just one mechanistic model. Nevertheless, because of the potentially strong link between demographic processes and species boundaries (Holt et al. 2005), it seems appropriate to construct a model that links species' life-history traits with the distribution of geographic range sizes for a species pool. Although the local (patch-scale) population dynamics in this model are completely deterministic, we have considered a fragmented landscape of patches and gaps in which the spatial heterogeneity is itself stochastic. This stochastic spatial structure, which juxtaposes landscape-level patch and gap characteristics against population-level critical patch sizes and maximum gap-crossing abilities, determines how far a novel species can spread from its evolutionary origin. Given reasonable assumptions about the distribution of patch and gap lengths in the landscape and about the distribution of critical patch sizes and critical gap lengths among species, we can obtain distributions of geographic range sizes that are qualitatively similar to those found in nature (Brown et al. 1996; Gaston 2003).

Geographic Ranges and Geographic Range Size Distributions

The analyses we have outlined afford insights on both the area occupancy and extent of occurrence measures of geographic range size (see Gaston 1991). A species' expected geographic range size using the extent of occurrence metric is given by equation (8), whereas the corresponding expectation for area occupancy would be obtained subtracting the intervening gap lengths, that is,

$$E(\Theta) = \frac{2E(L)E(\tau)}{1 - \Pr(L \geq L^*)\Pr(l \leq l^*)}. \quad (24)$$

In this framework, endemic species would be those with small geographic ranges as determined by their encounters with too-small patches or too-large gaps as the species expanded from their origin. In these scenarios, endemism would be expected to be more common for species with a high rate of leakage across patch boundaries relative to their population growth rates (high D/r; eq. [3]) or for highly habitat-specific species that could not tolerate being

outside a habitat patch and thus had a low rate of movement through the matrix relative to their in-matrix death rate (low d/s; eq. [6]). In addition, species with low average densities (low K) would be expected to be endemics, as would species that have a high threshold density for colonization (high m). Of course, endemism in nature may arise in many ways, including the evolution of habitat or resource specificity and range contraction by ancient lineages (Nekola 1999). However, it also seems likely that a broad suite of biotic and abiotic (or physical and evolutionary) mechanisms may act through only a few demographic parameters to enforce range boundaries (Holt et al. 2005). Consequently, it is interesting to note that many of the factors associated with endemism in this model are likewise associated with different types of spatial rarity in nature (e.g., Gaston and Blackburn 1996; Cofre et al. 2007).

We emphasize, however, that this modeling framework would allow species with identical life-history traits to attain very different geographic range sizes, depending on the specific landscape through which the species were spreading (which would dictate the distributions of patch sizes and gap widths that the species would have to contend with) and depending on the species' evolutionary origins (which would dictate the particular sequence of patches and gaps that species encountered). From this "context-dependent" perspective, our analytical results concerning the interplay between landscape structure and dispersal behavior confirm findings from simulation studies on stochastic neutral landscapes (e.g., Fahrig 1997; King and With 2002).

Links to Invasion Biology

In this article, we have focused our model development on the joint problems of geographic range boundaries and geographic range size. However, given the conceptual and biological links between the dynamics of biological invasions and the expansion of geographic ranges (e.g., Keitt et al. 2001), key aspects of our results are equally pertinent to understanding the spread of invasive species in patchy landscapes. Our efforts demonstrate that the interplay between population-level and landscape-level traits can determine not just how fast a species may spread (e.g., Shigesada et al. 1986; Van Kirk and Lewis 1997; Dewhirst and Lutscher 2009) but also the spatial limits of that spread.

Our results also pertain to the urgent call for improved understanding of the "landscape ecology of invasive spread" (With 2002). Nearly 2 decades ago, Mooney and Drake (1989) argued that the spread of a species through a patchy environment is likely to depend on the degree of habitat heterogeneity, size and distribution of patches, distance between suitable patches, and population char-

acteristics such as growth rate and dispersal ability. The framework we have presented captures all of these features and combines them to quantify how a species' spatial spread depends on measurable population- and landscape-level characteristics. Future work should explore how closely results predicted by this "population dynamics" perspective of invasive spread in stochastically fragmented landscapes correspond to predictions from other modeling frameworks.

Opportunities for Extending the Model

Last, we would emphasize that our model may be developed further in several ways. For example, as mentioned in "Model Setup," our full model does not allow for a situation in which a species may jump over a nearby too-small patch and still successfully colonize a sufficiently large patch remote from the species' origin. This is an important limitation of our model because it means that the geographic range size we calculate for a species that has both patch size and gap length constraints will be an underestimate of the true range size that would occur if jumping over were permissible. As a consequence, a multispecies distribution of range sizes calculated from our full model (e.g., case 3) will be necessarily biased downward compared with the true range size distribution (i.e., the size distribution will be left shifted). A more detailed consideration of this issue must wait for another article, but we note that we have already addressed this issue in this article in a limited fashion. We did this by constructing cases 1 and 2 as upper bounds on the general model (i.e., even a tiny patch may be successfully bypassed by an expanding species, and the full extent of a species' range size will be constrained only by the presence of a too-big gap in the landscape). Consequently, for the case of a landscape with exponentially distributed patch sizes and gap lengths, the true geographic range size distribution will lie, for a particular parameter combination, somewhere between the range size distribution predicted by case 1 and that predicted by case 3.

