

Effects of land use on population presence and genetic structure of an amphibian in an agricultural landscape

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Abstract

Context Species distributions are a function of an individual's ability to disperse to and colonize habitat patches. These processes depend upon landscape configuration and composition.

Objectives Using Blanchard's cricket frogs (*Acris blanchardi*), we assessed which land cover types were predictive of (1) presence at three spatial scales (pondshed, 500 and 2500 m) and (2) genetic structure. We predicted that forested, urban, and road land covers would negatively affect cricket frogs. We also predicted that agricultural, field, and aquatic land covers would positively affect cricket frogs.

Methods We surveyed for cricket frogs at 28 sites in southwestern Ohio, USA to determine presence across

different habitats and analyze genetic structure among populations. For our first objective, we examined if land use (crop, field, forest, and urban habitat) and landscape features (ponds, streams, and roads) explained presence; for our second objective, we assessed whether these land cover types explained genetic distance between populations.

Results Land cover did not have a strong influence on cricket frog presence. However, multiple competing models suggested effects of roads, streams, and land use. We found genetic structuring: populations were grouped into five major clusters and nine finer-scale clusters. Highways were predictive of increased genetic distance.

Conclusions By combining a focal-patch study with landscape genetics, our study suggests that major roads and waterways are key features affecting species distributions in agricultural landscapes. We demonstrate that cricket frogs may respond to landscape features at larger spatial scales, and that presence and movement may be affected by different environmental factors.

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Introduction

The distribution of a species across a landscape is regulated by two basic processes: extinction and

colonization (Hanski 1998). These processes are influenced by the composition and configuration of land cover types within landscapes, which must be suitable for individuals to disperse through and settle within (Pulliam 2000; Holt et al. 2005; Baguette and Van Dyck 2007). However, the vast majority of species distribution models correlate environmental variables with patterns of presence or abundance of a species, but do not directly address the process of dispersal (Elith and Leathwick 2009). Failure to consider the importance of dispersal could compromise our ability to predict long-term population dynamics as well as how species distributions might shift in response to habitat alteration or climate change. Indeed, recent research has demonstrated land cover that predicts presence does not necessarily predict successful dispersal between patches (i.e. 'functional connectivity'; Baguette and Van Dyck 2007; Spear et al. 2010; Mateo-Sánchez et al. 2015; but see Stevens et al. 2006). Further complicating the study of species distributions is the fact that responses of individuals to environmental factors often depend on spatial scale and the behavior or process in question (Pope et al. 2000; Angelone et al. 2011; Thornton et al. 2011). With regards to dispersal, for example, land cover types that are harder to move through, or are avoided at small spatial scales, may not be predictive of functional connectivity across a larger landscape (Stevens et al. 2006; Reding et al. 2013). It may be that the operative spatial scales for certain behaviors (i.e., habitat selection vs. dispersal) may differ. For these reasons, studies that account for settlement and dispersal across spatial scales are needed to accurately reflect the role of landscape composition and configuration on species distributions. Such studies are especially important to predict species responses to landscapes that are modified by anthropogenic activities.

One type of modified landscape are agricultural areas. Agriculture represents a dominant land use around the world (Ramankutty et al. 2008) and, for example, can exceed 60 % of land use in areas like the Midwest United States (Nickerson et al. 2011). Agricultural landscapes are often a mosaic of natural and modified land cover types, and are characteristically fragmented (Bennett et al. 2006). The composition and configuration of land cover within these landscapes can have significant consequences for the species native to these areas. Land uses, including

urban development and agricultural practices, can alter extinction and colonization probabilities. The likelihood of extirpation can increase due to degraded habitat quality and reduced recruitment (Bishop et al. 1999; Donald et al. 2001); the ability of individuals to colonize habitats can also be reduced because roads, cropland, and urban areas often act as barriers for dispersal (Goldberg and Waits 2010; Holderegger and Di Giulio 2010; Loos et al. 2014). However, responses to land cover are often species- and landscape-specific (Chetkiewicz et al. 2006; Baguette and Van Dyck 2007). For example, cropland, which is generally considered a dispersal barrier, may not negatively impact functional connectivity for some amphibian populations (Purrenhage et al. 2009; Goldberg and Waits 2010). Because the extent of agricultural landscapes is predicted to increase in the future with increasing human population (Tilman et al. 2001), it is vital that we understand how species respond to land cover and other features across these landscapes.

Pond-breeding amphibians depend on landscape connectivity at multiple spatial scales, which makes them ideal for investigating the impacts of land cover types within mosaic landscapes on wildlife. At smaller scales, aquatic and terrestrial habitats must be connected for seasonal migrations between breeding and overwinter habitats (Pope et al. 2000). At larger spatial scales, many species persist as patchy populations or metapopulations, and experience high rates of extinction and colonization (Trenham et al. 2003; Smith and Green 2005); therefore breeding habitats must be connected to maintain regional persistence. Despite the importance of dispersal and landscape connectivity, many distribution models used for species management, including GAP analyses (which compare the overlap of species distributions and protected habitat) conducted by state and federal agencies, generally focus only on species presence and the availability of aquatic habitats for amphibians (e.g. Southeast GAP Analysis Project 2014). Thus, comprehensive studies that account for habitat requirements across all life stages should lead to the development of more effective management strategies.

The objectives of our study were to assess how presence and functional connectivity of a declining amphibian species are affected by land cover types in landscapes dominated by agriculture. Blanchard's cricket frog (*Acris blanchardi*) is a pond-breeding anuran that is distributed across much of the

midwestern United States, but is experiencing decline across parts of its range (Gray et al. 2005; Lehtinen and Skinner 2006). It is an annual species (Lehtinen and MacDonald 2011), which means a single year of reproductive failure may equate to local extirpation in the absence of immigration. A short life span, together with an estimated maximum dispersal distance of 1.3 km (Gray et al. 2005) and annual colonization and extinction rates of 4 and 7 %, respectively (Lehtinen and Witter 2014), indicate that cricket frogs may be particularly dependent on dispersal for persistence. Previous studies have demonstrated that cricket frogs are more likely to be found in open canopy ponds and streams and are less likely to be found in highly urbanized areas (Lehtinen and Skinner 2006; Trumbo et al. 2012; Lehtinen and Witter 2014); cricket frog metamorphs also oriented away from forested habitat in a movement study (Youngquist and Boone 2014). We predicted that increases in percent forest, percent urban, and road presence would negatively affect movement and, therefore, reduce the likelihood of cricket frog presence. We also predicted that an increased proportion of field habitats, stream density, and pond density, would enhance dispersal and, thus, positively influence cricket frog presence. Agricultural habitat may have a neutral or positive effect on cricket frog movement and presence because cricket frogs do not appear to avoid moving through row crops (Youngquist and Boone 2014) and are commonly found in agricultural habitats (Lehtinen and Witter 2014).

