

META-ANALYSIS



Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat

James I. Watling^{1*}, A. Justin Nowakowski², Maureen A. Donnelly² and John L. Orrock³

¹Washington University in St Louis, Department of Biology, 1 Brookings Drive St Louis, MO 63130, USA, ²Florida International University Department of Biological Sciences, OE 167, University Park Miami, FL 33199, USA, ³University of Wisconsin Department of Zoology, Madison, WI 53706, USA

ABSTRACT

Aim Connectivity is a key determinant of the distribution and abundance of organisms and is greatly influenced by anthropogenic landscape modification, yet we lack a synthetic perspective on the magnitude and extent of matrix effects on connectivity. We synthesize results from published studies to understand the importance of matrix effects on fragmented animal populations.

Location Global.

Methods We conduct a meta-analysis of 283 fragmented populations representing 184 terrestrial animal taxa to determine the strength of matrix composition effects on the occurrence and abundance of animals in fragmented habitat.

Results Studies that use data on matrix composition report greater effects on abundance and occupancy of fragmented populations than studies that define connectivity without regard to the surrounding matrix (i.e. 'binary' studies that describe only characteristics of patch habitat).

Main conclusions Our findings underscore that conservation strategies must consider the importance of matrix habitat, have important implications for metapopulation and metacommunity paradigms, and provide direct large-scale, multi-taxa evidence that matrix habitat is an important driver of ecological dynamics in heterogeneous landscapes.

Keywords

Animals, biodiversity, connectivity, isolation, matrix, patch.

*Correspondence: James I. Watling, University of Florida, Ft Lauderdale Research and Education Center, 3205 College Avenue Ft Lauderdale, FL 33314, USA.
E-mail: watlingj@ufl.edu

INTRODUCTION

Understanding the distribution and abundance of organisms is the fundamental goal of ecology. This goal is of urgent pragmatic utility, because only by effectively characterizing the factors that govern organism distribution can we implement successful conservation and restoration strategies in the face of an anthropogenic biodiversity crisis that threatens many of the world's species with extinction (Brook *et al.*, 2008; Ehrlich & Pringle, 2008). Recent syntheses confirm that characteristics of habitat patches (e.g. size, shape, and isolation) can play an integral role in determining how organisms are distributed in patchy landscapes (Ewers & Didham, 2008; Prugh *et al.*, 2008; Prugh, 2009). However, patches do not exist in isolation from the matrix habitat in which they are embedded. Changes in abiotic conditions and fluxes of nutrients and organisms across habitat boundaries have important consequences for within-patch

dynamics (Polis *et al.*, 1997; Ries *et al.*, 2004; Turner, 2005), implicating connectivity as an important determinant of organism distributions at landscape scales (Turner, 2005; Kupfer *et al.*, 2006; Prugh, 2009). Although mounting evidence suggests that the matrix can mediate the strength and nature of connectivity effects in fragmented landscapes (Ricketts, 2001; Prugh *et al.*, 2008), existing syntheses have emphasized connectivity metrics that focus on patch characteristics alone, without explicit consideration of matrix quality as it pertains to connectivity (Moilanen & Nieminen, 2002; Prugh, 2009). Here we present the first quantitative synthesis describing whether and under what circumstances the matrix matters for connectivity in patchy habitat.

We performed a meta-analysis of 283 fragmented populations to determine the importance of matrix composition effects on the abundance and occupancy of animals on habitat patches. We describe matrix composition effects by comparing studies that

take two dichotomous views of patchy landscapes. The 'binary' perspective describes landscapes in which organisms aggregate within discreet habitat patches and disperse among patches through a homogeneous non-habitat matrix (MacArthur & Wilson, 1967; Moilanen & Nieminen, 2002; Hanski & Gaggiotti, 2004; Holyoak *et al.*, 2005). Many of the most widely-used connectivity metrics (Calabrese & Fagan, 2004) take a binary view of landscapes in which characteristics of the patch habitat (e.g. inter-patch distance, habitat amount) describe organism distribution and abundance, and characteristics of the intervening matrix are not quantified. A 'matrix composition' perspective (Mazerolle & Villard, 1999; Tischendorf & Fahrig, 2001; Cook *et al.*, 2002; Bender & Fahrig, 2005; Kupfer *et al.*, 2006; Fitzgibbon *et al.*, 2007) suggests that the land cover type(s) in which patches are embedded influences occupancy and abundance by differentially influencing rates of dispersal, colonization probability (Gustafson & Gardner, 1996; Bender & Fahrig, 2005), resource availability (Sisk *et al.*, 1997) and mortality risk (Aars & Ims, 1999; Storch *et al.*, 2005). The matrix composition perspective highlights an important distinction between structural connectivity (in which relationships among patches are described in terms of physical features of the environment) and functional connectivity (which focuses on movement of organisms themselves, rather than habitat features that facilitate or inhibit movement; Taylor *et al.*, 2006). Our meta-analysis focuses on structural connectivity by extracting data from studies that describe how matrix composition (e.g. amount and/or identity of non-patch land cover types) influences organism occupancy and abundance on patches.