This "jumping over" limitation of our model arises as a direct mathematical consequence of our reliance on the stopping time approach to the stochastic nature of fragmented landscapes and our choice to present results for a general model. At a technical level, the difficulty emerges because addressing the jumping over issue would require knowing how the probability density function for the sum of the combined gaps compares with the species' maximum gap-crossing ability. Such a calculation requires taking the convolution of the probability densities of the gap lengths, and explicit calculations are possible only in certain special cases. A mathematically similar issue arises if we try to determine the full probability density function

for the range size, as opposed to just computing its mean and variance.

Another key difference between our modeling approach and more typical (empirical or theoretical) studies of species boundaries is that we have completely ignored the potentially important roles played by biogeographic gradients of various types (e.g., temperature extremes, evapotranspiration potential, densities of resources, competitors, or natural enemies). For example, species interactions may certainly influence species geographic range sizes in the real world (Galen 1990), and from a modeling perspective, there may be some ways forward on this front because species interactions, such as consumer impacts, may help set a species' critical patch size (Cantrell et al. 2001). Alternatively, using the same modeling framework that we established here, one could impose spatial gradients in any of several life-history traits. For example, in many species, both local reproductive rate and local density may vary systematically over large spatial scales (e.g., Brown et al. 1995, 1996). Because these measures correspond closely to the parameters r and K in our model and these in turn help determine both a species' critical patch size and its maximum gap-crossing ability (table 1), it seems that a reasonable next step may be to consider the consequences of gradients in life-history traits for modeled geographic range sizes. Likewise, gradients in patch size or landscape "gappiness" also occur in nature, and the imposition of such specific spatial structure in a model would certainly affect the expectation and variance of geographic range sizes for particular species (and for distributions of range sizes across species). Many of these spatial gradient scenarios could not be treated analytically but could be systematically explored using numerical simulation techniques.

Moreover, similar modeling efforts should also be possible by exchanging the partial differential equation framework that we adopted for one of several alternative approaches. For example, our results should be extensible to discrete-time problems (e.g., seasonal systems) because integrodifference equations (Kot et al. 1996) can yield critical patch sizes just as RD models can (Van Kirk and Lewis 1997; Fagan and Lutscher 2006; Fagan et al. 2007). Likewise, there may be opportunities for developing a similar model for the case of geographic ranges in reaction-advection-diffusion models, which also generate critical patch sizes (e.g., Lutscher et al. 2005; Pachepsky et al. 2005). Such a model could shed light on the factors governing the distribution of geographic range sizes in reef fish (Lester and Ruttenberg 2005; Mora and Robertson 2005; Kiflawi et al. 2006) and other species that inhabit patchy landscapes in current-dominated systems.

Other extensions of the model, such as considering spatial spread and geographic range size distributions in two dimensions, would present substantial analytical challenges because of the greater difficulty of determining stopping times in two dimensions for generic probability distributions. Nevertheless, such generalizations are, at least in principle, possible. Given the potential conceptual and quantitative integration that is possible with models that link life-history traits to multispecies geographic range size distributions, future work on such models seems warranted.

Acknowledgments

Literature Cited

Abramowitz, M., and I. Stegun. 1965. Handbook of mathematical functions, with formulas, graphs, and mathematical tables. Dover, New York.

Bahr, D. B., and M. F. Meier. 2000. Snow patch and glacier size distributions. Water Resources Research 36:495–502.

Bakker, V. J., and D. H. Van Vuren. 2004. Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. Conservation Biology 18:689–697.

Barton, N., and B. O. Bengtsson. 1986. The barrier to genetic exchange between hybridizing populations. Heredity 57:357–376.

Berestycki, H., F. Hamel, and L. Roques. 2005. Analysis of the periodically fragmented environment model. II. Biological invasions and pulsating travelling fronts. Journal de Mathématiques Pures et Appliquées 84:1101–1146.

Botsford, L. W., A. Hastings, and S. D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecology Letters 4:144–150.

Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. Ecology 76:2028–2043.

Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27:597–623.

Cabrera, H. M. 1996. Low temperature and altitudinal limits in plant ecosystems: species responses to cold in tropical and subtropical mountains. Revista Chilena de Historia Natural 69:309–320.

