

MULTIVARIATE ANALYSIS OF SCALE-DEPENDENT ASSOCIATIONS BETWEEN BATS AND LANDSCAPE STRUCTURE

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Abstract. The assessment of biotic responses to habitat disturbance and fragmentation generally has been limited to analyses at a single spatial scale. Furthermore, methods to compare responses between scales have lacked the ability to discriminate among patterns related to the identity, strength, or direction of associations of biotic variables with landscape attributes. We present an examination of the relationship of population- and community-level characteristics of phyllostomid bats with habitat features that were measured at multiple spatial scales in Atlantic rain forest of eastern Paraguay. We used a matrix of partial correlations between each biotic response variable (i.e., species abundance, species richness, and evenness) and a suite of landscape characteristics to represent the multifaceted associations of bats with spatial structure. Correlation matrices can correspond based on either the strength (i.e., magnitude) or direction (i.e., sign) of association. Therefore, a simulation model independently evaluated correspondence in the magnitude and sign of correlations among scales, and results were combined via a meta-analysis to provide an overall test of significance. Our approach detected both species-specific differences in response to landscape structure and scale dependence in those responses. This matrix–simulation approach has broad applicability to ecological situations in which multiple intercorrelated factors contribute to patterns in space or time.

Key words: *Atlantic forest; bats; correlation; habitat fragmentation; landscape scale; matrix–simulation approach; meta-analysis; null model; Paraguay; permutation; phyllostomid bats; species-specific responses.*

INTRODUCTION

Fragmentation of natural habitats is one of the most important factors causing elevated rates of species extinction and the loss of biological diversity (Wilcox and Murphy 1985). Fragmentation reduces the amount of available habitat and subdivides or isolates populations (Hanski et al. 1995), thereby modifying behavior (Hargis et al. 1999), species interactions (Aizen and Feinsinger 1994), and ecosystem processes (Schwalter et al. 1981). For these reasons, the response of populations and communities to habitat fragmentation has become a central topic in conservation biology and landscape ecology.

Despite ample theoretical and empirical evidence that species and communities demonstrate nonlinear associations with gradients in habitat characteristics (e.g., Wiens 1989, Lord and Norton 1990, With and Crist 1995), many studies (e.g., McGarigal and McComb 1995, Villard et al. 1999, Gehrt and Chelsvig 2003, Numa et al. 2005) have explored such relationships at only a single landscape size. However, the detection of ecological relationships is determined, in

part, by the focal scale at which spatial characteristics are measured (Wiens et al. 1987, Lyons and Willig 1999, Gross et al. 2000, Scheiner et al. 2000, Steffan-Dewenter et al. 2002). Therefore, it is imperative that landscape attributes be quantified at a range of scales relevant to those at which individuals and populations interact. In the absence of prior knowledge, patterns measured across multiple spatial scales permit the comparison and detection of scale dependency in the association of species and communities with landscape structure. Nevertheless, comparing these relationships can be complicated by several issues. First, high correlation among predictor variables (i.e., multicollinearity) may result in incorrectly ascertaining the strength (i.e., magnitude) or direction (i.e., sign) of relationships between a biotic response variable (e.g., population- and community-level characteristics) and predictor variables (e.g., landscape characteristics). Second, matrices representing multivariate responses to habitat attributes may be (dis)similar to one another based on the strength or direction of association among matrix elements. Distinguishing among these types of matrix correspondence is a prerequisite to determining whether and how a biotic response changes as a function of scale. Finally, permutation methods are needed to test for the significance of observed differences among pairs of matrices, but current methods (e.g., Mantel test, analysis of similarities, Procrustes ordination; Legendre and Legendre 1998:552) do not read-

Manuscript received 18 March 2004; revised 24 November 2004; accepted 11 February 2005; final version received 9 March 2005. Corresponding Editor: N. T. Hobbs.

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FIG. 1. Landscape structure was measured in each of a nested sequence of concentric circles (1, 3, 5 km radius). Species abundance and community composition were estimated at sites located at the center of each nested set of circles. Land cover types were classified from Landsat Thematic Mapper imagery and include water (black), forest (dark gray), regrowth (mid-tone gray), pasture or grassland (light gray), and bare soil (white). Forest habitat was the focal landscape element in all quantitative analyses. The upper left and lower right corners are located at $23^{\circ}55'22''$ S, $55^{\circ}54'40''$ W, and at $24^{\circ}30'6''$ S, $55^{\circ}16'43''$ W, respectively. The figure is reproduced from Gorresen and Willig (2004) with permission.

ily handle the nonsymmetric matrices of partial correlation coefficients that we used to control for multicollinearity. We present a novel approach to address these concerns and distinguish patterns of association in multivariate data.

