Landscape context affects genetic diversity at a much larger spatial extent than population abundance

Nathan D. Jackson[1] and Lenore Fahrig

Geomatics and Landscape Ecology Research Laboratory, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6 Canada

Abstract. Regional landscape context influences the fate of local populations, yet the spatial extent of this influence (called the "scale of effect") is difficult to predict. Thus, a major problem for conservation management is to understand the factors governing the scale of effect such that landscape structure surrounding a focal area is measured and managed at the biologically relevant spatial scale. One unresolved question is whether and how scale of effect may depend on the population response measured (e.g., abundance vs. presence/absence). If scales of effect differ across population outcomes of a given species, management based on one outcome may compromise another, further complicating conservation decision making. Here we used an individual-based simulation model to investigate how scales of effect of landscapes that vary in the amount and fragmentation of habitat differ among three population responses (local abundance, presence/absence, and genetic diversity). We also explored how the population response measured affects the relative importance of habitat amount and fragmentation in shaping local populations, and how dispersal distance mediates the magnitude and spatial scale of these effects. We found that the spatial scale most strongly influencing local populations depended on the outcome measured and was predicted to be small for abundance, medium-sized for presence/absence, and large for genetic diversity. Increasing spatial scales likely resulted from increasing temporal scales over which outcomes were regulated (with local genetic diversity being regulated over the largest number of generations). Thus, multiple generations of dispersal and gene flow linked local population patterns to regional population size. The effects of habitat amount dominated the effects of fragmentation for all three outcomes. Increased dispersal distance strongly reduced abundance, but not presence/absence or genetic diversity. Our results suggest that managing protected species at spatial scales based on population abundance data may ignore broader landscape effects on population genetic diversity and persistence, lending support to the importance of managing large buffers surrounding areas of conservation concern.

Key words: *agent-based modeling; allelic richness; CLUMPY; focal patch; landscape buffers; landscape ecology; landscape genetics; midpoint displacement.*

Introduction

Predicting the spatial extent over which landscapes affect species in a "focal site" (such as a wetland, forest patch, or protected area) is a significant problem for conservation management. Protected areas are not islands, but are embedded within a landscape context that can strongly influence focal populations (Steffan-Dewenter et al. 2002, Martin et al. 2006). Landscape context around a focal site is comprised of a particular landscape structure, which is defined by the proportion and distribution of specific features of the landscape (e.g., forest, agriculture, roads, and urban areas) that are thought to affect local populations (e.g., populations in a focal site). The geographical extent over which landscape context most influences a given focal population (called the "scale of effect") may depend on a host of factors (Wiens 1989), including the home range, dispersal behavior, or reproductive rate of the species (Roland and Taylor 1997, Holland et al. 2004, Jackson and Fahrig 2012) or characteristics of the landscape of interest. Misspecifying the distance over which landscape context matters to focal populations can mislead predictions about how landscape characteristics (e.g., amount or configuration of habitat) will shape important population parameters (e.g., population abundance) and/or cause landscape effects to go undetected.

To accommodate uncertainty in scales of effect, a focal-site approach (Brennan et al. 2002) is increasingly being adopted in empirical studies (reviewed in Thornton et al. 2011). For this method, population outcomes (e.g., abundance or persistence) are sampled within a set of independent (e.g., geographically distant) focal habitat sites (which we also call "local" sites), whereas "regional" landscape structure (e.g., the amount or fragmentation of habitat) is sampled within a series of
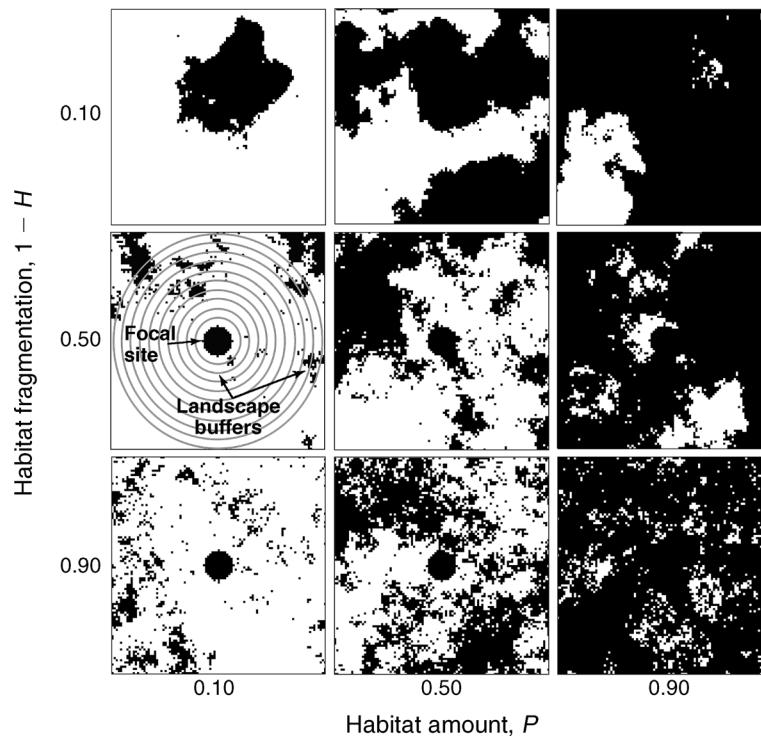
Fig. 1. An example of random simulated landscapes that were varied in their amount (x-axis; P) and fragmentation (y-axis; 1 − H [see Methods: Simulation model: Landscape simulation]) of habitat; although three levels of each are shown, five levels were simulated for each. Black cells represent habitat and white cells represent matrix. A seven-cell radius group of habitat cells (the focal site) was superimposed onto the center of each landscape within which demographic and genetic outcomes were sampled. We varied the spatial scale of the landscape around the focal site within which landscape structure was measured using 10 nested concentric buffers (shown in the center-left landscape).

spatially nested buffers of increasing radius around each focal site (Fig. 1). The scale of effect is that buffer radius for which landscape structure best predicts local population response (i.e., a given outcome measured in the focal site). In this way, relationships between landscape context and population outcomes are inferred at the spatial scale most relevant to a particular species–landscape interaction.

