THE RESPONSE OF BATS TO LANDSCAPE STRUCTURE IN AMAZONIAN FOREST: AN ANALYSIS AT MULTIPLE SCALES

by

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ABSTRACT

Habitat loss and fragmentation are currently the most serious threats to conserving biodiversity. This is especially the case in the Amazon Basin where species richness and diversity are at their peak, and deforestation is increasing at an alarming rate. Bats achieve their highest functional and taxonomic diversity in the Neotropics, and provide a suite of ecosystem services critical to maintaining tropical forests. However, very little is known regarding the response of populations and assemblages to spatially explicit aspects of landscape structure. The responses of 24 phyllostomid species and 4 assemblage characteristics to landscape structure were analyzed at each of 3 focal scales at 14 sites.

Satellite imagery was classified into two land-cover types (i.e., forest and non-forest) and processed with FRAGSTATS to quantify characteristics of landscape composition and configuration. Assemblage, trophic guild, and population responses to landscape characteristics were scale dependent. Frugivores responded more to landscape composition, whereas gleaning animalivores and assemblage characteristics responded only to landscape configuration. In general, the abundances and richness of species were higher in moderately fragmented forest than in continuous forest. This is likely due to the dominance of frugivores in assemblages and the abundance of fruits provided by successional plant species, suggesting that bats may be important in promoting secondary succession. Although frugivorous bats may increase when deforestation and fragmentation is small compared to the size of the regional landscape, changes in land use, specifically conversion of forest habitat, likely enhance the vulnerability of bats with

specialized ecological requirements. Consequently, even moderate amounts of fragmentation can affect local populations and may thereby alter the structure of assemblages.

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CHAPTER I
INTRODUCTION

Effects of Fragmentation

Deforestation and fragmentation of tropical forests have occurred at alarming rates in recent years, with an average of 15.2 million hectares of the world's tropical forest lost each year between 1990 and 2000 (FAO 2003). Habitat loss is the main threat to conservation of biodiversity (Hilton-Taylor 2000). Moreover, the rate of habitat loss associated with anthropogenic activities is increasing at startling rates (NRC 2001, 2003; Vitousek et al. 1997), especially in the Neotropics, which is home to a considerable proportion of the world's species (Heywood and Watson 1995). The present rate of deforestation in the Amazon is > 2 million hectares a year (Fearnside et al. 2005) and is predicted to increase as more paved roads are constructed within the region's core (Soares-Filho et al. 2006), fragmenting the remaining large continuous tracts of forest. Fragmentation in the tropics generally results in a landscape that comprises remnant islands of native vegetation surrounded by a matrix of areas disturbed by urbanization and agriculture, or by areas in various stages of secondary succession. The primary consequences of fragmentation are loss of original habitat, reduction in sizes of habitat patches, and increased isolation of habitat patches, all of which may influence the diversity and community composition of the area (Wilcox and Murphy 1985). Remnant forest patches often experience altered disturbance regimes and microclimate, invasion by exotic plant and animal species, and increased human exploitation in the form of hunting, burning, grazing, and resource extraction (Turner and Corlett 1996).

Importance of Scale

Even though fragmentation is a phenomenon that involves landscapes, surprisingly few studies have compared population characteristics among landscapes and even fewer have quantified differences between landscapes comprising unmodified habitat and landscapes exhibiting various degrees of fragmentation (Andrén 1994, Dooley and Bowers 1998). Most studies (e.g., McGarigal and McComb 1995, Villard et al. 1999) that analyze population and community responses to habitat fragmentation consider landscape characteristics at a single, arbitrarily delineated focal scale. Most studies of the effect of habitat fragmentation on bird and mammal abundances and distributions have employed a patch-based scheme (Andrén 1994). Moreover, relationships derived from patches (i.e., relatively homogeneous areas; Forman 1995) have been used to predict the response of populations and assemblages to landscape structure (i.e., the composition, spatial arrangement, and proportion of different patches) and fragmentation (McGarigal and McComb 1995). However, it is unclear if relationships between biodiversity and habitat characteristics derived at the focal scale of a patch can be extrapolated to those at the focal scale of a landscape (Wiens et al. 1987, 1993). Spatial patterns are scale dependent. The ability to detect patterns is a function of grain (i.e., size of individual units of observation, such as quadrats or pixels) and extent (i.e., the domain of analysis; Wiens 1989, Levin 1992), whereas the ability to describe, compare and attribute processes to patterns depends on the focus (i.e., the inference space to which the data points apply in an analysis; Scheiner et al. 2000). Attributes of species and communities demonstrate nonlinear associations with aspects of habitat

fragmentation. Moreover, abrupt changes in responses of species occur when the focal scale of analysis changes or when landscape structure changes in even a small way (With and Crist 1995). Species differ in the scales at which they secure resources or respond to heterogeneity (Wiens 1989, Milne et al. 1992, With 1994, Turner et al. 2001), implying that analyses at multiple focal scales are essential to elucidate how abundance, richness, or other aspects of biodiversity respond to variation in habitat characteristics (Wiens et al. 1987, Turner et al. 2001).