We conducted a two-part study in southwestern Ohio. First, we examined whether or not surrounding land cover affected cricket frog presence within ponds; we also assessed the spatial scale at which different features were most predictive of abundance. Second, we used landscape genetics to assess fine-scale patterns of genetic structure. Landscape genetics combines population genetics with landscape ecology, creating a powerful tool to test hypotheses of how landscape features affect dispersal (Storfer et al. 2010). We used genetic distance as a proxy for dispersal with the assumption that genetically similar populations are primarily the result of successful dispersal and breeding events (i.e. gene flow; e.g. Storfer et al. 2010; Van Strien et al. 2012). While genetic similarity may be the result of recent subdivisions and too little time for drift to occur, Ohio has been predominantly farmland since at least 1950 (Nickerson et al. 2011) and by 1980, 90 %

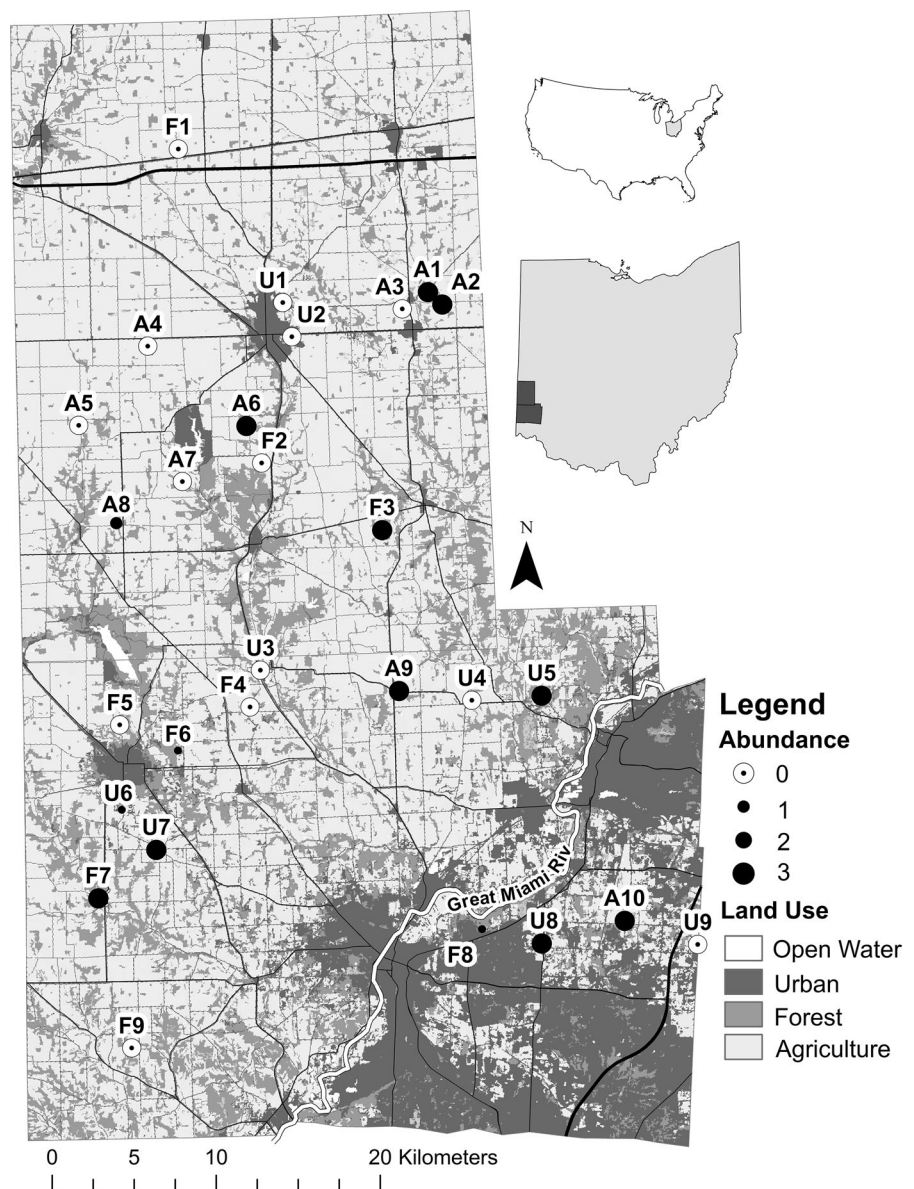
of its natural wetlands were lost (Dahl 1990). Because cricket frog generation time is one year, it is likely that enough generations have passed for drift to occur in response to land use changes. This approach allowed us to understand how landscape features impact the distribution of an amphibian in an agricultural landscape.

Methods

Sampling design

We conducted visual and call surveys at 28 permanent ponds in Butler and Preble counties, Ohio, USA, June 7–August 5, 2010 (Fig. 1). While this study area is near the edge of their eastern range in central Ohio, cricket frogs are common (Lehtinen and Skinner 2006). We used a stratified random design to select sites based on pond size and habitat surrounding the ponds (forest, agriculture, or urban habitat). We created a comprehensive water body dataset within the study area by digitizing 2009 aerial photographs of the two counties (total area: 2320 km²) in ArcGIS (ESRI v 9.3). We only included ponds that were between 200 and 5000 m². Ponds were then categorized based on the majority (>60 %) of land cover surrounding each pond within a 50 m buffer, which is the area where cricket frogs spend the majority of the year (Gray et al. 2005). We used the 2001 National Land Cover Database (NLCD; Homer et al. 2007) to initially categorize ponds and final selections were verified to ensure correct classification. We then used a random number generator to order ponds within a land cover category to use in the study and sampled those that we obtained landowner permission to visit. We selected ten agricultural ponds (including hay, pasture, and row crop surroundings), nine forested ponds, and nine urban ponds. The unequal sample size was the result of logistics (owner permission). For selection purposes, agricultural ponds included hay and pasture in the NLCD dataset because many ponds adjacent to row crop were actually in nearby grassy fields or surrounded by grassy buffers; all agricultural sites selected for surveys were within 100 m of row crop agriculture and most were within 50 m. The surface area of ponds varied between 426 m² and 4728 m² (average ± SE: 1648 ± 43 m²) and ponds were at least 1 km apart (average ± SE: 23.7 ± 0.6 km).