Although the impact of species characteristics on the scale of effect has received some attention (e.g., Roland and Taylor 1997, Holland et al. 2004, Jackson and Fahrig 2012), little is known concerning whether or how the scale of effect for a particular species may also depend upon the population response measured. Landscape impacts on populations are inferred using a variety of ecological or genetic outcomes (e.g., abundance, persistence, dispersal, reproductive rate, and genetic diversity or structure), yet the influence of a chosen outcome on scale of effect is unknown. Cushman and McGarigal (2004b) showed that for forest birds, landscape structure at larger spatial scales was somewhat more important for abundance than for presence/absence data. However, it is unclear how general these differences are. Also, little is known about how spatial scale of relationships between landscape factors and species responses based on abundance and presence/

absence (demographic outcomes) compare with those based on genetic data. The scale of effect for genetic diversity might be larger than the scale of effect for demographic outcomes because the size of the gene pool available to any local group of individuals is constrained by the regional population size, whereas local species abundance may be as dependent on local conditions as it is on regional landscape structure (Cushman and McGarigal 2004a, Thornton et al. 2011). If the scale of effect of landscape structure is generally similar for different demographic and genetic responses, this would simplify conservation management. On the other hand, if the scales significantly differ, conservation management tailored to one outcome might compromise the other, and a more complex decision-making process would be needed.

In this study, we investigated the strength, shape, and spatial scale of relationships between two components of landscape structure (habitat amount and fragmentation) and three measures of population diversity (abundance, persistence, and genetic diversity). Because species traits can influence landscape effects, we also varied average dispersal distance, which has been predicted to strongly shape the effective size and impact of landscapes (Jackson and Fahrig 2012). Our main goal was to determine how the spatial scale of landscape impacts are

mediated by population response. We also asked whether the relative importance of surrounding habitat loss and habitat fragmentation per se for shaping focal populations changes among the population outcomes measured, a question that also has important implications for conservation management (Fahrig 2003, Bruggeman et al. 2010). To accomplish this, we developed an individual-based population genetic simulation model in which hypothetical organisms disperse and reproduce within hypothetical landscapes that systematically vary in their structure.

METHODS

Simulation model

Overview.—We developed a spatially explicit individual-based model using NetLogo 4.1.3 (Wilensky 1999). The model simulates birth, dispersal, mating, reproduction, and death of individuals in stochastically generated heterogeneous landscapes. We simulated five hypothetical generic species (that differ only in dispersal potential) interacting with 25 different types of landscapes that varied in amount and fragmentation of habitat (Fig. 1). We investigated how and at what spatial scale landscapes and species characteristics impact three population outcomes: local abundance, presence/absence (i.e., persistence), and genetic diversity.

Landscape simulation.—We simulated landscapes composed of habitat and non-habitat ("matrix") using the midpoint displacement algorithm (Saupe 1988) as implemented in a previous model (TraitScape; Jackson and Fahrig 2012). This fractal algorithm produces landscapes that vary independently in the amount and fragmentation (the inverse of "clumpiness") of habitat. The proportion of habitat (P) was simulated at 10%, 30%, 50%, 70%, and 90%. Habitat fragmentation was varied by specifying the amount of habitat spatial autocorrelation (H). High values of H (e.g., near 1) yield landscapes with highly clumped habitat whereas low values of H (e.g., near 0) yield landscapes where habitat is highly fragmented into small patches. We simulated five degrees of fragmentation: H = 0.1, 0.3, 0.5, 0.7, and 0.9.

Each simulation run produces a random landscape composed of a 101 × 101 cell grid, according to the specified P and H. A small group of habitat cells (seven-cell radius) is superimposed onto the center of each landscape (called the "focal site," which is composed of 100% habitat) from which population outcomes are sampled at the end of each simulation (Fig. 1). Note, here we used "focal site" rather than the more usual "focal patch" since we sampled the population within equal-sized sites in the center of each landscape.

Population setup.—Each landscape is initially populated with 5000 individuals whose original coordinates are randomly assigned irrespective of landscape structure such that initial population densities are independent of the amount of habitat (Fahrig 2001). Individuals are endowed with five diploid loci and each gene copy is randomly assigned one of 20 alleles available at each locus. The sex of an individual is randomly assigned with an average ratio of 1:1.

Movement.—We simulated random female dispersal: each female in turn disperses one step (across a continuous surface) in a random direction. Female-biased dispersal is common in many groups of taxa such as birds and insects (Petit and Excoffier 2009). We selected random dispersal to maximize the opportunity for habitat fragmentation to impact populations (due to an increasing likelihood of dispersal into a hostile matrix as patches become smaller and more isolated [Hovestadt et al. 2001]). Distance travelled was drawn from a negative exponential distribution with a mean equal to the specified average dispersal distance (D_{av}). Negative exponential dispersal is often used to model "fat-tailed" dispersal kernels, which are exhibited by many species (Kot et al. 1996, DiLeo et al. 2013). Grid boundaries are reflecting. To account for the influence of an organism's dispersal potential on inferred relationships between landscape structure and population outcomes, D_{av} was experimentally varied to be 2, 4, 6, 8, or 10 cells.

Mating and reproduction.—After dispersal is complete, each female located in a habitat cell is given the opportunity to mate with the closest male within a radius equal to D_{av}. Note that in preliminary runs, having females mate with a randomly selected male (rather than the closest male) within radius D_{av} did not alter our results. If no male exists in habitat within this radius or if the female is located in the matrix, she does not mate. Thus all females mate one or fewer times whereas males may mate anywhere from zero to multiple times. The number of offspring per mated female (F) is drawn from a Poisson distribution with a mean calculated from the following logistic growth equation (Hassell and Comins 1976):

$$F = 2\left[\frac{\lambda}{1 + \left(\frac{\lambda - 1}{K}\right)N_F}\right].$$

Population growth rate (λ) and carrying capacity within a cell (K) were both set at 2 for all simulations, which achieved a balance of adequate persistence in low-habitat/high-fragmentation landscapes and computationally tractable population sizes (i.e., <25 000 individuals) in high-habitat/low-fragmentation landscapes. N_F represents the number of females occupying a given cell. To accommodate sexual reproduction, the equation was multiplied by two. Offspring occupy the same cell coordinates as their mother and are randomly assigned to be male or female. For all five diploid loci, offspring randomly inherit one allele from each parent. Mutation rate (μ) was set to 0.0001 (common for microsatellites in a wide range of plants and animals [Bhargava and Fuentes 2010]) and follows a *k*-allele mutation model where an allele mutates to any other available allele with equal probability. Note that males and females that

dispersed into the matrix do not contribute to the next generation.

Death.—After reproduction is complete, all adults (whether in habitat or matrix) die and juveniles become adults ready to disperse. Thus, generations are nonoverlapping. We refer to a completed cycle between dispersal and death as a single generation.