We assess the importance of matrix composition as a determinant of connectivity by comparing effect sizes of binary and matrix composition predictors of animal distribution in patchy landscapes. To explore how landscape context influences differences in binary and matrix effect sizes, we analyze data across two gradients: the amount of patch habitat and matrix heterogeneity in the landscape surrounding patches. Understanding the role of the matrix in the context of these descriptors of landscape change is critical because habitat loss and modification are key drivers of biodiversity erosion (Brook *et al.*, 2008; Ehrlich & Pringle, 2008). Our analyses provide the first synthetic, quantitative assessment of whether the matrix matters for organism distribution in patchy landscapes, and the landscape context in which the matrix matters most.

MATERIALS AND METHODS

We searched the ecological literature for studies quantifying patch and landscape effects on occupancy and abundance of terrestrial vertebrates. We combined the search terms 'landscape and occupancy and connectivity', 'landscape and abundance and connectivity' and 'landscape and connectivity and patch' in Web of Science and included all studies accessible as of 15 January 2009. We supplemented the results of keyword searches by acquiring studies used in previous synthetic treatments of individual species distributions in patchy landscapes (Moilanen & Nieminen, 2002; Prugh *et al.*, 2008). To be included, a study

needed to meet the following two requirements: (1) focus on a terrestrial vertebrate taxon in a terrestrial landscape; we excluded marine and estuarine studies, studies focusing on dendritic networks, and studies of fish on the grounds that the landscape context for those organisms and habitats are more different from the taxa and landscapes that we focused on than any of our foci are from one another; and (2) report univariate tests of an isolation term on occupancy or abundance or included raw data from which we could calculate effect sizes ourselves; studies that included multiple predictors of occupancy and abundance were excluded on the grounds that covariance among independent variables may influence the potential effect size of the isolation term(s).

The two broad connectivity metric classes that form the basis of our meta-analysis (binary vs. matrix composition) are comprised of several individual metrics. Most of the binary predictors included here have been the focus of previous synthetic treatments that compared the performance of different patch-based connectivity metrics (Moilanen & Nieminen, 2002; Prugh, 2009). We follow published terminology (Prugh, 2009) to describe five of the binary metrics included in the current study (Table 1). We include a sixth metric, the proximity index, which incorporates data on both patch area and isolation but has a different formula than the incidence function model (Table 1). We distinguished three types of metrics comprising our matrix composition predictors (Table 1). Diversity metrics describe variation in habitat composition around focal patches using an estimate of the diversity of cover types, usually the Shannon-Weiner diversity index, but also including metrics such as edge density (which are expected to increase in more heterogeneous landscapes; Fahrig, 2003). Cover metrics are similar to the concentric habitat binary metric, but describe habitat cover of some matrix type in a buffer around the focal patch. Modified distance metrics apply a weighting scheme based on measured or perceived differences in matrix permeability to weight distance from a focal patch to neighboring patches.

From the pool of studies we extracted data on ten parameters (Table S1): (1) species, (2) taxon (amphibian, arthropod, bird, mammal, reptile), (3) country in which study was conducted, (4) latitude, (5) area of the region in which the study was conducted, (6) matrix heterogeneity (scored on a three point scale, see below), (7) patch type, (8) range in patch area, (9) regional habitat cover (proportion of study landscape represented by the focal patch type, see below), and (10) number of patches. We considered a regional habitat cover gradient because simulations suggest that critical thresholds of habitat amount in a landscape may determine when area and isolation effects on patch patterns become apparent (Andr n, 1994; Fahrig, 1998). Our exploration of results across a gradient in matrix heterogeneity was based on simulations and translocation experiments (Bender & Fahrig, 2005) that suggest increasing matrix complexity may obscure area and isolation effects on patch patterns.