Bats

Bats are the second most species-rich order of mammals (Wilson and Reeder 1993). They occupy a variety of feeding guilds and may be the most abundant mammals at the local level, especially in tropical and subtropical habitats (Patterson et al. 2003). Many aspects of their biodiversity increase toward the tropics, including species density (Willig and Selcer 1989, Willig and Sandlin 1991) and a variety of metrics of taxonomic (Stevens and Willig 2002), functional (Stevens et al. 2004), and phenetic biodiversity (Stevens et al., *in press*). The form and parameterization of these patterns differ with spatial scale (e.g., Lyons and Willig 1999, 2002, Willig et al. 2003a, b). Moreover, bats, in general, and frugivorous and nectarivorous phyllostomids, in particular, may be keystone taxa in tropical

forests because of their effects in structuring plant communities and promoting secondary succession (Fleming 1988, Fleming and Heithaus 1981, Gorchov et al. 1993). Nonetheless, the response of particular bat species to complex spatial features and fragmentation across a range of spatial scales remains little explored. Fortunately, the fairly extensive area locally used by bats make this group amenable to an analysis in which remotely sensed imagery can be used to characterize forest fragmentation and landscape attributes. The analytical method that we present is applied to an assessment of scale dependence in the relationship of phyllostomid bats and landscape structure.

MATERIALS AND METHODS

Fourteen sites, spaced at ~ 10 -km intervals, were surveyed from 13 January 1997 to 24 May 1998 in a 3000-km² area of subtropical semideciduous forest (Hill and Hurtado 1996) within and adjacent to the Reserva Natural del Bosque Mbaracayú in the Departamento de Canindeyú of eastern Paraguay (Fig. 1). At each site, five two-night surveys were conducted every 2–3

months, for a total of 140 sampling nights. Each site was sampled once with 180 m of mist-net deployed the entire night, and four times with 228 m of net deployed for the first six hours of the night, for a total of >1000 hours of survey. Spacing of survey sites represented a compromise between establishing a study area sufficiently small that biogeographic factors did not differ among sites and an area sufficiently large that measures of species abundance more likely were to have been obtained from statistically independent sampling units. A complete description of the study area, sampling methods, landscape attributes, and regression models, as well as the relevance of the study to bat ecology, appear in Gorresen (2000) and Gorresen and Willig (2004).

“Scale” refers to the specific area from which measures of habitat characteristics and spatial patterns are derived (sensu Wiens 1989). As a focal area, it is also the inference space to which a particular datum in the analysis pertains (sensu Scheiner et al. 2000). We use “extent” to mean the domain of the study or the inference space to which a complete analysis pertains. “Landscape” is used more broadly to mean the larger area within which study organisms and habitat occur. The focal scales used in this study were chosen to include and describe the habitat encountered by individual bats (i.e., home range). Because little is known of the home range sizes of bats, circles of different diameters (1, 3, and 5 km radius) were centered on each sample site and were used to delimit a nested series of scales. The maximum scale (5 km radius) was constrained by the minimum distance between survey sites. The smallest scale (1 km radius) was selected to encompass the expected home range of smaller bat species in the study area (e.g., as large as a 0.5 km radius for *Glossophaga soricina*; Lemke 1984). “Response” is used to mean the functional relationship between landscape characteristics of the habitat and biotic characteristics of bats at the population level (i.e., species abundances) or community level (i.e., species richness and evenness).

Indices of abundance were based on number of captures per taxon. Measures of community structure (i.e., species richness and evenness) were standardized with rarefaction methods to permit the comparison of indices among sites with different sample sizes (Gotelli and Graves 1996). Species richness was calculated as the number of species within a rarefied sample. Evenness was estimated as the likelihood that a random selection of two individuals represents different species (Hurlbert 1971).

Forest served as the focal habitat type for all measures of landscape structure; all other habitat types comprised the matrix within which forest patches were situated. Landscape characteristics were estimated with the spatial analysis program LEAP II (Perera et al. 1997) for each of the three scales, and included forest cover, patch size, patch density, edge density, nearest

neighbor distances among patches, patch proximity, and patch shape.

Two approaches, multiple regression and the comparison of correlation matrices, were used to examine whether associations of phyllostomid bats with landscape characteristics change as a function of scale. At each scale, regression analyses were used to identify the specific suite of landscape characteristics associated with population- or community-level attributes. Correlation matrices were contrasted with a null-model approach (Gotelli and Graves 1996) to determine similarities or dissimilarities in response to landscape structure across spatial scales.

Multiple regression

Species presence and abundance often are related to the amount of available habitat (e.g., McGarigal and McComb 1995, Villard et al. 1999). Because landscape characteristics can be correlated with habitat area, the response of species abundance to these characteristics may be confounded. Therefore, the relationships of species abundance and community structure with landscape characteristics were evaluated after controlling for habitat area. Regression was used to remove linear effects of associations between each landscape characteristic and forest cover. Residuals from the regressions were used in subsequent analyses, but for the sake of simplicity, they are referred to solely by the name of the characteristics whose residuals were analyzed. The multiple regression of species abundances and community indices to landscape structure was performed with the REG procedure in SAS (SAS Institute 1985). Forward stepwise selection was used to identify a parsimonious combination of landscape characteristics that maximizes R^2 . Rare phyllostomid species were not subjected to species-specific analyses because of the ubiquity of zeros in the capture data. Species were classified as rare if they were captured fewer than 10 times during the course of this research. However, all phyllostomid species, regardless of abundance, were included in the calculation of diversity measures at the community level.