Simulation experiments

We carried out two simulation experiments (referred to as "habitable landscapes" and "all landscapes" and described in the next two subsections) to test the relative size and spatial scale of impacts of habitat amount and fragmentation on population (i.e., demographic and genetic) outcomes. In both experiments, we varied habitat amount (P; five levels), habitat fragmentation (H; five levels), and average dispersal distance (D_{av}; five levels) in a full factorial design (125 factor combinations). Each factor combination was repeated 100 times using a different random seed and each replicate was run for 1000 generations to ensure sufficient time for stabilization of global population size and arrival at genetic equilibrium.

Habitable landscapes.—Many scenarios resulted in both local (i.e., focal site) and regional (i.e., grid-wide) extinction. Due to the statistical challenges inherent in analyzing data with a large proportion of zeros (the outcome of extinct populations), for this first set of experiments, we only retained simulation runs that had extant local populations at the end of 1000 generations. For a given experimental scenario, simulations were thus repeated until the desired sample of 100 populations was reached. This experiment therefore investigated the impact of landscape structure on population outcomes, given that the population persists. To save computational time, runs were terminated if the focal site remained uninhabited for 30 generations; preliminary simulation runs showed that a focal site that was empty for 30 generations would not be recolonized.

All landscapes.—Because the above simulations focused only on patterns within persisting populations, we performed a second set of simulation experiments to investigate the effects of landscape structure on the probability of population persistence. Here, we carried out 100 iterations for each of the 125 factor combinations, retaining all simulation runs regardless of population outcome.

Because focal-site persistence is more likely when habitat is distributed near the center of the landscape, landscapes retained for the "habitable landscapes" experiments tended to contain less habitat near the periphery of landscapes compared to landscapes from experiments in which all landscapes were analyzed (this effect was mostly observed when P and D_{av} were low). To ensure that this did not influence inferred scales of effect, we repeated all analyses by including only those landscapes with an equal or greater proportion of habitat in the periphery of the landscape (outer most

buffer ring) compared to the center (inner most buffer ring). Results were the same; thus, we report results from analysis of the full data set.

Model output

For the experiments involving habitable landscapes, at the end of each retained simulation run, we recorded local population size (N) and genetic diversity. Genetic diversity was estimated using two common metrics: allelic richness (A; the number of unique alleles in a sample) and expected heterozygosity (H_e; the probability that any two chosen gene copies in a sample represent different alleles), averaged across loci. We also calculated the inbreeding coefficient F_{IS} to track deviations of observed heterozygosity (H_o) from expectations under random mating ($F_{IS} = H_e - [H_o/H_e]$). For the experiments involving all landscapes, we recorded whether the local population persisted until 1000 generations (i.e., presence/absence; PA), and if not, the generation at which the population went extinct.

To compare the impact of landscape structure on the three population outcomes at different spatial scales, we calculated landscape metrics within 10 nested circular buffers around the focal site of each simulated landscape, where buffer radii ranged from 9 to 50 cells. For each simulated landscape, we then calculated metrics of landscape structure for each of the 10 buffers using a moving window analysis in FRAGSTATS v3.3 (McGarigal et al. 2002). Habitat amount was calculated using the metric PLAND (the percentage of the landscape occupied by habitat). For habitat fragmentation, it was vital that we select a measure of fragmentation that is independent of habitat amount such that we could isolate its importance for mediating population outcomes (Fahrig 2003). For each landscape we thus calculated five metrics that are not expected to be strongly correlated with the amount of habitat in the landscape (where correlation with habitat amount was shown to be <0.25 by Neel et al. [2004]). Of these five, we chose to focus on the metric CLUMPY as it was generally the best predictor of population outcomes (see Appendix A for more details). CLUMPY tracks the extent that habitat is spatially aggregated and thus is expected to approximate simulated levels of H. CLUMPY ranges from −1 (highly fragmented habitat) to 1 (highly aggregated habitat).

Statistical analysis

Effects of landscape structure and dispersal distance on distinct population outcomes.—We first investigated relationships between the three experimental treatments (P, H, and D_{av}) and the three model outcomes (N, A, and H_e) from the "habitable landscapes" experiments using analyses of variance (ANOVA). We used logistic regression to examine relationships between experimental treatments and population persistence (i.e., presence/ absence; PA) from the "all landscapes" experiments. The four responses were each analyzed in separate analyses

and included all three treatments and two-way interactions. For these analyses, landscape structure (P and H) was defined for the entire grid ("regional" landscape structure), and all predictors were treated as categorical data.

Scales of effect of landscape structure across distinct population outcomes.—To determine the spatial scale at which P and H most strongly affect each simulated outcome (called the scale of effect, S), we repeated the above analyses, replacing regional estimates of landscape structure (P and H) with "scaled" estimates of landscape structure ($PLAND_i$ and $CLUMPY_i$) at each of the 10 scales (where $PLAND_i$ and $CLUMPY_i$ represent habitat amount and clumpiness, respectively, as measured at the ith buffer radius); thus 10 regressions were performed for each outcome, one for each of the 10 buffers. S for PLAND and CLUMPY was inferred to be the buffer radius for which model Akaike information criterion (AIC) was minimized (Holland et al. 2004). As in the regional landscape analyses, all four responses (N, A, H_e, and PA) were regressed separately against the two landscape predictors ($PLAND_i$ and $CLUMPY_i$), D_{av}, and all two-way interactions.

To account for the fact that PLAND and CLUMPY may exhibit different scales of effect, we performed these described regression analyses in two stages. First, because PLAND explained the vast majority of the observed variation in our data, we found S for PLAND alone by fitting regressions at the 10 scales without CLUMPY (e.g., $N \sim PLAND_i + D_{av} +$ two-way interactions). We then fit a second 10 models where PLAND was held constant at S and the scale of CLUMPY was varied (e.g., $N \sim PLAND_S + CLUMPY_i + D_{av} +$ two-way interactions, where CLUMPY was calculated across the 10 buffers). For H_e, two PLAND scales yielded low (but similar) AIC scores ($\Delta AIC < 1$). In this case, we varied the scale of CLUMPY using each $PLAND_S$ in turn and compared AIC from all 20 models to infer S for CLUMPY.