When a map of the study area was included in the paper as a figure, we digitized the figure to quantify landscape size and/or regional habitat cover as necessary. Because many studies did

Table 1 Summary information on nine individual metrics included in the meta-analysis.

Class	Metric	Description	Formula
Binary	Nearest-neighbor Distance	Shortest straight-line distance between adjacent patches	$ND_i = \min(d_{ij})$
	Distance to source	Shortest straight-line distance to a source population	$DS_i = \min(d_{im})$
	IFM	Unitless measure integrating area, distance and occupancy status of patches around a focal patch	$S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j^b * k$
	Proximity index	Unitless measure integrating area and distance of patches around a focal patch	$P_i = \sum_{j \neq i} \frac{A_j}{d_{ij}^2}$
	Concentric habitat	Proportional cover of focal habitat type in buffer around a patch	$CH_i = \sum_{d_{ij} \leq r} A_j$
Matrix composition	Diversity	Measure of diversity of habitat types in buffer around a patch	Varies, often based on Shannon diversity index, $H_i = -\sum_{i=1}^s (p_i * \ln p_i)$
	Cover	Proportional cover of non-focal habitat type in buffer around a patch	Varies, often $C_g = \sum_{d_{ij} \leq r} A_g$
	Modified distance	Shortest straight-line distance between adjacent patches weighted by habitat permeability	$MD_i = \sum_{j \neq i} \exp(p_g d_{ij}) A_j^b * k$

d_{ij} = distance between focal patch i and patch j d_{im} = distance between focal patch i and source m . α = parameter describing mobility of a species, usually $1/\text{average migration distance}$. A_j = area of patch j (patch $j \neq$ patch i). b = parameter scaling the effect of emigration to area k = occupancy or colonization of patch (1 = occupied/colonized, 0 = unoccupied/uncolonized). A_j = sum of areas of patch i + patch j r = radius of buffer around patch i s = number of habitat types in a landscape p_q = proportional cover of habitat type q g = non-focal patch habitat type (habitat type $g \neq$ habitat type i). p_g = proportional cover of non-focal patch habitat type.

not include detailed information on the proportion of the study landscape represented by the focal patch type, we pooled studies into three habitat cover categories: low habitat cover ($< 5\%$ of the study landscape), moderate habitat cover ($5\text{--}30\%$ of the study landscape), and high habitat cover ($> 30\%$ of the study landscape). We used 30% as a cutoff point to define relatively unfragmented landscapes because it has been suggested that fragmentation effects become apparent when habitat cover in a landscape drops below 30% (Andr n, 1994; Fahrig, 1998). We created a low habitat cover category ($< 5\%$) that roughly corresponds to the ‘relictual’ category used in Fischer & Lindenmayer (2007). Matrix complexity was scored based on an increase in the number and contrast of land cover types in the matrix. Patches embedded in a single cover type (e.g. agriculture or forest) or in matrices with multiple land cover types that varied little in structural contrast (e.g. hardwood and evergreen forest) were considered relatively homogeneous. Patches in landscapes with a mixture of two broad land cover types (e.g. forest and grassland, grassland and agriculture) represented an intermediate degree of complexity. Patches in landscapes with a mixture of three or more land uses, including agriculture, native vegetation and human habitation were considered heterogeneous.

We partitioned the total dataset into two subsets according to the dependent variable being studied. Studies for which a metric of patch abundance (density, relative abundance, calling rank, etc.) was analyzed were considered separately from studies in which patch occupancy was the dependent variable. For abundance-based studies, we extracted the r -value of the correlation between the predictor and abundance. In a few cases where abundance was not analyzed using correlation analysis (or data on predictors and abundance could not be calculated

from data included in a published table), we converted F -values to r (Rosenberg *et al.*, 1997), or Spearman rank correlations to r (Myers & Sirois, 2006). All r -values were converted to effect size metric z in MetaWin using Fisher’s z -transformation: $z = 0.5 * \ln((1 + r)/(1 - r))$ with variance $v_z = 1/(n - 3)$. Only one study with abundance as a response variable utilized nearest occupied neighbor as a metric of connectivity, so we grouped that study with studies utilizing the nearest-neighbor distance metric.