Correspondence of correlation matrices

Correlation matrices were developed at each scale to describe the multiple and intercorrelated relationships of a biotic response variable to a suite of landscape characteristics. Simple and partial correlations were calculated using the CORR procedure and PARTIAL statement in SAS (SAS Institute 1985). Each partial correlation between a response variable and a landscape characteristic controlled for the association with one other characteristic. For example, $r_{X:A,B}$ is the correlation of the abundance of species X to variable A controlling for the effect of variable B . For each species or community index (i.e., abundance, richness, evenness), a composite pattern matrix of simple and partial correlation coefficients summarized the overall

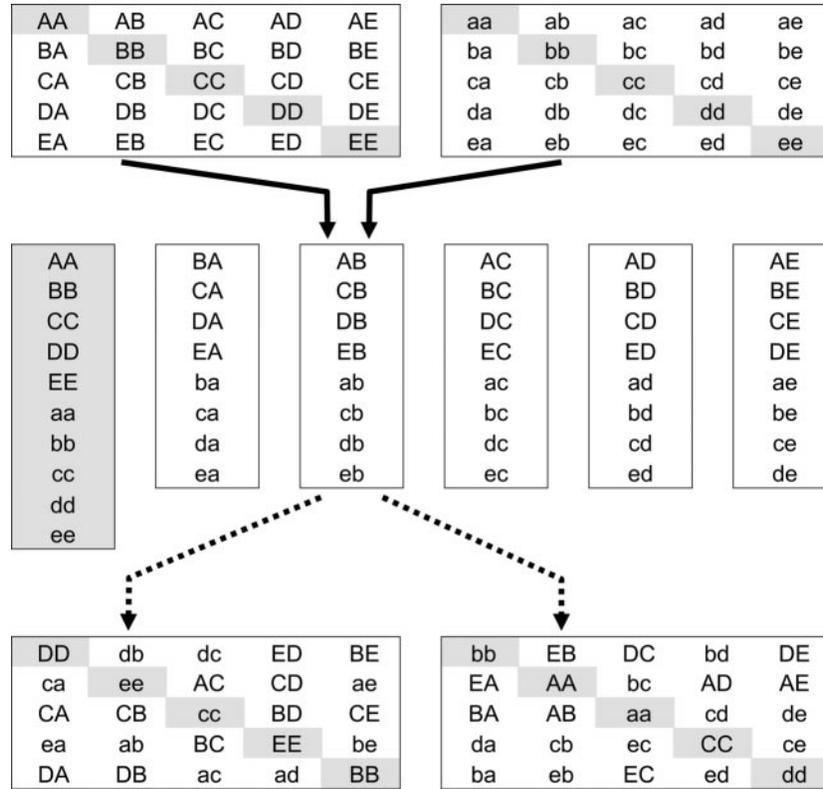


FIG. 2. Illustrative example of the random permutation method used to develop a null model for two matrices. Elements for each matrix are differentiated with upper- and lowercase letters (indicating row and column position; upper panel). Diagonal matrix elements correspond to simple correlation coefficients, and off-diagonal elements comprise partial correlation coefficients. Matrix elements from diagonal (shaded) and each of five off-diagonal columns are pooled separately (middle panel), and the locations of elements in each pool are permuted. Solid arrows portray an example of the pooling of off-diagonal elements from paired columns. Subsequently, elements from each pool are randomly reassigned a new position in one of two matrices, but the affiliation of an element with its original pool (i.e., column location) is retained (lower panel). Dashed arrows portray an example of the reallocation of off-diagonal elements into original column locations.

strength and nature of the relationship with spatial features of the landscape at each scale.

To determine whether the association of biotic response variables with landscape characteristics changed as a function of scale, pairs of matrices derived at different scales were compared using a null-model approach (Gotelli and Graves 1996). Null models were developed with permutation methods that randomized ecological data with constraints. Certain attributes of the data were varied stochastically while holding the remaining data structure constant, thereby creating a pattern that would be expected in the absence of the particular ecological mechanism of interest. More specifically, the association between patterns at two different scales (e.g., two correlation matrices) was compared to a distribution of analogous associations generated by randomizing the elements of the same two matrices. If the association between matrices is among the least frequent under the null distribution, the association is significant.

The structure of correlation matrices was related to three attributes of the data: (1) the identities of the

landscape variables correlated with a biotic response variable; (2) the identity of the landscape variable controlled (partialed) in each correlation; and (3) the distinction between simple and partial correlations. The ecological mechanism of interest and the attribute of the data that was varied stochastically in permutations were the identities of the landscape characteristics to which a biotic response variable was correlated. Null-model constraints maintained the identity of the partialled landscape variable, as well as the distinction between simple and partial correlations, in this manner retaining much of the original biological structure in the null model. That is, permutations randomly varied data attribute type 1 and constrained data attribute types 2 and 3, thereby generating a null pattern that removed the relationship between a biotic response variable and a suite of landscape characteristics.