The Role of Bats

Bat populations and communities have qualities that make them model organisms for the study of long- and short-term consequences of habitat fragmentation in the Neotropics. The Chiroptera is the second-most species-rich order of mammals, generally exhibiting the highest richness and abundance of any mammalian order in tropical forest communities (Handley 1967, Wilson and Reeder 1993, Stevens and Willig 2000, Patterson et al. 2003). Bats, similar to most taxa, increase in richness with decreases in latitude (Willig and Selcer 1989, Willig and Sandlin 1991, Willig et al. 2003), and achieve their highest taxonomic (approximately eighty percent of all bat species are found exclusively in the tropics) and functional diversity (i.e., all trophic groups represented) at sites in tropical regions (Stevens and Willig 2000, Patterson et al. 2003, Gianini and Kalko 2004). Bats fill a variety of trophic roles in tropical forests, interacting with a large number of other organisms and contributing to a number of ecosystem services. They are highly mobile and may travel long distances between roosts and foraging sites, making them efficient seed dispersers, pollinators, and predators of insects and small vertebrates (Findley 1993, Altringham 1996). The

exceptional mobility of bats, coupled with broad geographic distributions, make them ideal candidates for comparative macro-ecological studies with nonvolant mammals (e.g., rodents and marsupials) and birds (Willig et al. 2003). Furthermore, frugivorous bats of the family Phyllostomidae facilitate secondary succession and revegetation of deforested areas by dispersing seeds of pioneer plant species in the genera *Piper*, *Solanum*, and *Cecropia* (Fleming 1988). Being abundant, species-rich (as many as 110 species at localities in the Neotropics; Voss and Emmons 1996), and ecologically diverse makes bats a promising indicator group for analyzing the effects of habitat modification on biodiversity and community structure (Fenton et al. 1992, Kalko 1997, Medellín et al. 2000, Schulze et al. 2000). In addition, understanding the effects of habitat fragmentation and anthropogenic disturbance on bats is critical to designing a conservation program that is sensitive to maintaining natural ecosystem functions in tropical rainforests.

Previous Research

Studies throughout the Neotropics have quantified relationships between aspects of bat biodiversity and habitat fragmentation; however, the responses of bat assemblages and species to habitat fragmentation are equivocal. For example, phyllostomid diversity was higher in undisturbed than disturbed habitats, but species richness and total captures did not differ between habitats in Mexico (Fenton et al. 1992). Richness was less but abundance was greater in forest fragments than in continuous forest in French Guiana (Brosset et al. 1996), whereas no difference in species richness occurred between fragmented and unfragmented habitats and no relationship occurred between proportion of captures per guild and fragment size in Guatemala (Schulze et al. 2000). In contrast, diversity, richness and abundance are higher in continuous forest than in fragments, and

guild composition differed between fragmented and unfragmented habitat in French Guiana (Cosson et al. 1999). Diversity, richness, and the number of rare species are correlated with the structure of vegetation, and community structure is associated negatively with forest disturbance in Mexico (Medellín et al. 2000). All of these studies have relied on dichotomous and sometimes qualitative descriptions of habitats (e.g., disturbed vs. undisturbed, Fenton et al. 1992; fragmented vs. continuous forest, Schulze et al. 2000) or simple indices of landscape composition (e.g., size of forest fragments; Cosson et al. 1999) to investigate relationships between aspects of bat assemblages and habitat loss or fragmentation.