For studies investigating relationships between predictors and occupancy, our metric of effect size was beta (the coefficient obtained from a logistic regression model of occupancy as a function of connectivity), calculated separately for each fragmented population in the database. Beta is the $\ln(\text{odds ratio})$ and describes change in the odds of occupancy with each unit increase in the predictor variable. We calculated fully standardized logistic regression coefficients (Menard, 2004) because beta varies according to the scale at which an effect is measured (Menard, 2004), and predictors were measured on different scales (e.g. distance in meters, proportional cover in a buffer, etc.).

Analyses were conducted in R using a weighted means analysis of variance (ANOVA). We extracted the pooled variance estimate (σ^2_{pooled}) attributable to the random effect of study using the restricted maximum likelihood approach (Shadish & Haddock, 2009). The pooled variance estimate was incorporated into the weights for each effect as $w_i = 1/(v_i + \sigma^2_{\text{pooled}})$, and tests for the main effects of connectivity metric class, matrix heterogeneity, habitat cover and interactions were conducted as fixed effects (Raudenbush 2009). The sum of squares values are reported for main effects and their interaction as the heterogeneity statistic (Cochran’s Q) and tested against a chi-square

distribution with $p - 1$ degrees of freedom, where p is the number of groups being compared (Konstantopoulos & Hedges 2009). The mean and variance of effect sizes (T) for each factor level were calculated according to Konstantopoulos & Hedges (2009).

We were not able to ascertain habitat cover for several studies ($n = 14$ for studies of abundance and $n = 19$ for studies of occupancy) so we ran one analysis to test for the main effects of matrix heterogeneity (low, medium, high), connectivity metric class (binary vs. matrix composition) and their interaction, and a separate analysis to test for the main effects of habitat cover (low, medium, high), predictor and their interaction. Because we were not able to categorize habitat cover for all studies in the database, we report the main effect of connectivity metric class from the analyses including matrix heterogeneity. Complementing the analysis of interactions between connectivity metric class across the two gradients of landscape context, we also analyze effects of taxon (birds, mammals, amphibians and arthropods), connectivity metric class and their interaction, and describe variation in the individual metrics comprising the binary and matrix composition predictors. Post hoc contrasts were calculated for pairwise combinations of group mean effect sizes after adjusting α with a generalization of the Scheffé method as described by Konstantopoulos & Hedges (2009).

RESULTS

We analyzed effect sizes from 283 fragmented populations obtained from 63 studies published over a 38 year period from 1971–2009: abundance was the response variable for 108 fragmented populations and occupancy was the response measured in 175 fragmented populations (Table 2, Appendix S1). The vast majority of effects were for individual species, but we included five effects reported for multiple species (e.g. 'bees and wasps', 'seven amphibian species', see Appendix S1). All means are reported $\pm$ the 95% confidence interval calculated according to Konstantopoulos & Hedges (2009).

For studies of organism abundance, the effect size of matrix composition predictors ($\bar{T}_{\text{matrix}} = 0.415 \pm 0.104$) was over 65% greater than the effect size for binary predictors