Fig. 1 Sites surveyed for the presence of cricket frogs and subsequent population genetic analyses. Size and shading of dots indicates relative abundance: 0 = 0 collected, 1 = 1–5 collected, 2 = 6–10 collected, 3 = more than 10 collected. Categories (A agriculture, F forest, U urban) are based on the 50 m buffer. ‘Agriculture’ includes row crop, hay, and pasture. *Thin black lines* are state and US highways; *thick black lines* are interstates. Map insets show location of Ohio within the USA and location of the two county study area in southwest Ohio



We assessed cricket frog presence using call surveys and visual inspections June–August 2010. Surveys began at least 1 hour after sunset on dry, windless nights above 10 °C (Davis 2009). We waited 5 min after our arrival at a pond before beginning a 5 min call survey. Following call surveys, we visually inspected each pond for adult and juvenile cricket frogs for a combined time of up to six person-hours per site. While presence of calling males always indicated the presence of individuals, the absence of calling males did not always indicate the absence of

individuals; in July and August, 5 out of 11 calls surveys were false negatives. We collected tissue samples from individuals for genetic analyses by clipping the smallest toe on each front foot. We immediately released individuals at the point of capture. Tissues were stored in 95 % ethanol.

Study 1: effects of land cover on presence

Our first objective was to assess whether landscape features predicted the presence of cricket frogs. We

first tested for spatial autocorrelation in cricket frog presence using Moran's *I* in ArcGIS. We then determined the composition of land use and land cover at three scales: pond-shed (average area \pm SE = 3.2 ± 0.6 ha), 500 m buffer (78.5 ha), and 2500 m buffer (1963 ha) around surveyed ponds. These three scales represent (1) the area that drains into the pond, (2) the area where amphibians are most densely congregated and the scale at which cricket frogs are most likely to interact with upland habitat to overwinter (Gray 1971; Semlitsch and Bodie 2003) and (3) the scale at which an individual cricket frog may interact with the surrounding landscape throughout its lifetime, approximately twice the maximum recorded dispersal distance by cricket frogs (Gray et al. 2005). Pond-sheds were calculated with the ArcHydro data model in ArcGIS, using the 1/9 arc-second digital elevation model (USGS 3D Elevation Program) and high-resolution flowlines (USGS National Hydrography Dataset).

At each scale we calculated proportion crop land (row crop), field (grassland, pasture, and hay), forest (deciduous, coniferous, and mixed forest), and urban (low, medium, and high intensity). Land use was calculated from the 2001 NLCD (Homer et al. 2007). We also calculated pond density (number of ponds km^{-2}), stream density (m km^{-2}), and road density (m km^{-2}) at each spatial scale. These seven variables were used in univariate and multivariate models, described below. Ponds were digitized from 2009 aerial images, stream layers were obtained from the high resolution National Hydrography Dataset (USGS), and road layers were obtained from the Nation Transportation Dataset (USGS; U.S. Census Bureau).

We used logistic regression to test for effects of landscape context on cricket frog presence. We built 11 landscape models to test for individual and combined effects of land cover types on presence at three spatial scales. We built seven univariate models, three multivariate models, and a null model that included only the intercept. The multivariate models included a land use model (percent crop + percent forest + percent urban), a discrete features model (pond density + stream density + road density), and a full model (crop + forest + pond + stream + road). To reduce multicollinearity, as measured by variance inflation factors, we removed percent field from all multivariate models, percent urban from the full model, and pond

density from the full model at the 2500 m buffer scale. Percent field and pond density were correlated with percent crop (Spearman's rank $r > 0.70$). We compared models using bias-corrected Akaike information criteria (AICc), and considered that models with $\Delta\text{AICc} < 2$ (the difference in AICc between the candidate and the most parsimonious model) were similarly parsimonious; we also considered model weights in model evaluation. AIC-based model averaging was used to estimate parameters. Each scale (pond-shed, 500 m, or 2500 m) was tested separately because of the relatively small sample size ($N = 28$). We used the packages MASS (Venables and Ripley 2002) and AICcmodavg (Mazerolle 2015) in R (v3.1.0; R Core Team 2014).

Study 2: effects of land use on population genetics

Our second objective was to test whether landscape features affected functional connectivity, using genetic distance as a response. To ensure an adequate estimation of allele frequencies, we only used sites where we collected at least ten individuals for all genetic analyses; as a result we genotyped 182 individuals from ten pond sites. We extracted genomic DNA from toe clips using a standard phenol–chloroform procedure. We used single and multiplex polymerase chain reactions (PCR) to amplify ten microsatellite loci (Arc-3 and Arc-2, Arc-17 and Arc-36, Arc-28, Arc-14, Arc-34, Arc-29, Arc-8, and Arc-35), following the protocol of Beauclerc et al. (2007). Forward primers were labeled with fluorescent dyes (6-FAM, NED, HEX, or PET) for visualization. We performed fragment analyses on an ABI 3130 lx Genetic Analyzer using LIZ600 size standard (Life Technologies). We used Peak Scanner (v1.0; Life Technologies) to score allele fragment lengths and TANDEM (v1.07; Matschiner and Salzburger 2009) to assign integer values to fragment lengths. We tested for linkage disequilibrium and deviation from Hardy-Weinberg expectation with Bonferonni correction for both, using exact tests in Genepop (v4.2; Raymond and Rousset 1995; Rousset 2008). We tested for the presence of null alleles (fragments that failed to amplify and, thus, were not detected) using Micro-Checker (Van Oosterhout et al. 2004). We calculated population summary statistics in GenAlEx (v6; Peakall and Smouse 2006, 2012); these included mean number of alleles (N_A), number of private alleles (N_P), observed and expected heterozygosity (H_O and H_E),

and inbreeding coefficient (F_{IS}) for each population. To correct N_A for sample size bias, we estimated allelic richness (rarefied mean number of alleles per locus; A_R) with a standardized sample size of 11 individuals (smallest sample size across populations) in FSTAT (v2.9.2.3; Goudet 1995). We calculated pairwise genetic distance between pond sites (F_{ST}) for use in regression analyses (GenAlEx v6).