For scaled landscape analyses, all predictors were treated as continuous data because PLAND and CLUMPY varied across spatial scales in our simulated landscapes; they were not strictly controlled by P and H at these smaller scales. To achieve normality of residuals, we transformed H_e using $\log(1 - x)$ and rank ordered CLUMPY prior to analysis (see Appendix A). Large numbers of replicates can yield significant results, even when relationships are biologically trivial. Thus, for both regional and scaled landscape analyses we reported percent sum of squares (%SS) rather than statistical significance. The variable %SS gives the proportion of the variation in the data explained by a variable (Fletcher 2006). CLUMPY and PLAND were weakly collinear, particularly at small spatial scales (see Appendix A). For the scaled landscape analyses, we also calculated standardized regression coefficients, which are appropriate when comparing relative importance of collinear predictors (Smith et al. 2009).

RESULTS

Simulation experiments

Habitable landscapes.—In experiments involving only habitable landscapes, we were unable to obtain 100 replicates for six of the 125 factor combinations because the populations in these scenarios almost always went extinct (when P is = 0.1, H is = 0.3, and D_{av} is = 10, and for all five scenarios when H and P both are = 0.1). These scenarios were excluded from analysis. Population size usually stabilized by 100 generations and F_{IS} values were generally near zero, indicating that local populations were roughly in Hardy-Weinberg equilibrium at the end of the simulation ($F_{IS} \leq |0.20|$ in 99% of replicates). Simulation runs resulted in a wide range of population sizes (from ~100 to ~20 000 individuals) and levels of genetic diversity (H_e ranged from <0.0001 to >0.9).

All landscapes.—When tracking population persistence in all landscapes, nonviable populations usually went extinct quickly: out of populations that went extinct, 91% did so before 100 generations. Thus, in regression analysis, we used "persistence" (i.e., presence/absence at 1000 time steps) rather than "time to extinction" as the response.

Statistical analysis

Effects of landscape structure and dispersal distance on distinct population outcomes.—The proportion of habitat (P) had the greatest impact on all outcomes (%SS > 60%; Table 1, Fig. 2, and Appendix B), positively predicting both demographic and genetic responses. Habitat fragmentation (H) was the second strongest predictor of presence/absence (%SS = 8.7%) and genetic diversity (for A, %SS = 7.1; for H_e, %SS = 8.4), but was the weakest predictor of population abundance (%SS = 3.4%), and exhibited a negative effect in all cases. Average dispersal distance (D_{av}) was a strong and negative predictor of population abundance (%SS = 31.7%), but did not strongly predict presence/absence (%SS = 1.0%) or genetic diversity (for A, %SS = 1.6%; for H_e, %SS = 1.5%). The greatest increases in population abundance and allelic richness were observed when increasing from 70% habitat to 90% habitat (Fig. 2). That this same interval yielded the smallest increase in population persistence indicates that local populations in landscapes at or above 70% habitat were sustainable, although possibly far from carrying capacity. The two measures of genetic diversity were similarly predicted by landscape structure and D_{av}, thus we focus on allelic richness (but results for heterozygosity are reported in Appendix B). Inclusion of interaction terms improved AIC for all models, although the contributions of these interactions were generally small (%SS < 4; Table 1; Appendix B: Table B1).

Similar to the results we have described, habitat amount ($PLAND_S$) was a much better predictor of population outcomes (%SS > 60%) than was fragmen-

tation (CLUMPY$_S$; %SS < 14%) when these components of landscape structure were calculated at their "best" scales, S (i.e., the scales at which AIC was minimized; see Table 1, Appendix B: Table B1). Relative importance was also the same whether using standardized regression coefficients or %SS (Table 1 and Table B1 vs. Appendix C).

Scales of effect of landscape structure across distinct population outcomes.—The inferred scales of effect (S) were unambiguous (the change in AIC [ΔAIC] > 20 between best and second-best scales, except when the response was H_e, as noted in *Methods*), but differed across population outcomes (Fig. 3). Scale of effect for habitat amount (PLAND) was smallest for abundance (the radius is 18 cells or 10% of the total landscape) largest for genetic diversity (the radius is 45 cells or 62% of the total landscape for A; the radius is 50 cells or 77% of the total landscape for H_e), and intermediate for presence/absence (the radius is 31 cells or 30% of the total landscape). The influence of D_{av} on S for PLAND was apparent for all outcomes: as expected, S increased as D_{av} increased, although this trend was more striking for demographic than for genetic outcomes (Appendix D). For abundance and persistence, S for PLAND was between 3 and 6.5 times D_{av} (Appendix D). In contrast, for genetic diversity, S for PLAND was between 5 and 18 times D_{av}. Scales of effect for habitat fragmentation (CLUMPY) followed a similar pattern to S for PLAND, but were consistently one or two buffer radii smaller (Fig. 3).

DISCUSSION

The spatial scale of landscape effects on demographic outcomes

Landscape size is not an absolute quantity but is predicted to vary according to characteristics of the species, landscape, and process of interest (Wiens 1989). Here, we show that the spatial scale at which the landscape influences a given organism also depends on the chosen population response, which may create further challenges when attempting to provide scale-informative protection to species and areas of conservation concern.

First, we found that the scale of effect for presence/absence is larger than for abundance. One possible explanation for this pattern is that these different spatial scales of effect may, in part, result from the different temporal scales over which these two outcomes are regulated. Whereas the number of individuals (local abundance) can fluctuate every generation, a loss of all individuals (local extinction) usually requires many generations to occur (median time to extinction across our simulations was 17 generations). As the number of generations over which a process occurs increases, the potential geographical distance from over which a local population can recruit also increases, given that multiple generations of dispersal can result in greater total displacement than a single generation. Thus, the more

TABLE 1. Proportion of variation explained by habitat amount, habitat fragmentation, and average dispersal distance (D_{av}) when predicting three population outcomes (abundance, N; presence/absence, PA; and allelic richness, A).