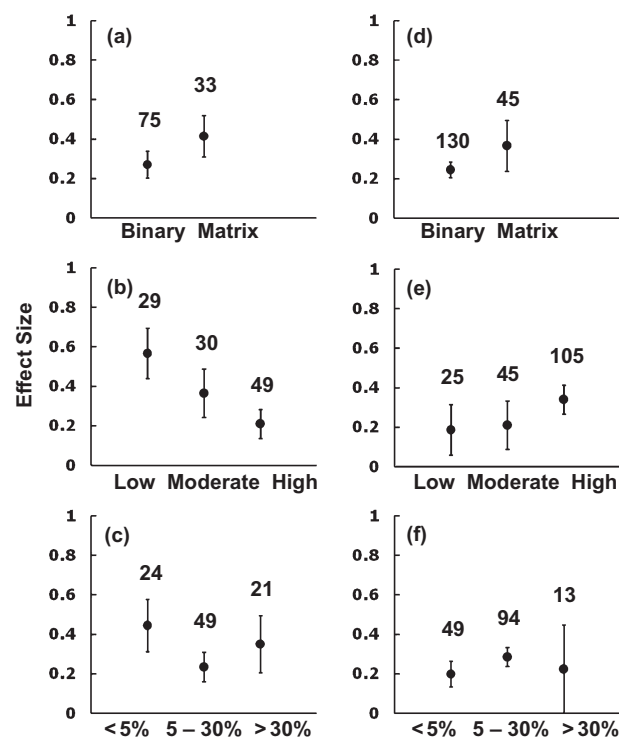


Figure 1 Plots of mean effects for predictors of organism distribution in patchy landscapes. All means are presented with 95% confidence intervals. (a) Mean effect sizes for predictors of organism abundance across all fragmented populations. (b) Mean effect sizes for predictors of organism abundance in landscapes characterized by low, moderate and high heterogeneity in land cover. (c) Mean effect sizes for predictors of organism abundance in landscapes with different proportions of focal habitat cover. (d) Mean effects for predictors of organism occupancy across all fragmented populations. (e) Mean effects for predictors of organism occupancy across the landscape heterogeneity gradient. (f) Mean effects for predictors of organism occupancy across the habitat cover gradient. The number of studies included in each calculation is indicated above the mean effect sizes.

Table 2 Cross-tabulation of number of effects in the total data set across levels of landscape context (matrix heterogeneity and habitat cover), response (abundance and occupancy), and predictor (binary and matrix).

	Binary			Matrix		
	Abundance	Occupancy	Total	Abundance	Occupancy	Total
Matrix heterogeneity						
Low	25	24	49	4	1	5
Medium	11	38	49	19	7	26
High	39	68	107	10	37	47
Habitat cover						
< 5%	13	28	41	11	21	32
5–30%	39	77	116	10	17	27
> 30%	15	7	22	6	6	12

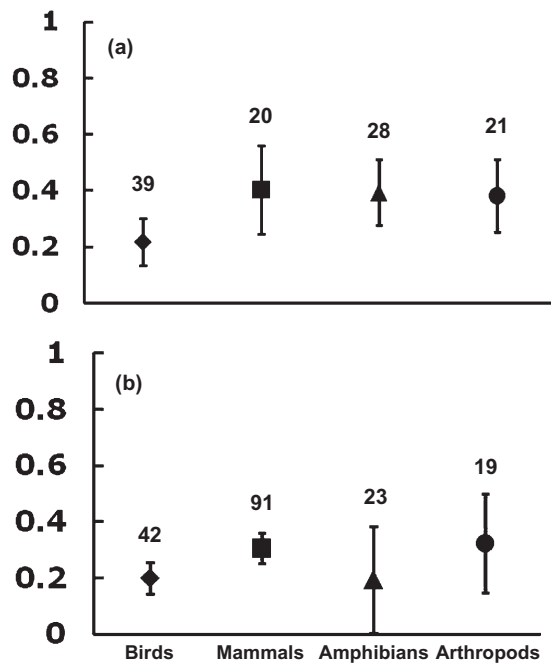


Figure 2 Plots of mean effects for predictors of organism distribution in patchy landscapes across four major groups of animals. All means are presented with 95% confidence intervals. (a) Mean effects for predictors of animal abundance. (b) Mean effects for predictors of animal occupancy. The number of studies included in each calculation is indicated above the mean effect sizes.

($\bar{T}_{\text{binary}} = 0.271 \pm 0.067$; $Q = 5.17$, $P = 0.023$, Fig. 1a). There was a significant difference in mean effect sizes across the three levels of matrix heterogeneity ($Q = 22.73$, $P < 0.001$; Fig. 1b) and post-hoc contrasts revealed that the contrast between low and high levels of matrix heterogeneity was significant ($\bar{T}_{\text{low}} = 0.568 \pm 0.128$, $\bar{T}_{\text{high}} = 0.211 \pm 0.073$, $\chi^2 = 22.70$, $P < 0.001$), whereas comparisons between low and medium levels of matrix heterogeneity ($\bar{T}_{\text{medium}} = 0.365 \pm 0.123$) and medium and high matrix heterogeneity were not significant ($\chi^2 = 5.04$, $P = 0.080$ and $\chi^2 = 4.43$, $P = 0.109$). The interaction between class and matrix heterogeneity was not significant ($Q = 1.89$, $P = 0.388$). The interaction between class and habitat cover was not significant ($Q = 0.640$, $P = 0.726$), nor was the main effect of habitat cover ($Q = 4.75$, $P = 0.093$, Fig. 1c).