Cantrell, R. S., and C. Cosner. 1991. Diffusive logistic equations with indefinite weights: population models in disrupted environments II. SIAM Journal of Mathematical Analysis 22:1043–1064.

———. 2001. Spatial heterogeneity and critical patch size: area effects via diffusion in closed environments. Journal of Theoretical Biology 209:161–171.

———. 2003. Spatial ecology via reaction-diffusion equations. Wiley, Chichester.

Cantrell, R. S., C. Cosner, and V. Hutson. 1996. Spatially explicit models for the population dynamics of a species colonizing an island. Mathematical Biosciences 136:65–107.

Cantrell, R. S., C. Cosner, and W. F. Fagan. 2001. How predator

incursions affect critical patch size: the role of the functional response. American Naturalist 158:368–375.

———. 2005. Edge-linked dynamics and the scale-dependence of competitive dominance. Mathematical Biosciences and Engineering 2:833–868.

Carter, R. N., and S. D. Prince. 1981. Epidemic models used to explain biogeographical distribution limits. Nature 293:644–645.

———. 1987. Distribution limits from a demographic viewpoint. Symposia of the British Ecological Society 28:165–184.

Castellón, T. D., and K. E. Sieving. 2006. An experimental test of matrix permeability and corridor use by an endemic understory bird. Conservation Biology 20:135–145.

Cofre, H. L., K. Bohning-Gaese, and P. A. Marquet. 2007. Rarity in Chilean forest birds: which ecological and life-history traits matter? Diversity and Distributions 13:203–212.

Creegan, H. P., and P. E. Osborne. 2005. Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach . Journal of Applied Ecology 42:678–687.

Cumming, S. G. 2001. A parametric model of the fire-size distribution. Canadian Journal of Forest Research 31:1297–1303.

Curriel, W. J. S., M. R. Claereboudt, and J. C. Roff. 1998. Gaps and patches in the ocean: a one-dimensional analysis of planktonic distributions. Marine Ecology Progress Series 171:15–21.

Dale, V. H., S. M. Pearson, H. L. Offerman, and R. V. O'Neill. 1994. Relating patterns of land-use change to faunal biodiversity in the central Amazon. Conservation Biology 8:1027–1036.

Dewhirst, S., and F. Lutscher. 2009. Dispersal in heterogeneous habitats: thresholds, spatial scales, and approximate rates of spread. Ecology (forthcoming).

Downing, J. A., Y. T. Prairie, J. J. Cole, C. M. Duarte, L. J. Tranvik, R. G. Striegl, W. H. McDowell, et al. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnology and Oceanography 51:2388–2397.

Drake, J. M., and D. M. Lodge. 2006. Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. Biological Invasions 8:365–375.

Fagan, W. F., and F. Lutscher. 2006. The average dispersal success approximation: linking home range size, natal dispersal, and metapopulation dynamics to reserve design. Ecological Applications 16:820–828.

Fagan, W. F., F. Lutscher, and K. Schneider. 2007. Population and community consequences of spatial subsidies derived from central place foraging. American Naturalist 170:902–915.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management 61:603–610.

Galen, C. 1990. Limits to the distributions of alpine tundra plants: herbivores and the alpine skypilot, *Polemonium viscosum*. Oikos 59:355–358.

Gaston, K. J. 1991. How large is a species geographic range? Oikos 61:434–438.

———. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford.

Gaston, K. J., and T. M. Blackburn. 1996. Global scale macroecology: interactions between population size, geographic range size and body size in the Anseriformes. Journal of Animal Ecology 65:701–714.

Gaston, K. J., and F. He. 2002. The distribution of species range size: a stochastic process. Proceedings of the Royal Society B: Biological Sciences 269:1079–1086.

Gaylord, B., and S. D. Gaines. 2000. Temperature or transport? range limits in marine species mediated solely by flow. American Naturalist 155:769–789.

Goldberg, E. E., and R. Lande. 2007. Species' borders and dispersal barriers. American Naturalist 170:297–304.

Groom, M. J. 1998. Allee effects limit population viability of an annual plant. American Naturalist 151:487–496.

Hanski, I. 1998. Metapopulation dynamics. Nature 396:41–49.

Holt, R. D., T. H. Keitt, M. A. Lewis, B. A. Maurer, and M. L. Taper. 2005. Theoretical models of species' borders: single species approaches. Oikos 108:18–27.

Johnson, N. L., S. Kotz, and N. Balakrishnan. 1994. Continuous univariate distributions. 2nd ed. Vol. 1. Wiley, Chichester.

Johnson, O. N., A. M. Liebhold, P. C. Tobin, and O. N. Bjornstad. 2006. Allee effects and pulsed invasion by the gypsy moth. Nature 444:361–363.