Factor	df	N (%SS)	PA (%CH)	A (%SS)
Regional landscape				
P	4	61.25	86.17	88.19
H	4	3.39	8.71	7.06
D_{av}	4	30.68	1.05	1.62
P:H	16	0.51	1.49	1.61
P:D_{av}	16	3.93	2.08	1.45
H:D_{av}	16	0.24	0.50	0.07
Scaled landscape				
PLAND$_S$	1	64.50	86.15	87.39
CLUMPY$_S$	1	3.60	13.64	9.84
D_{av}	1	26.17	0.12	0.55
PLAND$_S$:CLUMPY$_S$	1	5.17	0.05	1.06
PLAND$_S$:D_{av}	1	0.19	0.00	1.14
CLUMPY$_S$:D_{av}	1	0.33	0.03	0.02

Notes: N and A were analyzed using linear regression and PA was analyzed using logistic regression. Regional landscape refers to analyses using the full grid landscape where P is amount/proportion of habitat and H is fragmentation of habitat. Scaled landscape refers to analyses using the biologically relevant landscape size (scale of effect, S) for each population outcome, where PLAND$_S$ is habitat amount at S and CLUMPY$_S$ is habitat fragmentation at S. The R^2 values for regional landscape analyses were 0.698 (N), 0.719 (PA), and 0.830 (A). The R^2 values for scaled landscape analyses were 0.848 (N), 0.848 (PA), and 0.894 (A). The unit %SS is percent sum of squares, which gives the proportion of variation explained by a predictor; %CH is a χ^2 analog of %SS that is appropriate for binomial data (Agresti and Finlay 2008).

generations it takes to register a local response, the more important that geographically distant individuals should be in affecting that response. This link between temporal and spatial scales can be seen by plotting the correlation between local (focal site) responses and regional population size when "regional" population size is measured at different spatial extents and at different times prior to local sampling (Fig. 4). For example, when the regional landscape was defined at small spatial scales (e.g., the radius is 9), local abundance was best predicted by regional population size measured from the current generation. However, as the radius of the regional landscape was increased (e.g., to a radius of 45), local abundance was better predicted by past population size than present population size. This shows that population dynamics measured at greater distances from a local site tend to require more generations to influence local outcomes. Furthermore, allowing population dynamics more time to impact a response increases the relative importance of broad-scale population dynamics and decreases the relative importance of local population dynamics. In this way, the multiple generations required for local extirpation to occur may result in a larger spatial scale of effect for presence/absence than for abundance.

The distinct spatial scales at which these two demographic outcomes are expected to operate has not
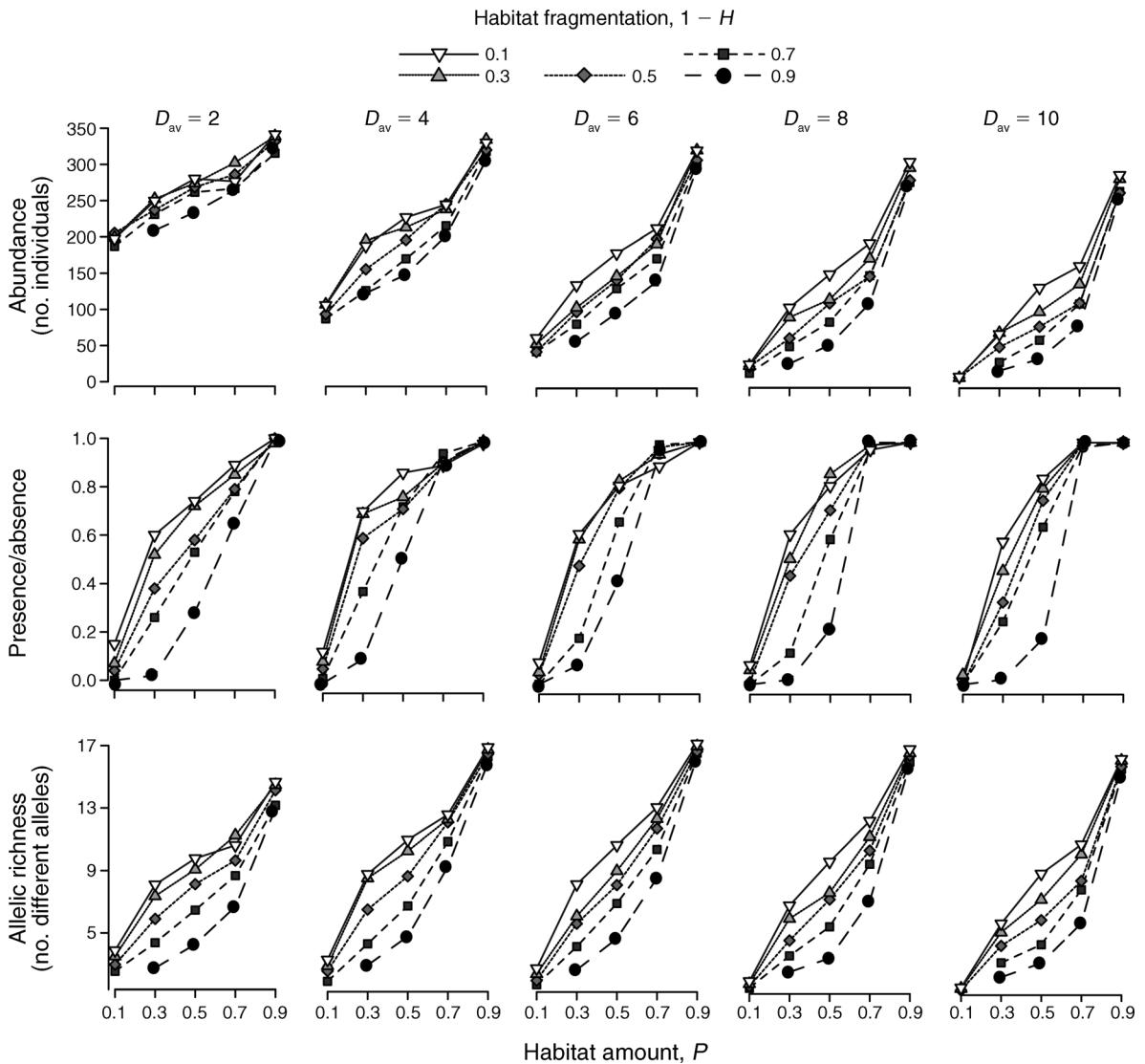
FIG. 2. Mean local abundance, presence/absence, and allelic richness plotted against the amount (proportion) of habitat (P) at different levels of habitat fragmentation ($1 - H$) and average dispersal distance (D_{av}).

before been fully appreciated, despite many landscape studies carried out using these measures (reviewed in Thornton et al. 2011). Note that in empirical data sets of abundance in which there are a lot of zeros (i.e., species absences, which were eliminated in our study), the scale of effect may be somewhat intermediate between those predicted here for presence/absence and abundance.