The random permutation algorithms separately pooled simple correlation coefficients (diagonal matrix elements) and each column of partial correlation coefficients (off-diagonal matrix columns) for a pair of matrices (Fig. 2). This generated $n + 1$ pools, where

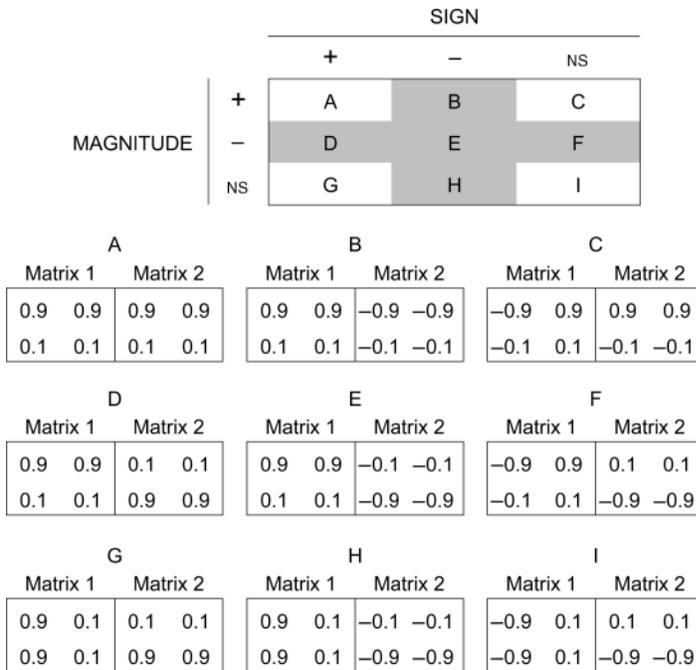


FIG. 3. Nine general types of matrix correspondences are possible based on tests of magnitude and sign patterns (upper panel). A plus (“+”) sign indicates a more similar correlation than expected by chance, a minus (“-”) sign indicates a more dissimilar correlation than expected by chance, and NS (not significant) indicates random associations. Shaded cells denote scale dependence. Examples that give rise to each of the empirical outcomes illustrate the nature of matrix correspondence and scale dependence (lower section A–I).

n is the number of landscape variables, and the content of each pool was derived equally as the union of elements from two matrices. The matrix elements from each pool were randomly reassigned a new position in one of two matrices, but their association with a particular pool was retained. That is, the location of an element was randomized with equal probability of its reassignment into the same column of either paired matrix. Randomization within these constraints produced null patterns that decoupled the association between a biotic response variable and landscape characteristics, but maintained the remaining data structure.

The test statistic used to compare matrices was the sum of squared deviations of corresponding matrix elements. Unlike the statistic based on the sum of cross-products, it works equally well for both continuous and binary data. The sum of squared deviations “counts” the differences in binary data matrices, whereas the sum of cross-products quantifies only paired nonzero elements and can “miss” differences between matrix elements. Parametric (Pearson) and nonparametric correlation coefficients (Spearman or Kendall) of ranked elements of paired matrices also may be used as alternative test statistics in a manner analogous to that used for Mantel tests (Legendre and Legendre 1998:552). The choice of appropriate statistic depends on the type of data examined (e.g., quantitative vs. semiquantitative) and its distributional assumptions.

Because the total number of possible random permutations for a pair of matrices may be very large (i.e., the factorial of the product of 2 and the number of matrix rows), the development of the null distribution was approximated with a sampled permutation test (Le-

gendre and Legendre 1998:25) of 5000 iterations. Significance was estimated as the proportion of iterations whose test statistic was less than or equal to the observed test statistic. Observed probabilities less than 0.500 (positive correspondence) were multiplied by 2 to account for the two-tailed nature of the test. Observed probabilities greater than 0.500 (negative correspondence) were subtracted from 1 prior to doubling the probability value [e.g., $P = (1 - 0.988) \times 2 = 0.024$]. The generation of a null model and the test of the difference between pairs of correlation matrices were programmed in MATLAB version 4.2c.1 (MathWorks 1995; see the Supplement).

A pair of correlation matrices may correspond to one another based on the strength of association among elements, the direction of association, or both. Consequently, two separate analyses were used to decompose the correspondence between matrices into their constituent and independent parts. The first analysis examined the difference between the absolute values of corresponding elements of paired matrices (magnitude test). The second analysis examined the difference in direction of the elements of paired matrices (sign test), and reassigned elements to binary values (1 for positive, 0 for negative). The case for separately analyzing correspondence in the magnitude and sign of paired matrix elements arose because preliminary tests based on the sum of squared deviations showed that elements with similar absolute values but different signs (e.g., 0.9 and -0.9) would cancel and result in small and nonsignificant test statistics.

A pair of matrices can exhibit one of nine possible structural correspondences (Fig. 3), as determined by

TABLE 1. Interpretation of focal scale dependence in the response of a species or a community parameter to landscape characteristics.

Magnitude	Sign	Fisher's	Scale	Correspondence between matrices	Pattern
+	+	*	independent	magnitude and sign similarity	A
+	-	*	dependent	magnitude similarity; sign dissimilarity	B
+	NS	*	inconclusive	magnitude similarity only	C
-	+	*	dependent	magnitude dissimilarity; sign similarity	D
-	-	*	dependent	magnitude and sign dissimilarity	E
-	NS	*	dependent	magnitude dissimilarity only	F
NS	+	*	inconclusive	sign similarity only	G
NS	-	*	dependent	sign dissimilarity only	H
NS	NS	NS	inconclusive	not significant	I
NS	+	NS	inconclusive	not significant, but with sign similarity	I
NS	-	NS	inconclusive	not significant, but with sign dissimilarity	I
+	NS	NS	inconclusive	not significant, but with magnitude similarity	I
-	NS	NS	inconclusive	not significant, but with magnitude dissimilarity	I