The association of assemblage structure and abundances of particular bat species with the spatial arrangement of habitat types within a landscape (i.e., landscape configuration) remains an area worthy of exploration. Measures of landscape composition (e.g., habitat area and number of patches) may not completely characterize the variance in abundance of individuals for birds or for mammals (Rotenberry and Wiens 1980, Andrén 1994, McGarigal and McComb 1995, Flather and Sauer 1996). Species may respond to a variety of additional attributes of landscape configuration (e.g., edge density, patch shape, and patch isolation), which represent more complex spatial characteristics. Correlations between richness or abundance of bats and a single measure of configuration (i.e., isolation of forest fragments) or a single measure of composition (i.e., forest area) returned conflicting results, supporting the idea that a more complete characterization of the landscape is required to extricate underlying relationships between bat biodiversity and habitat fragmentation. Abundance and richness were associated negatively with the distance between forest fragments, whereas no relationship occurred

between richness and forest area in Mexico (Estrada et al. 1993). Richness was correlated positively with forest area but was unrelated to the distance between fragmented and continuous forest in Sweden (de Jong 1995). Species-specific differences in response to forest fragmentation characterized the response of bats to a suite of indices concerning landscape structure (Gorresen and Willig 2004, Gorresen et al. 2005). Population and community responses were dependent on the focal scale of analysis, and species richness was correlated positively whereas species diversity was correlated negatively with measures of forest fragmentation.

In Iquitos, Peru, where habitat conversion currently occurs at a relatively small scale (i.e., 1 to 4 ha patches), abundance and richness of bats is higher in disturbed habitats than continuous forest, and 8 phyllostomid species from 4 sub-families (i.e., Glossophaginae, Phyllostominae, Carollinae, and Stenoderamtinae) significantly responded to habitat conversion (Willig et al. in press). The increasing rate of anthropogenic disturbance and resulting fragmentation of tropical forests make evaluating habitat fragments for their potential contribution to the maintenance of biological diversity a top priority for ecologists and conservation biologists (Turner and Corlett 1996). Moreover, conservation strategies must identify configurations of land-uses that sustain populations and maintain the composition of regional assemblages, while accommodating the needs of society (Martínez-Garza and Howe 2003, Cuarón 2005, Willig et al. in press). Variation in the responses of particular bat species to landscape characteristics (Gorresen and Willig 2004, Willig et al. in press), and equivocal evidence regarding response to fragmentation (Fenton et al. 1992, Estrada et al. 1993, Brosset et al. 1996, Cosson et al. 1999, Schulze et al. 2000, Bernard and Fenton 2002,

Gorresen and Willig 2004) at the population and assemblage level, suggest that the quantification of landscape structure at multiple focal scales is necessary to reveal associations between bats and their environment. This study assesses the scale-dependent responses of species abundances and aspects of biodiversity to landscape characteristics of Amazon rain forest that has been subjected to various degrees of fragmentation.

CHAPTER II
MATERIALS AND METHODS

Study Area

Research was conducted in lowland Amazonian forest to the southwest of Iquitos (3.74630˚S, 73.24333˚W), a city of moderate size in the Department of Loreto, northeastern Peru (Figure 2.1). The study area contains large areas of flooded and unflooded (terra firme) lowland tropical rain forests, white sand forests (varillal), and palm swamps (aguajals). Predominant plant families in the area are Palmae, Moraceae, Myristicaceae, and Leguminosae (Terborgh and Andresen 1998, Tuomisto et al. 2003). The climate is tropical, humid and almost aseasonal. Temperatures are relatively constant throughout the year, with mean monthly temperatures of 25˚-27˚C, and average daily high and nightly low temperatures of 32˚ and 21˚ C, respectively. Total annual precipitation ranges from 2600 to 3100 mm (Marengo 1998, Whitmore 1998, Madigosky and Vatnick 2000). Elevation ranges from sea level to 200 meters (Kalliola and Flores 1998).

Experimental Design

Fourteen sampling areas were established along the highway from Iquitos, southwest to Nauta (Figure 2.2). The number and placement of sites were determined so that sampling locations were > 4 km apart, included a representative range of habitat configurations (including deforestation), were accessible by field crews, and located on either side of the highway. The exact locations of sampling plot centers (Table 2.1) were

determined with the use of a Global Positioning System (Garmin® GPS 12 Personal Navigator®).

The bat fauna was sampled with mist nets (56,808 net meter hours) between September, 2003 and January, 2004. At each site, bats were captured during three two-night surveys, totaling 84 sampling nights. Each survey was separated by a minimum of 35 days and no more than 55 days. Repeated sampling of multiple sites in the region increased the likelihood of capturing uncommon species, and provided a comprehensive assessment of the regional assemblage. Sampling was not conducted on days immediately before, during, and following a full moon (i.e., when the moon is ≥ 90% illuminated), as these times may result in decreased activity of some species (i.e., lunar phobia; Erkert 1982, Gannon and Willig 1997). Twelve mist nets (12 m x 2.6 m) were erected in forest habitat only and positioned across trails and flyways on each sampling night. Nets were checked continually, with 30-45 minutes between visits to particular nets. Nets were opened at dusk for 5.5 hours (approximately until 23:30) each night, except during severe weather (i.e., strong wind or rain) because of increased health risks to bats. The number of deployed nets and the length of time they were open was recorded to facilitate comparisons of capture rates and species abundances among sites. Hair was trimmed from the back of each captured bat to facilitate identification of recaptures.