The spatial scale of landscape effects on genetic diversity

Our results predict that the scale of effect for genetic diversity is even larger than the scale of effect for presence/absence. If the link between temporal and spatial scales hypothesized above exists, then this may suggest that genetic diversity is also regulated over a larger temporal scale than are both abundance and presence/absence (Appendix E). Although local abun-

dance determines the number of gene copies in a sample (two times the population size for diploid organisms), thus directly influencing local genetic diversity (Frankham 1996), local abundance does not determine which gene copies locally occur (i.e., the diversity of gene copies). Genetic diversity is analogous to species diversity in that allelic richness is simply a summary of the presences/absences of each allele. Thus, because the loss or colonization of a given allele usually requires many generations, the relevant spatial scale is larger for allelic richness than for abundance. That the scale of effect is also inferred to be larger for genetic diversity than for presence/absence may result from a more rapid rate of local population extirpation (17 generation median wait time) than of allele extirpation (which occurred in our simulations at a median rate of one
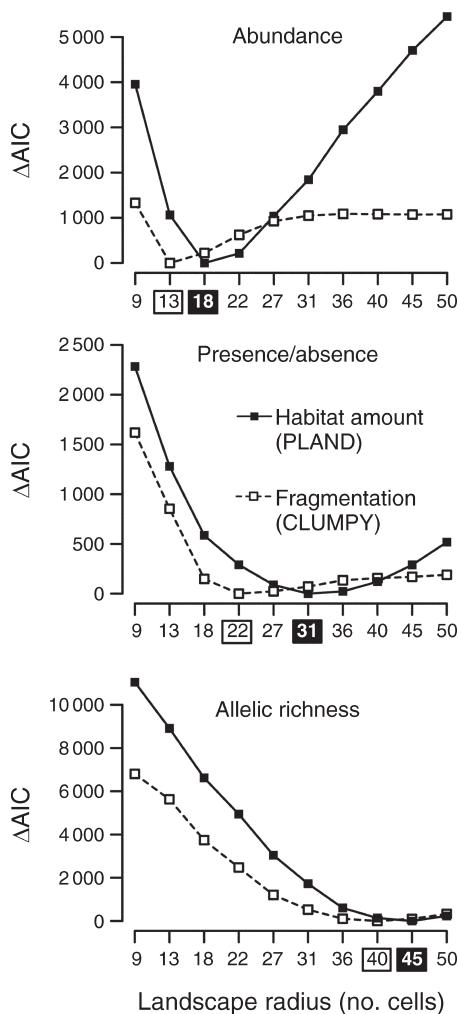
FIG. 3. Scales of landscape effect (S) calculated separately for habitat amount (PLAND) and fragmentation (CLUMPY) for demographic and genetic outcomes (where PLAND and CLUMPY are metrics that estimate scale-specific values of P and H, respectively). The value of S is smallest for abundance, medium-sized for presence/absence, and largest for allelic diversity. In all three cases, S is smaller for fragmentation than for habitat amount. Solid squares represent relative model fit (ΔAIC; the change in Akaike's information criterion) for regressions in which PLAND$_i$ was varied across 10 increasing radii, i (see *Methods: Statistical analysis: Scales of effect of landscape structure across distinct population outcomes* for regression model details). Hollow squares show ΔAIC for 10 regressions in which CLUMPY$_i$ was varied. The value of S for PLAND and CLUMPY is the spatial scale at which AIC was minimized. Note that S is highlighted on the x-axis for PLAND and CLUMPY using solid and hollow squares, respectively.

allele per 120 generations, calculated ignoring mutation). One reason that local species loss can occur more rapidly than allele loss is because the reduction of allelic richness due to loss of one allele can be reversed due to colonization by another allele (as long as the population persists). On the other hand, loss of the entire population cannot be rescued in this way, and thus, if landscape structure will not support a population,

extinction usually occurs relatively quickly. Thus, under this scenario, alleles are traveling on average over a larger region than are multiple generations of dispersing individuals during their respective wait times to extinction, resulting in a larger spatial scale for genetic diversity. We therefore suggest that it is through dispersal (for population persistence) and gene flow (for genetic diversity) that regional population dynamics are linked to local patterns of diversity and that it is the temporal scale of the process that determines the spatial scale of this linkage.

Relative effects of habitat amount and fragmentation on populations

As suggested in previous theoretical (Fahrig 1998, Flather and Bevers 2002, Bruggeman et al. 2010) and empirical studies (Dixo et al. 2009, Smith et al. 2011), the importance of habitat amount dominates the importance of habitat fragmentation for predicting demographic outcomes. Notably, we also found that this pattern holds for measures of genetic diversity. We note that the random dispersal behavior and inhospitable matrix simulated here likely maximize the chance of observing a strong negative effect of habitat fragmentation (Hovestadt et al. 2001); thus we have not likely underestimated its relative importance. From a conservation perspective, these results suggest that regardless of whether one is interested in preserving demographic or genetic diversity, efforts will be most productive if focused on preserving as much habitat as possible. The commonly held intuition that habitat fragmentation is a major contributor to genetic diversity decline may partly result from empirical studies that do not account for the effects of habitat amount when measuring the effects of habitat fragmentation on genetic diversity (Fahrig 2003). Furthermore, most landscape genetic studies to date have focused on the effects of landscape structure on gene flow and genetic divergence (Balkenhol et al. 2009), in which case fragmentation might play a larger role (e.g., Bruggeman et al. 2010, Jackson and Fahrig 2011, Cushman et al. 2012).