Notes: Thirteen outcomes are possible, based on separate tests of the correspondence in magnitude and sign of matrix elements, and Fisher's test of combined probabilities for both tests (see Fig. 3 for illustrative examples of test result combinations). Significant pattern similarity (+) in both the magnitude and sign tests, and a significant Fisher's test ($*P < 0.05$) indicate scale independence (pattern A). Scale dependence is indicated by significant pattern dissimilarity (-) in magnitude or sign tests combined with a significant Fisher's test (patterns B, D, E, F, and H). A significant Fisher's test with only pattern similarity in magnitude or sign tests indicates an inconclusive correspondence of matrix pattern (patterns C and G). A nonsignificant Fisher's test (NS) may also result in an inconclusive correspondence of matrix pattern (pattern I).

the combination of results from the magnitude and the sign tests (i.e., three possible results for each test: positive, negative, nonsignificant). Overall consistency in the structure of matrices was evaluated with a meta-analysis (Fisher's test for combined probabilities; Sokal and Rohlf 1995:794) of the results of the separate magnitude and sign tests. Because we wished to develop a test procedure that was sensitive to scale dependence, experiment-wise error rate was held constant at 0.10 with the Dunn-Sidak method (Sokal and Rohlf 1995:703). Consequently, the comparison-wise error rate was adjusted to 0.035 for each of three pairwise comparisons involving scale (1 km vs. 3 km, 3 km vs. 5 km, 1 km vs. 5 km). A combined probability less than or equal to the comparison-wise error rate was evidence of a significant correspondence between matrices. Significance in the separate magnitude and sign tests was based on the probability from each test being less than or equal to the average probability ($P = 0.075$) needed for obtaining significance in the Fisher's test.

A positive correspondence in both sign and magnitude tests, as well as a significant Fisher's test (pattern A; Table 1), demonstrated that the biotic response variables were associated with landscape characteristics in similar ways across scales (i.e., scale independence). A negative correspondence between matrices, with respect to either sign or magnitude, and a significant Fisher's test (patterns B, D, E, F, and H) demonstrated that biotic response variables were associated with landscape characteristics in dissimilar ways across scales (i.e., scale dependence). Outcomes in which Fisher's test was significant, but negative magnitude or sign tests were not evident, were considered to be inconclusive evidence of a scale-dependent response (patterns C and G). A nonsignificant Fisher's test with any combination of results for magnitude and sign tests

also resulted in an inconclusive correspondence between contrasted matrices (pattern I). Inconclusive outcomes may occur because one or both matrices are sets of random correlations. Cases in which only one of two matrices consists of random correlations may indicate dissimilar responses across scales (i.e., scale dependence). However, this case is not distinguishable from cases in which both matrices comprise random correlations (i.e., scale independence).

RESULTS

Multiple regression

The abundance of each species responded significantly to one or more landscape characteristics (Table 2). However, the identities of the characteristics and the strengths of the associations differed greatly as a function of scale. For example, edge density significantly accounted for 24% of the variation in abundance of *Artibeus lituratus* at the 5-km scale, but only (marginally) accounted for 18% at the 3-km scale, and did not significantly affect abundance at the 1-km scale. A regression model for *Sturnira lilium* at the 5-km scale identified four dependent variables (forest cover, patch density, patch size, and edge density) that together accounted for 73% of the variability in abundance. However, no landscape characteristic significantly accounted for variability at the 1-km scale.

In general, species showed a greater number of significant responses to landscape characteristics at larger than at smaller scales (Table 2). Multiple regression identified a total of five landscape characteristics at the 5-km scale associated with a total of 12 significant responses among all eight species. In comparison, two landscape characteristics at the 3-km scale elicited five significant responses, and only one landscape charac-

TABLE 2. Multiple regression analyses of bat species abundance and community indices (mean \pm SD) as a function of landscape characteristics for focal scales of 1 km, 3 km, and 5 km radii.