Use of a single sampling technique is rarely sufficient to accurately characterize diverse assemblages of species, and the biases associated with the use of ground-level mist-nets to sample bat communities have been discussed by a number of authors, including Handley (1967), Kunz and Brock (1975), Kunz and Kurta (1988), and Kalko

and Handley (2001). Ground-level mist-nets have been shown to effectively sample bats of the family Phyllostomidae, but other families (e.g., Vespertillionidae, Molossidae, Emballonuridae, and Thyropteridae) often are missed or under-represented as a result of their more sophisticated echolocation abilities or because they forage above the canopy or at edges of vegetation (Handley 1967, LaVal and Fitch 1977, Kalko and Handley 2001, Peters et al. 2006). As a result, analyses of the response of bats to landscape structure and tests for scale dependence in these responses were restricted to members of the family Phyllostomidae (Kalko1997, Gorresen and Willig 2004, Numa et al. 2005, Willig et al. in press).

Research involving live animals followed the guidelines for the capture, handling, and care of mammals approved by the American Society of Mammalogists and was approved by the Animal Care and Use Committee of Texas Tech University (ACUC# 01084-03). Data obtained from each captured bat included: species, sex, age reproductive condition, time and location of capture. External characteristics such as forearm length, total body length, ear length, and tibia length were measured to assist with subsequent verification of species identity for released specimens. A small number (≤ 20) of voucher specimens of each species were collected throughout the region during the study period to facilitate accurate taxonomic identification. Voucher specimens and incidentally collected individuals were processed as standard museum specimens (i.e., fluid preserved, full skeleton, or skin and partial skeleton) and were deposited at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos in Lima, Peru. Nomenclature follows the systematic recommendations of Simmons (2005) for bat taxa in lowland Amazonia, except for recognizing *Carollia benkeithi* (Solari and Baker

2006) rather than *C. castanea*, and *Artibeus planirostris* rather than *A. jamaicensis* (Lim et al. 2004).

Classification of Satellite Imagery

Measurement of landscape characteristics (Table 2.2) involved processing Landsat 5 Thematic Mapper data (path 6, row 63, recorded February 25, 2004) with ERDAS IMAGINE (ERDAS 1999), creating digital vegetation coverage and circular focal scales using ArcInfo 9.1 (ESRI 2005). Image data from the study area originally was classified into five land-cover classes: 1) closed canopy forest 2) secondary forest 3) agriculture and cleared areas 4) water or 5) roads and urban areas based on spectral reflectance properties. Classification accuracy of particular land cover classes was assessed by comparing habitat photos (identified by GPS points) collected during ground-truthing at each of the fourteen sites at the smallest focal scale (1 km radius) and aerial photographs encompassing the sites largest focal scales (5 km radius) to corresponding points on the classified imagery. Classification accuracy was 100 percent for the closed canopy forest, water, roads, and urban land cover classes. However, inconsistencies in the classification were found between the secondary forest and agriculture classes. To avoid misrepresentation of land cover classes, only the distinction between closed canopy forest and other habitats was retained (hereafter forest and nonforest). A digital vegetation coverage using two cover types was created in ArcMap (Figure 2.2) and was used in subsequent analyses to quantify landscape structure using FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps version 3.3 (McGarigal et al. 2002).