Dispersal effects on landscape–species relationships

When the matrix is hostile to fitness, short distance dispersers are expected to have an advantage due to their increased likelihood of settling in habitat (Murrell et al. 2002). This is particularly true when the proportion of matrix in the landscape is high (Hovestadt et al. 2001). Our findings that (1) increasing average dispersal distance (D_{av}) negatively influences abundance and (2) that this negative relationship is much stronger when habitat is scarce (slope $= -23.27$ and $R^2 = 0.63$ when $P = 0.1$ and $H = 0.5$) than when habitat is abundant (slope $= -8.89$ and $R^2 = 0.17$ when $P = 0.9$ and $H = 0.5$) are likely similarly due to reduced reproduction in species with higher D_{av} rates. The negative effect of D_{av} on abundance would likely decrease in cases where dispersal cost is reduced (Murrell et al. 2002), such as when
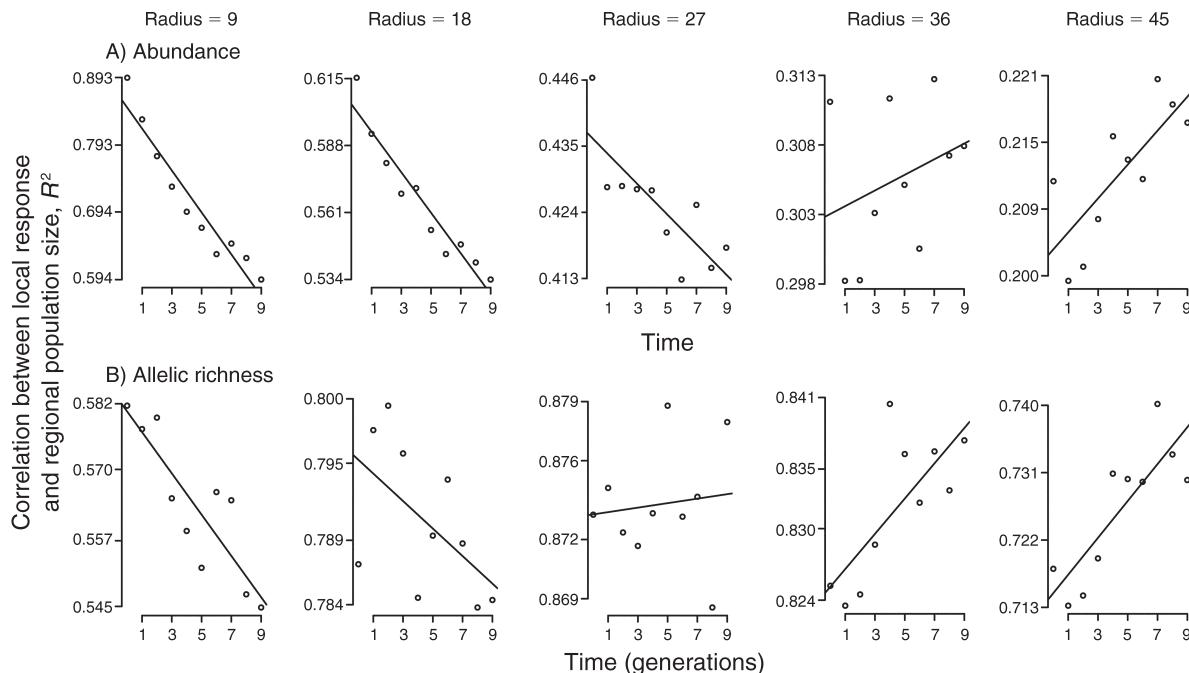
FIG. 4. Plots of the correlation between local (i.e., focal site) response ([A] abundance and [B] allelic richness) and regional population size, where regional population size was measured at 0–9 generations prior to local sampling, and where the radius of the landscape from which regional population size was measured was varied from 9 to 45 cells. These results show how increasing the lag time between regional and local sampling decreases the relative importance of regional population size in small landscapes and increases the relative importance of regional population size in large landscapes, suggesting that temporal and spatial scales of effect are linked. These plots were constructed from data collected from simulations run for 500 generations at average levels of habitat amount and fragmentation (0.5) and for the smallest dispersal distance ($D_{av} = 2$). Note the different scales on the y-axis. All relationships are significant at $P < 0.001$ except radius = 36 in A and radius = 27 in B.

organisms preferentially settle in habitat or when matrix is less hostile.

Despite its strong negative relationship with abundance, D_{av} had a negligible effect on population persistence and genetic diversity. These patterns are generally consistent with our proposed mechanism governing the different scales of effect observed among population outcomes. The more generations over which a process is regulated, the more closely the spatial extent over which these generations of individuals move will match the largest possible landscape radius (regardless of a species' D_{av}), making D_{av} less important. Thus, the larger time frames over which movement is relevant to the regulation of persistence and genetic diversity (as compared to abundance) may contribute to the smaller observed impacts of dispersal distance on these outcomes.

The impact of dispersal distance on presence/absence and genetic diversity might also be reduced due to positive effects of habitat connectivity that only arise at larger spatial scales. As D_{av} increases, demographic declines in local patches due to heightened emigration into the matrix (resulting in reduced local abundance) may be offset by increased connectivity among patches that can result in increased local persistence (e.g., due to

rescue effects; Brown and Kodric-Brown 1977) and larger local effective population sizes (Gilpin 1991).

Extrapolation to natural populations

This study is the first to build quantitative hypotheses about how the spatial scale at which landscape structure influences a population depends on the particular response being measured. Although these expectations are derived using simplified hypothetical species, they provide a set of concrete predictions that may hold in many real populations. In a recent simulation study, Jackson and Fahrig (2012) found that simulating "intelligent" dispersal behaviors (such as preferential settlement in habitat, exhibited by most vertebrates, or density dependent habitat selection, as seen in territorial animals) did not significantly change the scales of effect for abundance beyond those inferred under random dispersal behavior. Thus, our results may apply to many "informed" animal dispersers as well as plants (for which dispersal is often passive, as simulated here). However, Jackson and Fahrig (2012) found that one behavior, complete matrix avoidance, reduced scales of effect and lessened the difference in predictive power among scales. Thus, for groups such as many bird and insect species with strong gap avoidance behavior, scales of effect may be smaller and harder to define than

predicted here. Also, generalist species that are more tolerant of the matrix may exhibit increased population densities and decreased sensitivity to landscape structure than specialists (Fahrig 2001, Tischendorf et al. 2005), possibly resulting in smaller scales of effect (Jackson and Fahrig 2012).

Although variation in species traits and behaviors observed in natural populations may often influence scale of effect, our qualitative result that scale of effect is larger for genetic diversity than for presence/absence or abundance should be somewhat robust to this variation. For example, although we found that scales of effect generally increased with D_{av}, the rank order of these scales (i.e., S for genetic diversity > presence/absence > abundance) largely remained the same, regardless of D_{av} (see Appendix D). Nevertheless, the extrapolation of these results to any particular species group should await simulations that incorporate additional species traits and empirical studies that test our model predictions.

Implications for conservation

There is growing recognition that biodiversity management should be tailored to the spatial scale at which populations respond to the surrounding landscape and that this spatial scale will differ among species (Holland et al. 2004, Jackson and Fahrig 2012). Here, for simulated species we demonstrate that the spatial scale of effect for a given species also depends on the population outcome measured, suggesting that vastly different conclusions can be reached about the distances over which landscape alteration will affect populations simply based on how diversity is measured. This has important implications for conservation. For example, managing protected areas at a spatial scale known to regulate a species' abundance may underestimate the area of habitat needed to maintain the genetic diversity or even long-term persistence of that same species. Thus, we caution that scales of effect inferred from abundance data should be treated as the lower bound of a range of spatial extents that govern different aspects of biodiversity. In addition, the particularly wide reach of landscape effects on genetic diversity inferred here, which often go unnoticed, supports the contention that landscape structure should be managed within substantial regions surrounding protected areas (e.g., using buffer zones [Shafer 1999, Wade and Theobald 2010]), as landscape context will have lasting impacts on protected populations.