Population structure

We tested for the presence of genetic clustering using STRUCTURE (v2.3.4; Pritchard et al. 2000), which creates a Bayesian model based on allele frequencies that probabilistically assigns individuals to genetic clusters independent of sampling location and then infers the number of distinct genetic populations (k). We used a batch run in which we tested for $k = 1$ through 10 (because we had 10 sites), with 10 replicates per each k ; each run had a burn-in period of 2×10^5 iterations (initial iterations that were discarded) followed by 2×10^6 iterations (sufficient for model convergence; Gilbert et al. 2012); all other parameters were set to default. Using STRUCTURE HARVESTER (Earl and vonHoldt 2012), we evaluated the most likely number of population clusters (k) based on the maximum log probability ($\ln \Pr(X|k)$), as well as the second order rate of change (Δk ; Evanno et al. 2005). In general, Δk detects the strongest patterns of population structure, while log probability detects finer scale population structure (Evanno et al. 2005; Coulon et al. 2008a; Fisher-Reid et al. 2013). We used CLUMPP (v1.1.2; Jakobsson and Rosenberg 2007) and DISTRUCT (v1.1; Rosenberg 2004) to average across runs and visualize the most likely values of k .

Landscape genetics

To examine effects of land cover on genetic structure, we tested for isolation-by-resistance (IBR; McRae 2006) among populations by regressing landscape resistance distances with genetic distance (F_{ST}). Isolation-by-resistance assumes that some landscape features are more permeable (less resistant) to dispersing individuals than others. Landscape features are assigned different resistance values and pairwise landscape distances are calculated based on least-resistant paths between populations. To prevent bias

associated with assigning weights to each land cover layer when creating a multivariate landscape surface (Spear et al. 2010; Zeller et al. 2012), we tested the singular effects of different landscape features as well as a combined model that assumed equal weights.

We tested nine models corresponding to resistances of different land covers that fell into four categories: corridor, barrier, full, and null (Table 1). We constructed four corridor models (Field, Crop, Stepping Stone, and Riparian) based on the predictions that aquatic features (streams and ponds), field (natural grasslands, hay, and pasture) and row crop land uses would enable dispersal (Lehtinen and Witter 2014; Youngquist and Boone 2014). Stepping Stone and Riparian models were based on aquatic features. For the Riparian Model, we calculated distance from the nearest stream or pond at each cell; movement becomes more costly as individuals move further away from aquatic features. In the Stepping Stone Model, we used a binary landscape where only aquatic features were permeable to dispersal. We constructed three barrier models (Highway, Urban, and Forest) based on the predictions that major roads, urban land cover, and forested land cover would hinder dispersal (Holderegger and Di Giulio 2010; Trumbo et al. 2012; Youngquist and Boone 2014). For the Highway Model, we assigned resistance values for major roads based on relative traffic densities (i.e., state routes, US highways, and Interstate highways; Ohio Department of Transportation). For the Combined Model, we added three models into a single resistance layer: land cover (where each cell was assigned a resistance value based on the majority land cover), Highway Model, and Riparian Model. We constructed a single null model, the Isolation-by-distance Model, in which all land uses and features were equally permeable to dispersal. Landscape resistance surfaces were created in ArcGIS with a 100 m cell. This cell size enabled us to size to increase computational processing speed (needed for resistance distance analysis) and calculate percentages of land cover type from 2001 NLCD, which has a 30 m cell size, while retaining relatively high resolution across the landscape. Land cover, road, pond, and stream layers were the same as those used in Study 1.

We used Circuitscape (v4.0; McRae 2006; McRae et al. 2008) in ArcGIS to calculate resistance distances between populations for each model. Circuitscape uses circuit theory to model the flow of current (i.e.

Table 1 Description of mixed effects models used for testing effects of landscape resistance on genetic distance

Hypothesis category	Model	Resistance scale
Corridor	Stepping stone	Streams and ponds = 1; terrestrial = 100
	Riparian ^a	Nearest to aquatic features = 1; farthest = 100
	Field	100 % field = 1; 0 % field = 100
	Crop	100 % crop = 1; 0 % crop = 100
Barrier	Highway ^b	State route = 50; US highways = 75; interstate = 100
	Urban	0 % urban = 1; 100 % urban = 100
	Forest	0 % forest = 1; 100 % forest = 100
Full	Combined ^c	Corridor = 3; barrier = 264
Null	Isolation-by-distance	1

Percent land cover and riparian resistance were continuous variables and all others were categorical. We used three scales: 1–10, 1–100, and 1–10,000. This table shows resistance based on 1–100 range. The full model is a summation of resistance for majority land cover, highway, and riparian layers; the scale is relative to complete corridor and complete barrier

^a For the Riparian model, we reclassified distance from stream and ponds into 10 groups and assigned resistance accordingly. The maximum distance between aquatic features was 2163 m; distances 0–216 m from aquatic features had a resistance of 1 and distances 1950–2163 m had the maximum resistance

^b Relative resistance values for state routes, US highways, and interstates were based on differences in traffic counts between road types and values were either square-rooted or squared for the 1–10 and 1–10,000 resistance ranges, respectively; all non-highway cells were assigned a value of 1

^c The full model is a summation of resistance for majority land cover, highway, and riparian layers. The scale is relative to complete corridor and complete barrier; the minimum resistance is 3 and max is 28, 264 and 24,096 for each scale

dispersal) between populations through a resistance surface and allows for multiple pathways. We used the pairwise mode and eight-neighbor connection option. We initially assigned landscape resistances for each land-cover layer on a scale of 1 to 100 (1 = completely permeable and 100 = complete barrier to dispersal; Table 1). However, because calculating the resistance distance is sensitive to the range of values used for parameterization (Koen et al. 2012b), we created two additional scales of landscape resistances by taking the square-root and square of the first dataset (i.e., scales of 1–10 and 1–10,000 respectively; e.g. Koen et al. 2012a, b; Van Strien et al. 2012). Because the combined model was the summation of three layers, resistances ranged from 3 to 28, 3 to 264, and 3 to 24,096.