Landscape Structure

A landscape may be defined as a heterogeneous area comprising an interacting mosaic of patches at any scale relevant to the species under consideration (McGarigal and Marks 1995). To identify relationships between characteristics of the landscape and aspects of bat biodiversity, it is desirable to measure landscape attributes at a focal scale that would include the home ranges of individuals that compose local populations. The relationship between abundance and landscape characteristics may be weak or non-existent if landscape attributes are quantified at a focal scale different from that at which species perceive environmental variation. However, little is known about the sizes of bat home ranges, especially those in the Amazonian rain forests of northeastern Peru. Therefore, following the approach of Gorresen and Willig (2004) and Gorresen et al. (2005), concentric circles (1, 3 and 5 km radius) centered on each sampling locale delimited landscape boundaries for subsequent analyses (Figure 2.2). The smallest focal scale (1 km) was chosen to encompass the home ranges of smaller bat species that occur in the study area (e.g., *Glossophaga soricina* and *Mesophylla macconnelli*) as well as home ranges of gleaning insectivores that forage short distances from their roosts (e.g., *Lophostoma silvicolum* may travel only 500 meters from roosts while searching for prey; Lemke 1984, Arita et al. 1997, Kalko et al. 1999). Scales greater than 5 km radius were not examined because focal areas would overlap substantially, producing spatial dependence among observational units. Moreover, the selected focal scales facilitate comparison with previous research in Paraguay on scale-dependent habitat associations of bats with landscape structure (Gorresen and Willig 2004, Gorresen et al. 2005).

Landscapes are differentiated by spatial relationships among their component parts. A landscape can be characterized by its composition and configuration (collectively known as landscape structure), which can independently or in combination affect organisms and ecological processes (McGarigal and Marks 1995). Landscape composition refers to habitat types and their relative proportions, without reference to location or connectivity. Metrics used to quantify composition include total area, percent cover (of a particular habitat type), number of patches, patch density, mean patch size, and measures of patch richness, diversity, and evenness. Indices of landscape configuration describe the physical distribution and spatial arrangement of habitat types or patches. Habitat patches are distributed within landscapes, forming a complex mosaic, and their spatial pattern may strongly influence the abundance, distribution, or dynamics of resident populations (Wiens et al. 1993). Indices of landscape configuration include mean nearest neighbor distance, contagion, mean patch shape, proximity, total edge, and edge-to-area ratios (Turner et al. 2001, McGarigal and Marks 1995). Although numerous metrics are available to describe and quantify landscape structure, many are correlated strongly and contain redundant information (McGarigal and Marks 1995, Riitters et al. 1995, Turner et al. 2001, McGarigal et al. 2002). Consequently, a subset of indices (Table 2.2) associated with the presence and abundance of species in previous studies (for birds Rolstad 1991, McGarigal and McComb 1995, Villard et al. 1999 and for bats Gorresen 2000, Gorresen and Willig 2004) were selected to characterize associations between aspects of bat biodiversity and landscape structure.

The forest class served as the principal habitat type for all measures of landscape structure and the nonforest class represented the matrix within which forest patches were

dispersed. Landscape characteristics (i.e., forest cover, patch size, patch density, edge density, mean nearest neighbor distances among patches, patch proximity, mean patch shape and habitat diversity; see McGarigal et al. 2002, Gorresen and Willig 2004) were estimated at each of the 3 focal scales for each of the 14 sites (Table 2.3). Forest cover was expressed as the percentage of a site (i.e., a focal circle of known area) designated as forest in the classified image. Patch density was the number of forest patches within a site divided by the total area of the site, and was expressed as number of patches per 100 ha. Mean patch size was the average size of a forest patch within a site. Edge density was the total perimeter of all forest patches divided by the area of a site, standardized as meters per hectare. Mean shape index is an average perimeter to area ratio for all forest patches within a site. Calculated for one forest patch, it equals the patch perimeter divided by the minimum perimeter possible for a square patch of the same area. Mean nearest neighbor index describes the average distance between each forest patch and the shortest edge to edge distance to the most proximate forest patch. The index of mean proximity measures relative isolation by weighting distances between neighboring forest patches with the area of those neighbors. It is a mean of $\sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^2}$ calculated for each forest patch at each focal scale where a_{ijs} = area (m^2) of patch ijs and h_{ijs} = distance (m) between all possible pairwise patches, based on edge-to-edge distance (Table 2.2). Patch diversity index equals 1 minus the sum of the squared proportional areas of each patch type within the site. This value represents the probability that any 2 pixels selected at random from the site would be from different patch types based on the forest or nonforest classification.