Biotic variable	1-km landscape			3-km landscape			5-km landscape		
	ΔR^2	<i>P</i>	Sign	ΔR^2	<i>P</i>	Sign	ΔR^2	<i>P</i>	Sign
<i>Artibeus fimbriatus</i> (13.8 \pm 8.1)									
Patch density				34	0.03	+	39	0.02	-
Patch size									
Model <i>R</i> ²				30	0.03		33	0.02	
<i>Artibeus literatus</i> (382.1 \pm 111.0)									
Edge density				25	0.07	-	30	0.04	-
Patch proximity	52	0.01	-						
Model <i>R</i> ²	46	0.01		18	0.07		24	0.04	
<i>Carollia perspicillata</i> (11.6 \pm 8.8)									
Forest cover				21	0.04	+	16	0.10	+
Patch density				36	0.02	+			
Patch size							34	0.03	-
Patch shape	36	0.05	+						
Patch proximity							10	0.14	-
Model <i>R</i> ²	29	0.05		48	0.01		49	0.02	
<i>Chrotopterus auritus</i> (0.9 \pm 1.4)									
Forest cover				26	0.06	+	29	0.05	+
Patch proximity	29	0.09	+						
Model <i>R</i> ²	21	0.09		20	0.06		24	0.05	
<i>Glossophaga soricina</i> (1.6 \pm 1.7)									
Patch density				23	0.08	+			
Patch size	42	0.03	+				14	0.11	-
Patch proximity							38	0.02	-
Model <i>R</i> ²	35	0.03		16	0.08		43	0.02	
<i>Platyrrhinus lineatus</i> (3.7 \pm 3.1)									
Patch density				28	0.05	+			
Patch size							31	0.04	-
Model <i>R</i> ²				22	0.05		30	0.04	
<i>Pygoderma bilabiatum</i> (37.3 \pm 17.1)									
Forest cover				38	0.02	+	43	< 0.01	+
Patch size	48	0.02	-						
Patch proximity							22	0.02	+
Model <i>R</i> ²	43	0.02		32	0.02		59	< 0.01	
<i>Sturnira lilium</i> (100.0 \pm 57.2)									
Forest cover				49	< 0.01	+	44	< 0.01	+
Patch density							11	0.01	+
Patch size	24	0.12	-				14	0.04	+
Edge density							7	0.04	-
Nearest neighbor				14	0.07	+	7	0.11	+
Model <i>R</i> ²	16	0.12		56	< 0.01		73	0.01	
Richness (6.9 \pm 1.2)									
Patch density							11	0.08	+
Forest cover	28	0.09	+						
Patch density							15	0.03	-
Patch size				42	0.01	-	44	0.01	-
Patch proximity							12	0.07	-
Model <i>R</i> ²	20	0.09		37	0.01		62	0.01	
Evenness (0.5 \pm 0.1)									
Forest cover				60	< 0.01	+	56	< 0.01	+
Patch density							11	0.08	+
Patch shape	40	0.04	+						
Nearest neighbor				22	< 0.01	+			
Model <i>R</i> ²	33	0.04		78	< 0.01		62	< 0.01	

Notes: The term ΔR^2 is the individual contribution of variables to the regression model. Coefficients of multiple determination (model *R*²) are adjusted for the number of selected variables in the model. Significant regression models or parameters (*P* \leq 0.05) are indicated in bold. Symbols (+, -) under "Sign" refer to the sign of the regression parameter estimates. (Table modified from Gorresen and Willig [2004].)

TABLE 3. Tests of the similarity or dissimilarity in response of species or community parameter to landscape characteristics at different focal scales are given by significance levels (upper section) and test results (lower section).

Species	Correlation matrix comparisons								
	1 km–3 km tests			3 km–5 km tests			1 km–5 km tests		
	Magnitude	Sign	Fisher's	Magnitude	Sign	Fisher's	Magnitude	Sign	Fisher's
<i>Artibeus fimbriatus</i>	0.492	0.010	0.030	< 0.001	< 0.001	< 0.001	0.775	0.383	0.658
<i>Artibeus lituratus</i>	0.237	0.071	0.086	< 0.001	< 0.001	< 0.001	0.799	0.003	0.018
<i>Carollia perspicillata</i>	0.345	0.016	0.035	< 0.001	0.001	< 0.001	0.628	0.004	0.019
<i>Chrotopterus auritus</i>	0.111	0.004	0.004	< 0.001	< 0.001	< 0.001	0.032	0.010	0.003
<i>Glossophaga soricina</i>	0.225	0.002	0.003	0.031	0.002	0.001	0.505	0.044	0.106
<i>Platyrrhinus lineatus</i>	0.715	< 0.001	0.003	< 0.001	0.002	< 0.001	0.913	0.248	0.563
<i>Pygoderma bilabiatum</i>	0.728	0.031	0.108	< 0.001	0.112	0.001	0.219	0.238	0.206
<i>Sturnira lilium</i>	0.033	0.102	0.023	< 0.001	0.001	< 0.001	0.456	0.001	0.003
Species richness	0.773	0.001	0.007	< 0.001	< 0.001	< 0.001	0.076	0.046	0.024
Species evenness	< 0.001	0.126	0.001	< 0.001	< 0.001	< 0.001	0.006	0.182	0.009
<i>Artibeus fimbriatus</i>	NS	+	G	+	+	A	NS	NS	I
<i>Artibeus lituratus</i>	NS	–	I	+	+	A	NS	–	H
<i>Carollia perspicillata</i>	NS	–	H	+	+	A	NS	–	H
<i>Chrotopterus auritus</i>	NS	–	H	+	+	A	+	–	B
<i>Glossophaga soricina</i>	NS	–	H	+	+	A	NS	–	I
<i>Platyrrhinus lineatus</i>	NS	+	G	+	+	A	NS	NS	I
<i>Pygoderma bilabiatum</i>	NS	–	I	+	NS	C	NS	NS	I
<i>Sturnira lilium</i>	+	NS	C	+	+	A	NS	+	G
Species richness	NS	–	H	+	+	A	NS	–	H
Species evenness	+	NS	C	+	+	A	+	NS	C

Notes: Tests for consistency in the magnitude or direction of response to landscape characteristics are combined via Fisher's test. Comparison-wise error rates for the three pairwise contrasts were adjusted to 0.035 to hold experiment-wise error rate constant at 0.10 via the Dunn-Sidak method (Sokal and Rohlf 1995). Significance in magnitude or sign tests was established at $P \leq 0.075$ (the average probability required in Fisher's test to produce significance at 0.035). Significant tests are shown in bold. Symbols + and – indicate that the response was more similar or more dissimilar than expected due to chance; NS indicates nonsignificance. Letters A–I represent the type of similarity or dissimilarity in response between focal scales as a result of separate tests of the correspondence in magnitude and sign of matrix elements, and Fisher's test of combined probabilities for both tests (see Table 1). Focal scale-dependent responses are shown in bold.

teristic at the 1-km scale was associated with two significant responses.