We used linear mixed effects models (Van Strien et al. 2012) to determine which IBR models best explained pairwise genetic distance (F_{ST}). This method accounts for the non-independence of pairwise distances using maximum-likelihood population effects modeling and estimates parameters using residual maximum-likelihood criteria (REML; Clarke et al. 2002). Each predictor variable (effective resistance distance) was centered around the mean and

tested individually in univariate models. We compared models using R^2_{β} (Edwards et al. 2008), calculated from the Kenward-Rogers approximation of F and denominator degrees of freedom (Kenward and Roger 1997): the mixed model with the fixed effect (landscape resistance distance) and random effect (covariate structure of distance matrix) was compared to a null model with only an intercept and random effect (Edwards et al. 2008). We used R^2_{β} to compare models rather than AIC because AIC is not suitable to compare fixed effects when using REML (Clarke et al. 2002). The different scales (1–10, 1–100, and 1–10,000) were compared separately. We used the packages lme4 (Bates et al. 2014) and pbkrtest (Halekoh and Højsgaard 2014) in R v3.1.0 (R Core Team 2014).

Results

Study 1: effects of land use on presence

Across all sites, average proportion crop, field, forest, and urban, along with pond density, were similar

among the three spatial scales, while density of streams and roads was greater at the 2500 m scale (Table 2). The increase in streams and roads from pond-shed to 2500 m resulted because most sites were at least 300 m from these features. The range and standard error of land use and pond density were narrower at the 2500 m scale, indicating that the landscape mosaic became more similar among sites at the larger spatial scale. Most focal ponds, even if in an urban or forested area near the pond, were embedded in landscapes that consisted mostly of open habitat (crop and fields). Therefore, landscape composition at larger spatial scales was similar.

We detected cricket frogs at 50 % of the sampled sites: 6/10 field, 4/9 urban, 4/9 forest. There was no spatial autocorrelation among sites with cricket frogs (Moran's $I = 0.02$, $p = 0.72$), indicating that populations were not spatially clustered in the study region. There was weak support for some land cover types being predictive of cricket frog presence at different spatial scales (Table 3). At the pond-shed scale, the null model had the best support. At the 500 m scale, there were four competing models that explained the presence of cricket frogs. The null model again had the best support; road density and percent crop had a negative association with cricket frog presence; and percent forest had a positive association with cricket frogs. At 2500 m, the null model ranked first, followed by stream density, percent crop, pond density, percent field, and percent urban. Overall, the null model was 30–40 % more likely to be the best model compared to the next competing model (Table 3).

Study 2: effects of land use on population genetics

Overall, two sites at one locus (Arc-29) departed from Hardy-Weinberg equilibrium ($p < 0.0005$) and two pairs of loci showed signs of linkage disequilibrium at one or two sites (Arc-3/Arc-14; Arc-36/Arc-8); these could result from small sample sizes, genetic drift, or outcrossing. Acr29 had null alleles at three sites and Acr35 had null alleles at one site. However, there were no overall patterns and removal of Acr29 did not significantly alter results (data not shown); therefore, we used all loci in further analyses. The ten loci had between 4 and 27 alleles each (average = 12.5 ± 2.3) across all samples. Mean allelic richness and heterozygosity over the ten loci were similar across sites (Table 4). All pairwise F_{ST} values were significantly different from zero ($p < 0.0001$) and ranged from 0.03 to 0.15 (Table S1 in supplementary material). Site U5 had consistently higher pairwise F_{ST} values compared to other sites as well as fewer alleles per locus and lower observed heterozygosity (Table 4), indicating that this site was the most genetically isolated of the sites.

STRUCTURE analyses showed evidence of genetic clusters. Using the Δk method, STRUCTURE showed five clusters across the 10 focal ponds ($k = 5$; Table 4; Figs. 2, S1). The five clusters showed a pattern in which Clusters 1 and 4 were separated from all others by US highways and Cluster 5 was separated from all others by the Great Miami River (Fig. 2). Cluster 2 was bisected by a US highway. The log probability method supported the presence of nine

Table 2 Average \pm SE and ranges of land use and landscape features at two spatial scales across all surveyed sites around focal ponds

Scale	Urban (%)	Forest (%)	Field (%)	Crop (%)	Pond (N/km ²)	Stream (m/km ²)	Road (m/km ²)
Pond-shed							
Average \pm SE	28.8 \pm 6.7	17.1 \pm 5.9	12.3 \pm 4.7	39.2 \pm 8.4	0.6 \pm 0.6	0	1691.3 \pm 466.0
Range	0–100	0–100	0–83.3	0–100	0–17.9	0	0–9103.7
500 m							
Average \pm SE	16.7 \pm 3.4	19.1 \pm 3.5	20.4 \pm 4.2	42.9 \pm 6.3	2.5 \pm 0.6	1028.5 \pm 163.1	3273.8 \pm 355.8
Range	0–72.0	0–61.9	0–68.5	0–94.2	0–14.2	0–2475.8	1412.1–9743.1
2500 m							
Average \pm SE	15.8 \pm 2.7	17.7 \pm 1.8	21.5 \pm 3.3	43.9 \pm 4.8	2.1 \pm 0.3	1178.7 \pm 61.6	3174.4 \pm 279.3
Range	3.7–59.0	3.0–39.0	0–49.7	5.5–90.6	0–5.8	559.1–1726.9	1722.0–6919.4

Table 3 Competing models ($\Delta\text{AICc} \leq 2$) for effects of landscape variables on cricket frog presence from logistic regression at the pond-shed, 500 m and 2500 m spatial scales

Scale	Model	ΔAICc	Model weight	-LL	Parameter (SE)
500 m	Null	0.0	0.43	19.41	N/A
	Null	0.0	0.25	19.41	N/A
	Road density	0.6	0.18	18.56	-0.0003 (0.0003)
	Forest	1.3	0.13	18.88	2.16 (2.23)
2500 m	Crop	2.0	0.09	19.24	-0.60 (1.26)
	Null	0	0.22	19.41	N/A
	Stream density	0.48	0.17	18.49	0.0018 (0.0014)
	Crop	1.15	0.12	18.82	-1.73 (1.68)
	Pond density	1.3	0.11	18.89	0.23 (0.23)
	Field	1.68	0.09	19.09	1.77 (2.23)
	Urban	1.97	0.08	19.23	1.51 (2.93)

LL is log likelihood. Parameter estimates are model averages; unconditional SE are in parentheses

Table 4 Sample size (N), average number of observed alleles (N_A), rarified allelic richness (A_R) number of observed private alleles (N_P), observed and expected heterozygosity (H_O , H_E), and inbreeding coefficient (F_{IS}) for each site included in genetic analyses