Assemblage Structure

Taxonomic components of biodiversity (i.e., species richness, evenness, diversity, dominance, and rarity) are useful for assessing and quantifying the effects of anthropogenic activities on biological systems and may represent integrated indicators of stress (May 1986). In particular, diversity and richness of bat assemblages are responsive to habitat disturbance and have been used to assess the conservation value of particular sites in the Neotropics (Fenton et al. 1992, Wilson et al. 1996, Medellín et al. 2000). Species richness is the simplest and most intuitive way to describe and compare the biodiversity of an assemblage, and can be a reliable means of differentiating among assemblages (Magurran 1998), especially if sampling effort is standardized. Richness was calculated as the number of species captured at each site. However, comprehensive assessment of biodiversity from a taxonomic perspective requires consideration of measures based on relative abundance (i.e., evenness, dominance, rarity, and diversity; Chapin et al. 2000, Purvis and Hector 2000, Stirling and Wilsey 2001, Stevens and Willig 2002, Wilsey et al. 2005) in addition to richness, because these measures may not respond to habitat fragmentation in the same manner (Gorresen and Willig 2004). For example, evenness and richness respond differently to landscape characteristics (Gorresen and Willig 2004), and the number and identity of rare species differs in disturbed versus undisturbed habitats (Willig et al. in press) in New World bat communities.

Taxonomic diversity is a product of the number of species and equability of their importances, which can be estimated based on relative abundances. Several reviews

provide descriptions and guidelines in the use of indices of taxonomic diversity for assessment of biodiversity (e.g., Camargo 1995, Magurran 1988, Stevens and Willig 2002). I used the Shannon index (Pielou 1975) to estimate species diversity. I used Hurlbert's probability of interspecific encounter (PIE) to estimate evenness because it is unbiased with respect to sample size and measures the likelihood that the random selection of two individuals from a sample represent different species (Hurlbert 1971). I estimated dominance with the Berger-Parker index (Berger and Parker 1970), which describes the proportional abundance of the most abundant species. I estimated rarity as the number of rare species at a site, where species were rare if $p_i < 1/S$, and p_i equals the proportional abundance of species i and S is species richness (Camargo 1992).

Spatial Autocorrelation

Many ecological attributes (e.g., phytoplankton distributions in lakes, plant and animal distributions across continents, soil types, and fertility) display geographic patchiness across a range of spatial scales (Hutchinson, 1953, Simpson 1964, Tilman 1984, Cloern et al. 1992). Organisms are distributed neither uniformly nor at random in nature, but respond to factors such as temperature, water availability, competition and food availability, via immigration, emigration, reproduction, and mortality (Legendre 1993). The resultant spatial autocorrelation in abundances, a general statistical property most often observed as heterogeneity in or gradients of ecological characteristics, occurs when values of characteristics from geographically proximate locations are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected from random pairs of observations (Legendre 1993). Spatially autocorrelated data violate assumptions of many parametric and non-parametric approaches to data analysis and may

lead to inaccurate conclusions by biasing Type 1 (declaring significance too frequently under the null hypothesis in cases of positive autocorrelation) or Type 2 (declaring non-significance too frequently under the null hypothesis in cases of negative autocorrelation) error rates (Legendre 1993).

The degree to which differences in species composition are related to geographic distances between sites was assessed by correlation analysis. Ecological and geographical distance matrices were based on percent dissimilarity (Renkonen index) of species abundances between sites (Krebs 1989) and straight-line distances between geographic centers of sites, respectively (Table 2.4). Although this one tailed test of the null hypothesis of no association could be performed on all possible pair-wise combinations of sites (91 pair-wise combinations for n = 14 sites), it would lack power. To overcome this obstacle, a subset of pair-wise combinations was selected to increase the power of the test by obtaining the highest possible correlation coefficient, via elimination of combinations of sites that are less likely to be autocorrelated spatially. Selection of sites most likely to show compositional similarities was accomplished by generating a geographic connectivity graphic known as a Gabriel network (Gabriel and Sokal 1969, Matula and Sokal 1980, Gorresen 2000). A Gabriel network represents a compromise between methods that are too selective (e.g., the minimum spanning tree network) or too inclusive (i.e., all possible pair-wise comparisons) for this analysis. Gabriel networks employ a connectivity criterion such that "any two localities (A and B) are considered contiguous (connected) if no other locality lies on or within the circle whose diameter is the line AB" (Sokal and Oden 1978). The advantage of this method is that sites separated by large distances may be linked if they are the most proximate

candidates, even though other criteria such as mean nearest neighbor distance or average distance among sites may leave them unconnected. Although the Gabriel network connects more sites than do other methods (i.e., the minimum spanning tree network), it was quite selective (15 links) compared to the number of possible pairwise comparisons (91). This selectivity is likely due to the linear arrangement of sites. Consequently, connectivity between sites was calculated with an adjusted Gabriel network, and sites that were proximate or separated by only one site were used as the subset most likely to show spatial autocorrelation (Figure 2.3). This adjusted Gabriel network identified 28 pairwise comparisons, whereas only15 pair-wise comparisons were identified with a traditional Gabriel network. Ecological and geographic distances between sites identified with the adjusted Gabriel network formed the basis of a test for spatial autocorrelation (Table 2.4). Because this methodology is novel, results from a test of spatial autocorrelation using sites identified with a traditional Gabriel network were included for comparison. Because no *a priori* assumptions were made regarding the kind of association between ecological and geographic distances, Spearman rank correlation (Sokal and Rohlf 1995) was used to quantify associations (Gorresen and Willig 2004). Percent dissimilarity and Gabriel connectivity were calculated with script files (PCTDISM and GABRIEL; Gorresen 2000) in Matlab version 6.5 (Mathworks Inc. 2002).