Kawasaki, K., and N. Shigesada. 2007. An integrodifference model for biological invasions in a periodically fragmented environment. Japan Journal of Industrial and Applied Mathematics 24:3–15.

Keitt, T. H., D. L. Urban, and B. T. Milne. 1997. Detecting critical scales in fragmented landscapes. Conservation Ecology 1:4, http://www.consecol.org/vol1/iss1/art4/.

Keitt, T. H., M. A. Lewis, and R. D. Holt. 2001. Allee effects, invasion pinning, and species' borders. American Naturalist 157:203–216.

Kierstead, H., and L. B. Slobodkin 1953. The size of water masses containing plankton bloom. Journal of Marine Research 12:141–147.

Kiflawi, M., J. Belmaker, E. Brokovich, S. Einbinder, and R. Holzman. 2006. The determinants of species richness of a relatively young coral-reef ichthyofauna. Journal of Biogeography 33:1289–1294.

King, A. W., and K. A. With. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? Ecological Modelling 147:23–39.

Kot, M., M. A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. Ecology 77:2027–2042.

Lawton, R. O., and F. E. Putz. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology 69:764–777.

Lester, S. E., and B. I. Ruttenberg. 2005. The relationship between pelagic larval duration and range size in tropical reef fishes: a synthetic analysis. Proceedings of the Royal Society B: Biological Sciences 272:585–591.

Lewis, M. A., and P. Kareiva. 1993. Allee dynamics and the spread of invading organisms. Theoretical Population Biology 43:141–158.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20:223–228.

Lutscher, F., E. Pachepsky, and M. A. Lewis. 2005. The effect of dispersal patterns on stream populations. SIAM Journal of Applied Mathematics 65:1305–1327.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Mooney, H. A., and J. A. Drake. 1989. Biological invasions: a SCOPE program overview. Pages 491–506 *in* J. A. Drake, H. A. Mooney, F. Di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, eds. Biological invasions: a global perspective. Wiley, Chichester.

Mora, C., and D. R. Robertson. 2005. Factors shaping the range-size

frequency distribution of the endemic fish fauna of the Tropical Eastern Pacific. Journal of Biogeography 32:277–286.

Nekola, J. C. 1999. Paleorefugia and neorefugia: the influence of colonization history on community pattern and process. Ecology 80:2459–2473.

Pachepsky, E., F. Lutscher, R. Nisbet, and M. A. Lewis. 2005. Persistence, spread and the drift paradox. Theoretical Population Biology 67:61–73.

Pereira, H. M., and G. C. Daily. 2006. Modeling biodiversity dynamics in countryside landscapes. Ecology 87:1877–1885.

Pereira, H. M., G. C. Daily, and J. Roughgarden. 2004. A framework for assessing the relative vulnerability of species to land-use change. Ecological Applications 14:730–742.

Pialek, J., and N. H. Barton. 1997. The spread of an advantageous allele across a barrier: the effects of random drift and selection against heterozygotes. Genetics 145:493–504.

Shigesada, N., and K. Kawasaki. 1997. Biological invasions: theory and practice. Oxford University Press, Oxford.

Shigesada, N., K. Kawasaki, and E. Teramoto 1986. Traveling periodic waves in heterogeneous environments. Theoretical Population Biology 30:143–160.

Skellam, J. 1951. Random dispersal in theoretical populations. Biometrika 38:196–218.

Tobin, P. C., S. L. Whitmire, D. M. Johnson, O. N. Bjornstad, and A. M. Liebhold. 2007. Invasion speed is affected by geographical variation in the strength of Allee effects. Ecology Letters 10:36–43.

Urban, D., and T. H. Keitt. 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82:1205–1218.

van der Ree, R., A. F. Bennett, and D. C. Gilmore. 2004. Gap-crossing by gliding marsupials: thresholds for use of isolated woodland patches in an agricultural landscape. Biological Conservation 115: 241–249.

Van Kirk, R. W., and M. A. Lewis. 1997. Integrodifference models for persistence in fragmented habitats. Bulletin of Mathematical Biology 59:107–137.

Veit, R. R., and M. A. Lewis. 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. American Naturalist 148:255–274.

Vidondo, B., Y. T. Prairie, J. M. Blanco, and C. M. Duarte. 1997. Some aspects of the analysis of size spectra in aquatic ecology. Limnology and Oceanography 41:184–192.

Virgos, E., and J. G. Casanovas. 1999. Environmental constraints at the edge of a species distribution, the Eurasian badger (*Meles meles* L.): a biogeographic approach. Journal of Biogeography 26:559–564.

Webb, T. J., and K. J. Gaston. 2000. Geographic range size and evolutionary age in birds. Proceedings of the Royal Society of London B: Biological Sciences 267:1843–1850.

With, K. A. 2002. The landscape ecology of invasive spread. Conservation Biology 16:1192–1203.