Cluster	Site ID	N	N_A	A_R	N_P	H_O	H_E	F_{IS}
1	A1	11	5.6	5.5	1	0.745	0.66	-0.137
	A2	17	5.6	4.9	2	0.64	0.596	-0.059
2	A6	20	7.1	5.9	1	0.746	0.732	-0.035
	F3	12	4.7	4.5	2	0.658	0.634	-0.036
	A9	16	6.2	5.5	8	0.637	0.665	0.020
3	U5	20	3.9	3.5	0	0.538	0.534	-0.003
4	U7	21	6.6	5.2	4	0.591	0.624	0.041
	F7	20	6.5	5.4	2	0.668	0.686	0.078
5	U8	24	5.0	4.4	0	0.676	0.629	-0.067
	A10	21	5.8	4.7	3	0.604	0.645	0.071

The first column indicates clustering based on STRUCTURE results for $k = 5$

clusters (Figs. 2, S1), indicating that each sampled site was a unique genetic cluster separated by state routes and US highways; the exception was the clustering of sites A1 and A2, which were not separated by a major road and formed a single genetic population. Overall, this suggests that populations were moderately to highly isolated and that US highways and the Great Miami River played a role in isolating these populations.

The best-supported mixed effects model, regardless of specification of resistance values, was the Highway Model ($R_\beta^2 = 0.67$, $p < 0.0001$; Table 5); state routes and US highways were impediments to gene flow. The Isolation-by-distance Model was the second best model, overall, indicating that all other land uses and landscape features were permeable to dispersal. Using

different ranges of resistance values affected the number and width of paths calculated by Circuitscape such that paths became fewer and more strictly defined as the maximum resistance value increased (Fig. 3). These differences resulted in Forest, Riparian, and Stepping Stone models being sensitive to the initial specification of resistances. While forest was supported as a barrier to gene flow when resistances were 1–10 ($R_\beta^2 = 0.45$, $p < 0.0001$), it was not the case when the maximum resistance was 100 or 10,000 (1–100: $R_\beta^2 = 0.00$, $p = 0.92$; 1–10,000: $R_\beta^2 = 0.01$, $p = 0.34$; Table 5). The Riparian and Stepping Stone models were ranked 3rd at the 1–10 and 1–100 ranges, but were least supported and not significant when resistances ranged

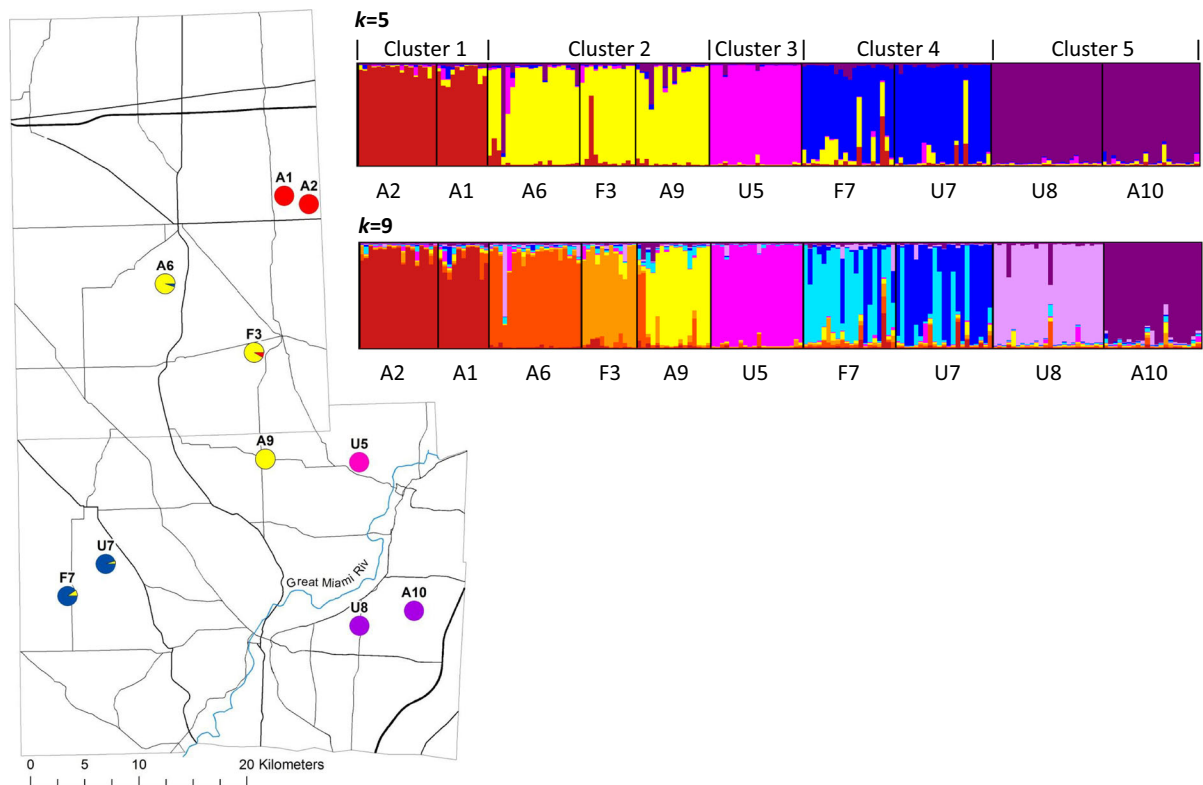


Fig. 2 Genetic cluster results from STRUCTURE, showing $k = 5$ and $k = 9$. Each bar represents an individual and colors correspond to the probability of that individual being assigned to a given cluster. Pie charts on map correspond to $k = 5$

proportion of individuals assigned to each of the five clusters; labels correspond to the surveyed sites. Major roads are depicted as black lines; thinnest state route, medium US highway, thickest interstate. Blue line is the Great Miami River

Table 5 Mixed effects model ranking based on R^2_{β} (list order is based on R^2_{β} across all scales) for effects of landscape features on genetic distance (F_{ST})

Model	Range of resistances					
	1–10		1–100		1–10,000	
	R^2_{β}	p	R^2_{β}	p	R^2_{β}	p
Highway (B)	0.67	<0.0001	0.67	<0.0001	0.67	<0.0001
Isolation-by-distance (N)	0.60	<0.0001	0.60	<0.0001	0.60	<0.0001
Field (C)	0.59	<0.0001	0.57	<0.0001	0.54	<0.0001
Urban (B)	0.46	<0.0001	0.46	0.003	0.55	0.01
Row crop (C)	0.39	<0.0001	0.37	0.003	0.34	0.04
Riparian (C)	0.59	<0.0001	0.57	<0.0001	0.00	0.95
Stepping stone (C)	0.59	<0.0001	0.56	<0.0001	0.03	0.64
Combined (C + B)	0.56	<0.0001	0.36	<0.0001	0.07	0.37
Forest (B)	0.45	<0.0001	0.00	0.92	0.11	0.34