Response of Species, Guilds, and Assemblages to Landscape Structure

The presence and abundance of species are related to the amount and quality of available habitat. Additionally, measurements of landscape structure (Table 2.5) are correlated with habitat area (Rolstad 1991, McGarigal and McComb 1995, Gorresen and Willig 2004, Gorresen et al. 2005). To avoid the confounding of assessments of the

relationships between species abundance and landscape characteristics, it was necessary to partition and remove the effects of habitat (forest) area from each measurement of landscape structure using regression analyses (Table 2.6). The residuals from these regression analyses were independent of habitat area, and were used along with forest cover in its original form as independent variables in subsequent analyses of population and assemblage responses to landscape structure (Table 2.7).

The abundance of each species was double square-root transformed prior to multiple regression analysis with residuals of landscape characteristics (hereafter landscape characteristics). This reduces the influence of outliers on mean values, normalizes distributions, homogenizes variances, and improves the linear nature of regression relationships (Neter et al. 1996, Gorresen 2000). The variables describing assemblage structure (diversity, richness, evenness, rarity, and dominance) were not transformed because values are not raw data (as in abundance counts) and in some cases (e.g., H′, PIE) are already transformations of empirical data.

Multiple regression analysis assessed the relationship between a biotic response characteristic at the population (i.e., the local abundance of a particular bat species) or assemblage (i.e., diversity, richness, evenness, rarity, and dominance) level with each of a suite of landscape characteristics (i.e., forest cover, patch density, mean patch size, diversity, edge density, mean shape, mean nearest neighbor distance, and mean proximity). Regression models were evaluated using SPSS 9.0 (SPSS Inc. 1999). At each focal scale, stepwise selection identified a parsimonious combination of landscape characters that maximized R^2 with respect to variation in a biotic response characteristic. Additionally, the association between a biotic response characteristic and each landscape

characteristic was identified by correlation analysis to identify particular characteristics of the landscape to which bats respond, and to facilitate comparisons among focal scales. Species captured less than 10 times during the study were excluded from population-level analyses due to the ubiquity of zeros in the empirical data. However, all 42 phyllostomid species regardless of abundance were included in estimates of biodiversity for assemblage-level analyses.

Scale Dependence

Habitat fragmentation refers to the connectivity of habitat types within a landscape. Ultimately, connectivity depends on the ability of a species to move through various habitats that compose landscapes (O'Neill et al. 1988, With and Crist 1995). Because of differences in mobility, habitat requirements, and life history, species differ in the scales at which they interact with the environment (Kotliar and Wiens 1990, Andrén 1994, With 1994, With and Crist 1995, Gorresen et al. 2005). Consequently, the connectedness of a landscape is dependent on the scale at which species interact with spatial heterogeneity of the landscape (O'Neill et al. 1988, With and Crist 1995). As a result, a species-centered view of fragmentation is necessary, and a single arbitrarily defined focal scale is insufficient to characterize relationships between species or assemblages and spatial pattern (Turner et al. 2001).

Indices that measure the composition and configuration of landscapes are scale dependent. As the focal scale selected to quantify a landscape changes, descriptive attributes such as the proportion or number of cover types, patch density, and amount of edge may change (Table 2.3). Accordingly, the detection of ecological relationships is influenced to some extent by the spatial scale at which landscape characteristics are

measured (Wiens 1989, Gross et al. 2000, Turner et al. 2001, Lyons and Willig 2002, Gorresen et al. 2005). Consequently, it is essential that habitat characteristics be quantified at a range of scales relevant to the study organisms. In the absence of adequate data, as is the case regarding home ranges of Neotropical bats, patterns measured at multiple spatial scales facilitate the detection of scale dependency in the association of a biotic response characteristic with landscape structure (Gorresen et al. 2005).