Literature Cited

Agresti, A., and B. Finlay. 2008. Statistical methods for the social sciences. Prentice Hall, Upper Saddle River, New Jersey, USA.

Balkenhol, N., F. Gugerli, S. A. Cushman, L. P. Waits, A. Coulon, J. W. Arntzen, R. Holderegger, and H. H. Wagner. 2009. Identifying future research needs in landscape genetics: where to from here? Landscape Ecology 24:455–463.

Bhargava, A., and F. F. Fuentes. 2010. Mutational dynamics of microsatellites. Molecular Biotechnology 44:250–266.

Brennan, J. M., D. J. Bender, T. A. Contreras, and L. Fahrig. 2002. Focal patch landscape studies for wildlife management: optimizing sampling effort across scales. Pages 68–91 in J. Liu and W. W. Taylor, editors. Integrating landscape ecology into natural resource management. Cambridge University Press, Cambridge, Massachusetts, USA.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449.

Bruggeman, D. J., T. Wiegand, and N. Fernandez. 2010. The relative effects of habitat loss and fragmentation on population genetic variation in the red-cockaded woodpecker (*Picoides borealis*). Molecular Ecology 19:3679–3691.

Cushman, S. A., and K. McGarigal. 2004a. Hierarchical analysis of forest bird species–environment relationships in the Oregon Coast Range. Ecological Applications 14:1090–1105.

Cushman, S. A., and K. McGarigal. 2004b. Patterns in the species–environment relationship depend on both scale and choice of response variables. Oikos 105:117–124.

Cushman, S. A., A. Shirk, and E. L. Landguth. 2012. Separating the effects of habitat area, fragmentation and matrix resistance on genetic differentiation in complex landscapes. Landscape Ecology 27:369–380.

DiLeo, M. F., J. D. Rouse, J. A. Dávila, and S. C. Lougheed. 2013. The influence of landscape on gene flow in the eastern massasauga rattlesnake (*Sistrurus c. catenatus*): insight from computer simulations. Molecular Ecology 22:4483–4498.

Dixo, M., J. P. Metzger, J. S. Morgante, and K. R. Zamudio. 2009. Habitat fragmentation reduces genetic diversity and connectivity among toad populations in the Brazilian Atlantic Coastal Forest. Biological Conservation 142:1560–1569.

Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? Ecological Modelling 105:273–292.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation 100:65–74.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Flather, C. H., and M. Bevers. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. American Naturalist 159:40–56.

Fletcher, R. J., Jr. 2006. Emergent properties of conspecific attraction in fragmented landscapes. American Naturalist 168:207–219.

Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. Conservation Biology 10:1500–1508.

Gilpin, M. 1991. The genetic effective size of a metapopulation. Biological Journal of the Linnean Society 42:165–175.

Hassell, M. P., and H. N. Comins. 1976. Discrete time models for two-species competition. Theoretical Population Biology 9:202–221.

Holland, J. D., D. G. Bert, and L. Fahrig. 2004. Determining the spatial scale of species' response to habitat. BioScience 54:227–233.

Hovestadt, T., S. Messner, and H. J. Poethke. 2001. Evolution of reduced dispersal mortality and "fat-tailed" dispersal

kernels in autocorrelated landscapes. Proceedings of the Royal Society B 268:385–391.

Jackson, H. B., and L. Fahrig. 2012. What size is a biologically relevant landscape? Landscape Ecology 27:929–941.

Jackson, N. D., and L. Fahrig. 2011. Relative effects of road mortality and decreased connectivity on population genetic diversity. Biological Conservation 144:3143–3148.

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

Martin, T. G., S. McIntyre, C. P. Catterall, and H. P. Possingham. 2006. Is landscape context important for riparian conservation? Birds in grassy woodland. Biological Conservation 127:201–214.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst, Massachusetts, USA. http://www.umass.edu/landeco/research/fragstats/fragstats.html

Murrell, D. J., J. M. J. Travis, and C. Dytham. 2002. The evolution of dispersal distance in spatially-structured populations. Oikos 97:229–236.

Neel, M. C., K. McGarigal, and S. A. Cushman. 2004. Behavior of class-level landscape metrics across gradients of class aggregation and area. Landscape Ecology 19:435–455.

Petit, R. J., and L. Excoffier. 2009. Gene flow and species delimitation. Trends in Ecology and Evolution 24:386–393.

Roland, J., and P. D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386:710–713.

Saupe, D. 1988. Algorithms for random fractals. Pages 71–113 in H.-O. Peitgen and D. Saupe, editors. The science of fractal images. Springer-Verlag, New York, New York, USA.

Shafer, C. L. 1999. US national park buffer zones: historical, scientific, social, and legal aspects. Environmental Management 23:49–73.

Smith, A. C., L. Fahrig, and C. M. Francis. 2011. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. Ecography 34:103–113.

Smith, A. C., N. Koper, C. M. Francis, and L. Fahrig. 2009. Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. Landscape Ecology 24:1271–1285.

Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83:1421–1432.

Thornton, D. H., L. C. Branch, and M. E. Sunquist. 2011. The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. Landscape Ecology 26:7–18.

Tischendorf, L., A. Grez, T. Zaviezo, and L. Fahrig. 2005. Mechanisms affecting population density in fragmented habitat. Ecology and Society. http://www.ecologyandsociety.org/vol10/iss2/art17/

Wade, A. A., and D. M. Theobald. 2010. Residential development encroachment on US protected areas. Conservation Biology 24:151–161.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Wilensky, U. 1999. Netlogo. Center for Connected Learning and Computer-Based Modelling. Northwestern University, Evanston, Illinois, USA. http://ccl.northwestern.edu/netlogo/

SUPPLEMENTAL MATERIAL

Appendix A

Supplementary methods: selecting a fragmentation metric and assessing collinearity (*Ecological Archives* E095-073-A1).

Appendix B

Simulation results for heterozygosity (*Ecological Archives* E095-073-A2).

Appendix C

Standardized and mean-centered regression coefficients (*Ecological Archives* E095-073-A3).

Appendix D

Plots of scales of effect across dispersal distance cohorts (*Ecological Archives* E095-073-A4).

Appendix E

Plots showing how local abundance responds more strongly to nearby and current population size than does genetic diversity (*Ecological Archives* E095-073-A5).

Supplement

AlleleScape: source code for the simulation model used in this study (*Ecological Archives* E095-073-S1).