Model descriptions are in Table 1. Bolded R^2_{β} are significant based on log likelihood ratio test
B barrier hypotheses;
C corridor hypotheses;
N null hypothesis

from 1 to 10,000 ($R^2_{\beta} < 0.03$). Field, Urban, and Crop models significantly explained genetic distance across all ranges of resistance values ($p < 0.04$). However,

based on R^2_{β} , they did not explain variation better than the uniform resistance model (Table 5). The Combined Model was generally ranked low and did not

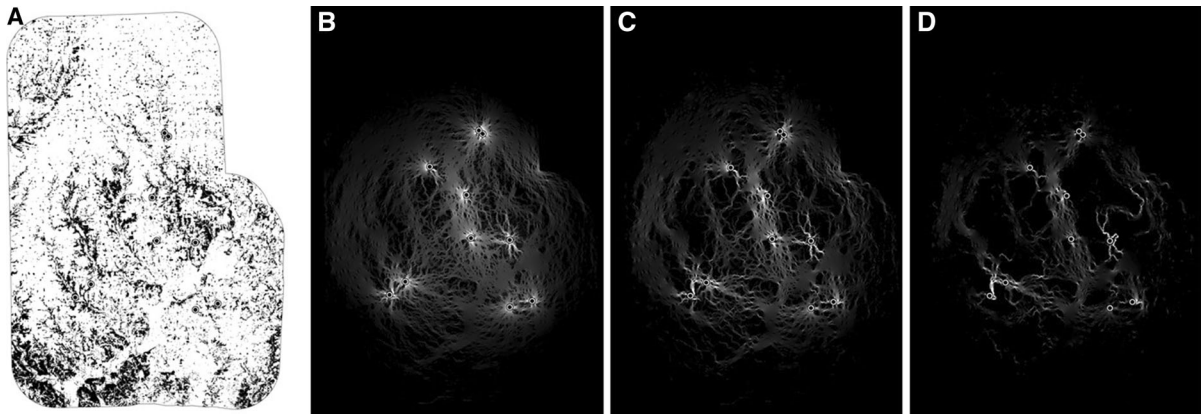


Fig. 3 Relationship between parameterizing resistance values and Circuitscape current maps, which are used to calculate average effective resistance distance. All figures relate to the hypothesis that forest is a barrier. High current paths (*white*) are analogous to least cost paths. **a** Resistance surface of percent forest. *Black* high resistance; *white* low resistance. **b** Current

map for resistance values 1–10. **c** Current map for resistance values 1–100. **d** Current map for resistance values 1–10,000. For **b–d**, *black* low current and *white* high current. **b–d** demonstrate that higher contrast between high- and low-resistance values (larger range) results in narrower, more restricted paths

explain genetic distance better than the univariate models (Table 5).

Discussion

By combining landscape approaches with population genetics, we demonstrate that cricket frog distribution was affected by the composition of the landscape. Our results indicate that the effects of specific landscape features depend on the metric in question—in this case, presence and functional connectivity. Furthermore, results from this study, in conjunction with other research (e.g. Pope et al. 2000; Angelone et al. 2011; Thornton et al. 2011), point to the importance of considering spatial scale when studying effects of environmental factors on species distributions.

Counter to our predictions, our results indicate that cricket frog presence was not strongly affected by the surrounding landscape context. Support for the null model (intercept only) at all scales suggests that all land cover types were equally likely to influence presence and relative abundance of cricket frogs at smaller spatial scales. These results could be explained by cricket frog tadpoles not being directly impacted by land use near ponds (Youngquist and Boone, unpublished; but see Puglis and Boone 2012). However, there were multiple competing models at the 500 and 2500 m spatial scales. Model weights were low

indicating high uncertainty regarding the best model. Percent crop, despite having low Akaike weights, was a competing model at the larger spatial scales and was negatively related to cricket frog presence. This contrasted with our predictions based on observation of cricket frogs being common in agricultural ponds (Lehtinen and Witter 2014; Youngquist, pers. obs.). However, perhaps this result is not surprising given the negative effects of intensive agriculture on wildlife in general (Donald et al. 2001; Dudgeon et al. 2006; Potts et al. 2010). We also found a negative correlation between cropland and pond density, indicating that areas under intensive agricultural production may not have an abundance of habitat for cricket frogs. At the 2500 m scale, stream and pond density were positively associated with cricket frog abundance. Cricket frogs are frequently found along streams (Lehtinen and Witter 2014), which may increase landscape connectivity, and thus presence at multiple sites, by providing corridors for movement. Other studies have also found positive associations between aquatic features and amphibian presence, suggesting the importance of these features for maintaining regional population structure (Vos and Stumpel 1995; Denoël and Lehmann 2006). Despite the model uncertainty, our results indicate that cricket frog adults may be habitat generalists across spatial scales. We must note, however, that our landscape matrix was dominated by agriculture. The optimal spatial scale to assess the

relationship between landscape composition and species presence may change as a function of landscape heterogeneity. Because our study was a snapshot of regional cricket frog presences over a single year, and because cricket frogs have relatively high rates of local extinction (7 %) and colonization (4 %) per year, the observed abundances could change from year to year (Lehtinen and Witter 2014). However, our random selection of ponds should be representative of available habitats in the study area and we would not expect species to dramatically alter their habitat preferences between years.