We grouped the three reptile populations with amphibian populations for analysis of effect size across taxa. The interaction between class and taxon was not significant ($Q = 6.24$, $P = 0.100$), but there was a significant main effect of taxon ($Q = 9.25$, $P = 0.026$). Post hoc contrasts revealed that the mean effect size for birds ($\bar{T}_{\text{birds}} = 0.217 \pm 0.083$) was lower than for all other taxa ($\bar{T}_{\text{amphibian}} = 0.393 \pm 0.117$, $\bar{T}_{\text{mammal}} = 0.403 \pm 0.157$, and $\bar{T}_{\text{arthropod}} = 0.382 \pm 0.129$), but the only significant contrast was between birds and mammals ($\chi^2 = 22.59$, $P < 0.001$; Fig. 2a). There were also significant differences in mean effect sizes across the eight individual metrics ($Q = 22.81$, $P = 0.002$), driven largely by the significantly lower mean effect size of the proximity index relative to other metrics (Fig. 3a). When fragmented popula-

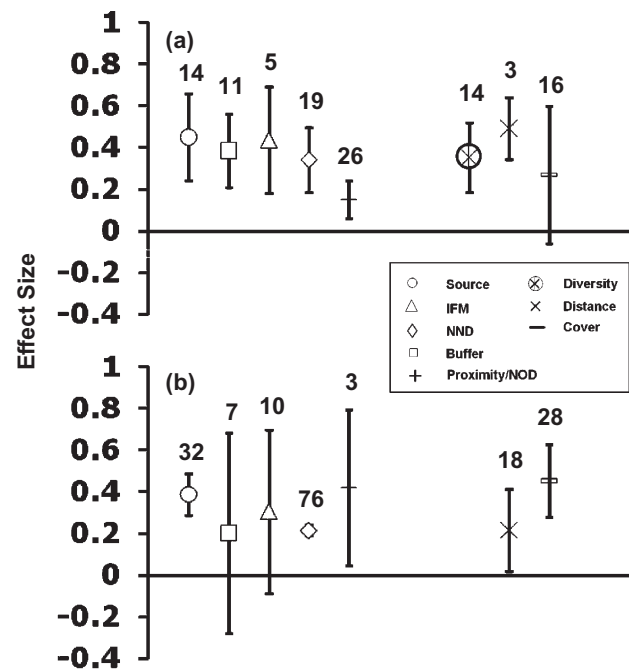


Figure 3 Plot of mean effects of connectivity metrics on organism distribution in patchy landscapes. Binary metrics include information on patch characteristics only whereas matrix composition metrics describe structural aspects of land cover in the matrix separating patches. All means are presented with 95% confidence intervals. (a) Mean effects of connectivity metrics on organism abundance. (b) Mean effects of connectivity metrics on organism occupancy. The number of studies included in each calculation is indicated above the mean effect sizes.

tions that were described using the proximity index are removed from the analysis, the main effect of connectivity metric class is not significant for studies of abundance ($Q = 3.48$, $P = 0.746$). Comparing just the subset of studies that report effects of both binary and matrix composition predictors of organism abundance ($n = 37$ observations) indicated no difference in mean effect size between connectivity metric classes ($Q = 0.15$, $P = 0.699$).

For occupancy studies, the effect size of matrix composition predictors ($\bar{T}_{\text{matrix}} = 0.368 \pm 0.129$) was about 50% greater than the effect size for binary predictors ($\bar{T}_{\text{binary}} = 0.246 \pm 0.039$; $Q = 3.15$, $P = 0.076$; Fig. 1d). Because alternative estimates of variance associated with the random effect of study (Shadish & Haddock, 2009) indicated an even greater difference in mean effect sizes, we consider this to be a conservative estimate of the difference between binary and matrix composition predictors. There was a significant difference in effect sizes across the three levels of matrix heterogeneity ($Q = 10.71$, $P = 0.005$, Fig. 1e), and post hoc contrasts indicated that differences in mean effect size were significant for comparisons between low and high levels of matrix heterogeneity ($\bar{T}_{\text{low}} = 0.187 \pm 0.072$, $\bar{T}_{\text{high}} = 0.341 \pm 0.060$; $\chi^2 = 10.47$, $P = 0.005$) and medium and high levels of matrix heterogeneity ($\bar{T}_{\text{medium}} = 0.211 \pm 0.064$, $\chi^2 = 8.44$, $P = 0.015$), but not between low and medium levels of

matrix heterogeneity ($\chi^2 = 0.24$, $P = 0.888$). The interaction between class and matrix heterogeneity was not significant ($Q = 0.020$, $P = 0.990$). There was no interaction between class and cover ($Q = 0.28$, $P = 0.872$), and the difference in effect sizes across the three levels of habitat cover was not significant ($Q = 4.67$, $P = 0.097$, Fig. 1f).