As with the regression analyses of species-specific responses, the identity of the landscape characteristics and strength of the association with community indices ranged greatly as a function of scale (Table 2). For example, patch size significantly accounted for 44% of the variability in species richness at the 5-km scale, somewhat less (42%) at the 3-km scale, and was not associated significantly with species richness at the smallest (1-km) scale. Regression models also differed in the number of landscape characteristics associated with community indices. For instance, regression models identified patch density and patch size at the 5-km scale that together accounted for 62% of the variation in species richness, whereas no landscape characteristic accounted significantly for community-level variability at the 1-km scale. In general, community parameters showed a greater number of significant responses to landscape characteristics at larger than at smaller scales (Table 2). For both the 3-km and 5-km scales, multiple regression identified a total of three landscape characteristics associated with a total of three significant responses in species richness and evenness. In comparison, only one landscape characteristic at the 1-km scale was associated with a significant response.

Correspondence of correlation matrices

The comparison of correlation matrices with tests of magnitude and sign correspondence identified both scale-dependent and scale-independent responses of species to landscape characteristics (Table 3). Scale dependence was detected for four of eight species: *Artibeus lituratus*, *Carollia perspicillata*, *Chrotopterus auritus*, and *Glossophaga soricina*. All scale-dependent responses were attributable to the association of species abundance with landscape characteristics acting in opposite directions across scales (i.e., sign dissimilarity; patterns B and H). That is, abundances were associated positively with landscape characteristics at one scale and negatively with characteristics at another scale. Scale-dependent responses were only apparent between the smallest and either of the two larger scales (i.e., 1 km–3 km, or 1 km–5 km contrasts). With one exception (*Pygoderma bilabiatum*), each species responded similarly to landscape characteristics at the middle and large scales (i.e., 3 km and 5 km). Three (*Artibeus fimbriatus*, *Platyrrhinus lineatus*, and *Sturnira lilium*) of eight species exhibited a combination of similar (i.e., scale-independent; pattern A) and inconclusive responses between scales (i.e., patterns C, G, and I).

Null-model analyses detected both scale-dependent and scale-independent responses of community indices to landscape characteristics (Table 3). Species richness demonstrated scale dependence because it responded in opposite directions to landscape characteristics across scales (i.e., sign dissimilarity, pattern H). In contrast, evenness did not show scale-dependent responses to landscape characteristics.

DISCUSSION

Landscape characteristics

This study corroborates theoretical and empirical findings that ecological patterns depend greatly on focal scale (Allen and Starr 1982, Kolasa and Pickett 1991, Lyons and Willig 1999, Waide et al. 1999, Gross et al. 2000, Willig et al. 2003a, Graham and Knight 2004). Most landscape studies evaluate species responses to the spatial structure of habitat measured from areas of a single size (e.g., watersheds [McGarigal and McComb 1995]; quadrats [Hargis et al. 1999, Villard et al. 1999, Numa et al. 2005], 2 km radius plots [Gehrt and Chelsvig 2003]). However, we found the identity of landscape characteristics associated with population and community attributes to be dependent on scale (Table 2). The *size* of the landscape to which an organism responds may be determined by the *identities* of landscape variables. Consequently, there is no single focal scale of the landscape to which species or communities respond. This conclusion is intuitively reasonable. Typically, organisms are cognizant of resources and habitat features at a range of scales (Kotliar and Wiens 1990), and may respond to both local and regional characteristics of a landscape. For example, an individual bat may respond to the presence of a resource that is small relative to its range of movement (e.g., a small body of water), and yet simultaneously be sensitive to features at larger scales (e.g., woodland cover; Gehrt and Chelsvig 2003). Conversely, a bat may be sensitive to an aspect of its immediate neighborhood (e.g., patch edge) not important at large scales. Ecological considerations of associations between landscape structure and population and community attributes of phyllostomid bats are treated in greater detail in Gorresen and Willig (2004).

Focal scale of response

Bat abundances were associated significantly with landscapes characteristics at focal scales as large as 5 km in radius. Although the home range sizes of bats are poorly known, this scale probably would include all or most of the home range of captured individuals, at least for species with small- to mid-sized territories. For example, mid-sized species such as *Carollia perspicillata* probably have home ranges <3 km in radius (Heithaus and Fleming 1978, Fleming 1988). Similarly, the maximum recorded distance between foraging sites visited by a single *Glossophaga soricina* was 1450 m

(Lemke 1984). The fact that species abundance is associated with features of landscapes larger than the home range of individual bats suggests that local abundance reflects a number of factors operating at different scales, including dispersal, habitat selection, species-specific autecological requirements, and the collective sampling of individuals.