The landscape genetics analyses considered effects of landscape composition on cricket frog distribution at a larger scale than the focal-pond study. The results of these analyses demonstrated that functional connectivity was affected by the landscape matrix, with certain features acting as barriers or corridors to gene flow. The IBR model in which highways were partial barriers to gene flow best explained variation in pairwise genetic distance between sampled ponds, across all three scales of resistance values. These results match with the fine-scale (log probability; $k = 9$) Bayesian clustering results showing nine clusters: all clusters were separated by either state routes or US highways. However, when looking at higher-level patterns of structure (Δk ; $k = 5$), the effect of highways was not as apparent. This suggests that some individuals were able to successfully disperse across these roads, enabling gene flow. Streams may provide one conduit for traversing roads. While resistance surfaces including streams did not explain genetic distance better than a uniform landscape, the Riparian and Stepping Stone models were ranked third and fourth when resistance values were scaled 1–10 or 1–100. With proper management, waterways could connect habitats on opposite sides of roads via underpasses (Lesbarrères and Fahrig 2012). The lack of a strong genetic signature supporting streams or ponds as pathways, despite their moderate importance for presence, may be an outcome of cricket frogs dispersing terrestrially. For instance, although we rejected crop and field land cover types as corridors, there was no evidence that these land cover types hindered functional connectivity of the landscape. This can be explained by the willingness of cricket frog metamorphs to move through corn fields and grassy fields (Youngquist and Boone 2014). Our Combined Model, which summed the resistances of land cover, streams, and roads, was one of the lowest ranked

models. These results indicate that the landscape matrix in southwest Ohio is permeable to cricket frog dispersal. There were some differences in model ranking among the different ranges of resistance values and we must note that there is not yet a formal method to compare between models based on R_{β}^2 . Despite this, the consistency in the ranking of the top models suggests our conclusion that major roads are an impediment to dispersal, while other land cover types are permeable, is robust.

The observed differences in model significance among different resistance scales highlights the importance of resistance parameterization. Because Circuitscape allows individuals to travel across multiple paths, instead of calculating a single least-cost-path between sites, the relative contrast between high and low resistance habitats can alter conclusions (e.g., Koen et al. 2012a). Therefore, when parameterizing models for habitat suitability or dispersal resistance, the range of resistance values should match the biology and behavior of the organism. For example, if a species is highly sensitivity to habitat edges, it would be prudent to have a large range of resistance values (high contrast between suitable and unsuitable land cover) to reflect this behavior. Furthermore, using a high-contrast map will ensure that paths are restricted to the feature in question (Fig. 3) and enables researchers to test feature-specific hypotheses. In our study, using a high contrast resistance layer for the Riparian Model helped us conclude that cricket frog dispersal was not limited to riparian habitat.

In our present study, highways were the main predictor of genetic distance. These results are not surprising because the negative effects of roads on gene flow and population connectivity are supported by a plethora of studies (e.g., Holderegger and Di Giulio 2010). However, road density was only weakly predictive of abundance: it only ranked as a competing model to explain cricket frog presence at the 500 m scale. Genetic distance may have responded more strongly than presence to road density for a couple reasons. First, high road density, a proxy for urban development, may not reflect habitat suitability for amphibians because ponds in urban areas may be in city parks where populations are able to persist. Secondly, roads are often leaky barriers to dispersal and might not completely prevent movement (Holderegger and Di Giulio 2010), and therefore,

colonization. Detecting effects of roads on genetic distance, but not presence, indicates that roads may affect species over longer temporal scales, even if they are leaky barriers.

Other than the effects of roads on cricket frog distribution at larger spatial scales, our results show relatively weak effects of land cover on cricket frog presence and genetic structure. These results contrast with other studies showing that cricket frog presence and movement behavior are sensitive to forest and urban land cover types (Lehtinen and Skinner 2006; Trumbo et al. 2012; Youngquist and Boone 2014). The area used in our study was relatively homogeneous agricultural habitat: dominated by crop, pasture, and hay (Fig. 1). High intensity urban land cover, where impervious surface is the majority of the surface area, and forest land cover were relatively sparse in our study area (3 % medium-high intensity development and 16 % forest). Individuals may be able to find alternative routes to bypass these unfavorable habitats when they cover a small fraction of the landscape, taking advantage of slightly longer routes around small patches of unfavorable land cover. This is especially likely considering the lack of effect of other land cover types on genetic structure. Finally, the majority of urban ponds in this study were backyard ponds in suburban areas, thereby limiting our ability to detect effects of high intensity urban land use on presence. At other spatial scales or in landscapes dominated by forest or high intensity urbanization, these factors could become more significant in affecting cricket frog distribution.

Conclusions

Our study adds to a growing body of literature suggesting that agricultural landscapes can provide suitable habitat for a wide range of species and are permeable to wildlife movement (Field et al. 2007; Céréghino et al. 2008; Purrenhage et al. 2009; Goldberg and Waits 2010; but see Donald et al. 2001; Benton et al. 2003). Overall, our results indicate that cricket frogs are tolerant of large variation in landscape composition; they are able to inhabit permanent ponds in a variety of habitat matrices and most land uses are permeable to gene flow. Only highways appeared to impede movement among

populations. However, the effects of landscape configuration and composition on cricket frogs at larger spatial scales remain unknown. Our results do not negate the fact that conversion of natural wetlands, grasslands, and forests for agriculture has overall had negative consequences for many species (Donald et al. 2001; Dudgeon et al. 2006; Potts et al. 2010). Maintaining landscape heterogeneity within agricultural landscapes may be the best way to conserve biodiversity (Benton et al. 2003).

Finally, our results indicate that landscape connectivity may be particularly important for species that, like cricket frogs, tend toward being habitat generalists and have high population turnover. In agricultural landscapes where the majority of land use is crop and pasture, roads and waterways may act as key features across the landscape and play disproportionate roles in species distributions. However, species with similar ecologies can respond differently to the same landscape (e.g., Richardson 2012); other open canopy species may be more sensitive to agricultural activities than cricket frogs (e.g., Row et al. 2010; Loos et al. 2014).

The importance of a multivariate approach when examining how landscape context may affect the distributions of species cannot be understated. A number of studies have shown that the effects of landscape composition and configuration on the processes that affect distributions often do not translate across spatial scales (Pope et al. 2000; Murphy et al. 2010; Angelone et al. 2011; but see Stevens et al. 2006). One reason, for example, is that different aspects of dispersal—crossing into the matrix, finding new habitat, and establishing or integrating into a new population—occur at different spatial scales (Leidner and Haddad 2011). Similarly, for species with complex life cycles, habitat requirements for larval and adult stages may lead to differences in perceived optimal spatial scales between life stages. All of this culminates in the reality that observed habitat preferences within the home ranges of individuals may not reflect functional connectivity at the population/metapopulation level (Coulon et al. 2008b; Reding et al. 2013; Mateo-Sánchez et al. 2015). Management goals must consider taxon- or species-specific behaviors, match the scale at which individuals interact with the landscape, and target the process of interest. Only through comprehensive, multi-scale studies, can we

develop an understanding of the relationship between organisms and their habitats.

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