We grouped the one reptile population with the amphibian populations for analysis of effect sizes across taxa, and found no interaction between predictor class and taxon ($Q = 0.03$, $P = 0.986$), but a significant main effect of taxon ($Q = 7.84$, $P = 0.049$). Effect sizes for mammals and arthropod were larger than effect sizes reported for other taxa ($\bar{T}_{\text{mammal}} = 0.305 \pm 0.054$, $\bar{T}_{\text{arthropod}} = 0.324 \pm 0.176$, $\bar{T}_{\text{amphibian}} = 0.195 \pm 0.189$, $\bar{T}_{\text{bird}} = 0.200 \pm 0.056$; Fig. 2b), but the only contrast that approached statistical significance after the α level correction was between birds and mammals ($\chi^2 = 6.87$, $P = 0.076$). There were significant differences in effect size across individual metrics ($Q = 16.26$, $P = 0.012$), with distance to the nearest occupied neighbor (binary) and distance (matrix composition) having the greatest effect sizes (Fig. 3b). Comparing just the subset of studies that report effects of both binary and matrix composition predictors of organism occupancy ($n = 46$ observations) indicated no difference in mean effect size between connectivity metric classes ($Q = 0.03$, $P = 0.865$).

DISCUSSION

Our study provides quantitative evidence, across a wide variety of taxa and geographic contexts, suggesting that the matrix matters for connectivity in patchy landscapes. Although the matrix is rarely considered when predicting occupancy and abundance for conservation and restoration, our results suggest that connectivity is more influenced by matrix composition than binary measures of connectivity that focus on attributes of patches alone. For studies of both abundance and occupancy, the mean effect size of matrix composition predictors was approximately 50% greater than the mean effect size of binary predictors. The greater effect size of matrix composition predictors for studies of organism abundance is a function of the poor performance of one particular metric, the proximity index (Fig. 3). Below we discuss the implications of our results for metapopulation and metacommunity studies, and the main effects of landscape context we observed.

Structural connectivity is an important phenomenon that influences species distributions and evolutionary processes (Mazerolle & Villard, 1999; Tischendorf & Fahrig, 2001; Fischer & Lindenmayer, 2007; Fitzgibbon *et al.*, 2007), but there is little consensus over how it should be measured. Although many binary connectivity metrics are readily calculated and provide a numerically tractable means of modeling landscape structure (Prugh, 2009), we argue that matrix composition metrics may provide more insight into connectivity-distribution relationships at little or no additional computational or interpretive cost. The information content of many landscape metrics (e.g. diversity and cover metrics of matrix composition, Table 1) is comparable to that included in many binary metrics (e.g. the

IFM, proximity index, and concentric habitat metrics, Table 1). Matrix composition metrics focus explicitly on how different land cover types or landscape features exert varying levels of resistance to organism movement (Storfer *et al.*, 2007; McRae *et al.*, 2008), and ultimately affect connectivity by influencing the probability of movement, colonization and rates of gene flow among patches (Ricketts, 2001; With, 2004; Fitzgibbon *et al.*, 2007). Increasing effort directed at describing data-driven estimates of species- or taxon-specific resistance values for different land cover types in the matrix will likely further improve the performance of matrix composition metrics. Recent work suggests that matrix composition metrics can better explain patterns of genetic divergence between local populations than Euclidian distances (Greenwald *et al.*, 2009). Our observation that organism occupancy and abundance are better predicted by matrix composition metrics than binary metrics underscores the importance of matrix effects on population attributes that provide the foundation of the metapopulation and metacommunity framework.

A large body of literature has been devoted to the application of binary models to fragmented landscape in the context of island biogeography, metacommunity, and metapopulation models (MacArthur & Wilson, 1967; Hanski & Gaggiotti, 2004; Holyoak *et al.*, 2005). The utility of these models for understanding dynamics in patchy landscapes and for conservation planning depends on the validity of the assumptions made and the predictive power of the model parameters. However, previous quantitative syntheses have found that distance-based measures tend to be poor predictors of species richness and patch occupancy (Watling & Donnelly, 2006; Prugh *et al.*, 2008). Binary metrics implicitly assume that the composition of the landscape matrix has negligible effects on patch dynamics. Our results suggest that the matrix assumption is often violated in terrestrial systems and provides further support for the conclusion that binary connectivity measures tend to explain little variation in species distributions.