Regional and local species densities are linked by the dispersal of individuals across habitats and among populations (i.e., source-sink populations [Pulliam 1988]; internal colonization [Gotelli 1991], and meta-population connectivity [Rolstad 1991]). Consequently, large-scale (regional) conditions indirectly determine local abundance by the movement of individuals among sites. Local populations also may respond to landscape features within areas greater than the home ranges of resident individuals for reasons other than source-sink and regional population dynamics. A local population may shift foraging areas over time to track resource availability, avoid predators, reduce competition, or explore new territory. For instance, *C. perspicillata* individuals that share a roost may change foraging areas within and between seasons (Fleming 1988). Therefore, the area affecting local abundance reflects habitat selection over time, and encompasses an area greater than the size of individual home ranges. In addition, species may have specialized resource requirements that demand a shift in location at different life stages. For example, bat species that move elevationally between wintering and maternity sites have large annual home ranges (e.g., Cryan et al. 2000). Finally, some bats are likely to have been netted at the edge of their home ranges. Because the home ranges of bats captured at a single location are unlikely to be coincident, they must collectively comprise an area larger than that of any single home range. Consequently, an aggregate of individual responses to landscape characteristics served to define population-level responses, and these were associated with habitat patterns at least as large as the extent of the landscape addressed in this study. The implication of this result for studies in landscape ecology is that habitat characteristics must be measured over areas sufficiently large to incorporate the collective response of individuals in a local population.

Because so little is known about the autecology and spatial dynamics of bats, in general, especially those in subtropical and tropical forests, it is difficult to construct directional hypotheses about scale-dependent responses. Nonetheless, our results suggest that multiple-scale assessments are necessary to adequately characterize features of habitats and their spatial configuration that affect the abundance of populations or their assembly into local communities. Consequently, multiscale approaches may be critical to the success of management and conservation strategies, whether they focus on target species or on assemblages of taxa.

Analytical applications

The matrix-contrast method presented here shares a number of features with other analytical methods such as Mantel tests (Legendre and Legendre 1998:552) and 4th corner problems (Legendre and Legendre 1998:565) in that they allow for comparison of multivariate data in matrix format and test for significance with permutation methods. However, there are two main differences between our approach and that of other matrix comparison methods: (1) the matrices developed here comprise partial correlation coefficients and thus are nonsymmetric; and (2) the test of matrix differences is decomposed into comparisons of correlation strength and direction (i.e., magnitude and sign).

The use of partial correlation coefficients provides measures of association that account for multiple intercorrelated factors among predictor variables, a trait frequently found in ecological data. The (dis)similarity matrices used in methods such as Mantel tests do not afford this flexibility and do not control for collinearity among variables. Partial Mantel tests do compute partial correlations *among* three matrices (Legendre and Legendre 1998:558), but do not control for the interrelationships *within* matrices.

Correlation matrices can correspond to one another based on the strength or direction of associations between response and predictor variables. Tests that do not distinguish between these aspects risk confounding their respective effects. Therefore, our analyses separately examined the magnitude and sign correspondence and subsequently recombined the results via a meta-analysis to provide an overall test of significance. Methods such as Mantel tests conceivably can distinguish among magnitude and sign correspondence by appropriately coding input data, separately testing and recombining results in a manner similar to that applied here.

Our method may be further adapted to include an examination of the contribution and significance of a particular predictor variable to the empirical pattern. In this case, the test statistic and null distribution can be limited to the sum of squared deviations from the subset (i.e., matrix row) of elements corresponding to the predictor variable in question. Significant correspondence would indicate that the particular predictor variable was more (dis)similar in correlation strength or direction than expected by chance.

Our method may be generalized in a manner similar to a Mantel test to assess the presence of a specific ecological structure. This approach entails the comparison of a matrix of empirical observations with a matrix comprising a hypothetical pattern established a priori (i.e., model matrix; Legendre and Legendre 1998:555). For example, one may wish to test whether the abundance of a species is correlated strongly and negatively with a suite of variables indicative of fragmented habitat. In this case, the matrix of observed

correlations is contrasted with that of a matrix of hypothesized correlations, and one-tailed tests of magnitude and sign measure the degree of negative correspondence between matrices. Various combinations of predictor variables and levels of correlations may be examined, and the significance of the magnitude and sign tests may be evaluated for patterns indicative of increasing correspondence between empirical and hypothesized ecological structure.

ACKNOWLEDGMENTS

We thank S. Andelman, S. Scheiner, and two anonymous referees for reviewing drafts of this manuscript. E. Fish and R. Owen provided encouragement, support, and critical reviews. Logistical assistance was provided by the Fundación Moisés Bertoni para la Conservación de la Naturaleza, CITES-Paraguay, Dirección de Parques Nacionales y Vida Silvestre. We are grateful to W. Baker, P. Cryan, C. Kanebuachapegi, G. McMillan, J. Padwe, and D. Taylor for field assistance. Financial support was provided by the Wildlife Conservation Society, the Conservation and Research Foundation, Bat Conservation International, the National Science Foundation (DEB-94009226), and the Department of Biological Sciences and the Graduate School of Texas Tech University. This research was executed as partial fulfillment of the requirements of the M.S. degree at the Texas Tech University.

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SUPPLEMENT

MATLAB source code for the generation of a null model via matrix permutation models and the test of the difference between pairs of correlation matrices is available in ESA's Electronic Data Archive: *Ecological Archives* A015-065-S1.