Our work also suggests that matrix composition may influence the degree to which alternate metacommunity paradigms describe community dynamics (Chase, 2003; Leibold *et al.*, 2004; Cadotte, 2006). For example, when the matrix is heterogeneous, colonization probability may be less influenced by Euclidian distance than the permeability of different land cover types (e.g. patch dynamics approach). Differential permeability of the matrix implies that local communities embedded in less permeable matrices should be more prone to community drift and therefore more divergent in composition than local communities that exchange greater numbers of migrants (e.g. neutral metacommunity approach). If different land cover types in the matrix provide supplemental resources that benefit some species but not others, competitive outcomes may be altered within patches, leading to faulty conclusions about the relative importance of priority effects and local environmental conditions (e.g. species-sorting approach). For example, local conditions may be similar across patches, but community composition may differ because of variation in matrix composition, which could be interpreted as multiple stable equilibria

arising from different invasion histories (Chase, 2003). Most theoretical and simulation work to date has focused on dynamics at one end of a matrix complexity gradient, when the matrix is of one neutral type and is relatively uniform across the landscape. Future simulation studies should examine the degree to which matrix composition influences patch dynamics and alters community patterns from those observed when a relatively homogeneous landscape is assumed.

Our results suggest that landscape context plays a significant role in determining the ability to predict organism occupancy and abundance. One hypothesis predicts a critical threshold of 30% habitat cover below which organism responses to fragmentation effects (e.g. patch area and isolation) become pronounced (Andrén 1994). We expected that if such a threshold exists, we would see relatively greater effect sizes of binary predictors compared with matrix predictors in landscapes with low and moderate habitat cover (e.g. a significant interaction between class and habitat cover) and a main effect of cover with greater mean effect sizes in landscapes with relatively little habitat cover. In contrast, our analyses failed to detect an interaction between class and habitat cover, and the main effects of cover were marginal and inconsistent: for abundance, effect sizes in both low and high cover landscapes were greater than effect sizes in moderately-fragmented landscapes whereas in the occupancy dataset effect sizes were greatest in the moderately-fragmented landscape. Our results are not consistent with predictions of a critical 30% threshold of habitat loss (Andrén 1994). Although many empirical studies have reported results consistent with a roughly 30% threshold (reviewed in Swift & Hannon, 2010), other factors, including time lags in population responses to habitat alteration or confounding of habitat cover with other metrics of landscape structure not considered here (e.g. edges, Ewers & Didham, 2008) may preclude our ability to detect a signal consistent with the 30% habitat cover threshold.

The effect of matrix heterogeneity differed for studies of organism abundance and occupancy; mean effect size was greatest in the most heterogeneous landscapes when occupancy was the response measured, whereas the mean effect size was lowest in heterogeneous landscapes when abundance was the response. In other words, habitat heterogeneity may obscure connectivity effects when abundance is the response, but not when describing organism occupancy. In our analysis, fragmented populations that exist in heterogeneous landscapes almost always included human activities (e.g. settlements and/or land used for agriculture). This makes our results particularly relevant in the context of biodiversity hotspots, which are defined in part by human disturbance of natural habitat and therefore exist in relatively heterogeneous landscapes (Brooks *et al.*, 2002).

By documenting the important role of matrix composition for terrestrial animals, our work has several implications for future research. Our analysis highlights that data regarding how animals use multiple habitat types are needed to understand the mechanistic basis for matrix heterogeneity as a driver of patch dynamics in complex landscapes. Our work also has important implications for metacommunity theory (Chase, 2003; Leibold *et al.*, 2004; Cadotte, 2006) because matrix effects on connectiv-

ity and resource availability have the potential to alter competitive and trophic interactions (Cronin, 2007), although more work is needed to describe how matrix effects alter the relative strength of alternative metacommunity paradigms. Although additional studies of matrix effects are needed to understand the consequences of interacting habitat elements in landscapes, our work emphasizes that the matrix matters for connectivity of terrestrial animal populations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Summary data for effects included in meta-analysis.

Appendix S1 Studies used in the meta-analysis.

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BIOSKETCHES

James Watling studies how the amount, arrangement and quality of habitat in landscapes influences the distribution and abundance of species.

Justin Nowakowski conducts research related to amphibian conservation and the effects of land use on community and genetic diversity.

Maureen Donnelly is broadly interested in the ecology and evolution of the Neotropical herpetofauna.

John Orrock studies the consequences of biotic interactions for the spatial distribution of species.

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