The response of a particular biotic response characteristic to landscape characteristics was analyzed to assess scale dependency. Correlation analyses between a biotic response characteristic at the population or assemblage level and a suite of landscape metrics were performed at each focal scale. Simple and partial correlations were calculated using the bivariate and partial options following the correlation command in SPSS 9.0 (SPSS Inc. 1999). Each partial correlation between a response characteristic (X) and a landscape characteristic (A-F) controlled for the association with one other characteristic. For example, $r_{X \cdot A,B}$ is the correlation of *X* to landscape characteristic *A* controlling for the effect of landscape characteristc *B* (Figure 2.4). Empirical matrices created from simple and partial correlation coefficients summarized the overall strength and nature of the relationship between a biotic response characteristic and landscape characteristics at each focal scale.

Pairs of correlation matrices derived at different focal scales were compared using a null model approach (Figure 2.5) developed by Gorresen et al. (2005). Specifically, the association between patterns at two different focal scales (e.g., 1 km vs. 3 km) was compared to a distribution of like associations generated by randomizing the elements of

the same two matrices. If the association between matrices is among the rarest under the null distribution, the association is significant. Null models were developed with permutation methods that randomized ecological data with constraints to disentangle the association between a particular response characteristic and multiple landscape characteristics (Figure 2.5). This was accomplished by holding some aspects of the data constant while allowing other elements to vary stochastically, creating a pattern expected in the absence of a particular ecological mechanism (Gotelli and Graves 1996). The distinction between simple and partial correlations, along with the identity of the landscape characteristic controlled (X_2) in each correlation was preserved by null model constraints, thereby maintaining some biological structure. The particular landscape characteristic to which a biotic response characteristic was correlated (X_1) was permuted randomly. Randomization within these constraints generated a null pattern that lacked the relationship between a biotic response characteristic and a suite of landscape characteristics but maintained the remaining correlation structure of the data (Gorresen et al. 2005).

The test statistic used to compare matrices was the sum of squared deviations of corresponding elements in the 2 matrices. The total number of possible random permutations for a pair of matrices may be very large (in this case 16!). Consequently, the development of the null distribution was approximated with a sample permutation test (Legendre and Legendre 1998) based on 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 (Gorresen et al. 2005). The generation of a null model and the test of the difference between pairs of correlation matrices were executed with random permutation algorithms (PERMDIFF and PERMCORR; Gorresen 2000) programmed in MATLAB version 6.5 (MathWorks 2002).

A pair of correlation matrices may correspond to one another based on the strength or direction of association among elements, or both. Consequently, two separate analyses were used to characterize the correspondence between matrices. The first analysis examined the difference between the absolute values of corresponding elements of paired matrices (magnitude test). The second examined the difference in direction of the elements of paired matrices (sign test), and was accomplished by reassigning a binary value (1 for positive, 0 for negative) to each element. Individually analyzing correspondence in the magnitude and sign of paired matrix elements is necessary when using the sum of squared deviations as a test statistic, because elements with similar absolute values but different signs (e.g., 0.9 and -0.9) misleadingly result in small and nonsignificant test statistics (Gorresen et al. 2005). Combining the results from magnitude and sign tests for a pair of matrices may result in one of nine possibilities regarding correspondence of matrix structure (Fig. 2.6). Overall consistency in the structure of matrices was evaluated with Fisher's test for combined probabilities (Sokal and Rohlf 1995). To maintain experiment-wise error rate constant at 0.10, comparison-wise error rate was adjusted to 0.035 with the Dunn-Šidák method (Sokal and Rohlf 1995) for each of three pairwise comparisons involving scale (1 km vs. 3 km, 1 km vs. 5km, 3 km vs. 5 km). Significant correspondence between matrices was indicated by a

combined probability less than or equal to the comparison-wise error rate. 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 (Gorresen et al. 2005). A significant Fisher's test with positive correspondence in both sign and magnitude tests (pattern A; Table 2.8), demonstrates that particular biotic response characteristics were associated with landscape metrics similarly regardless of scale (i.e., scale independence). A negative correspondence between matrices in either sign or magnitude tests, and a significant Fisher's test (patterns B, D, E, F, and H) demonstrated that biotic response characteristics were associated with landscape characteristics in dissimilar ways among scales (i.e., scale dependence). Inconclusive evidence of a scale-dependent response (patterns C, G, and I) was the result of a nonsignificant Fisher's test with any combination of results for magnitude and sign tests, or outcomes in which Fisher's test was significant, but negative magnitude or sign tests were not apparent (Gorresen et al. 2005).

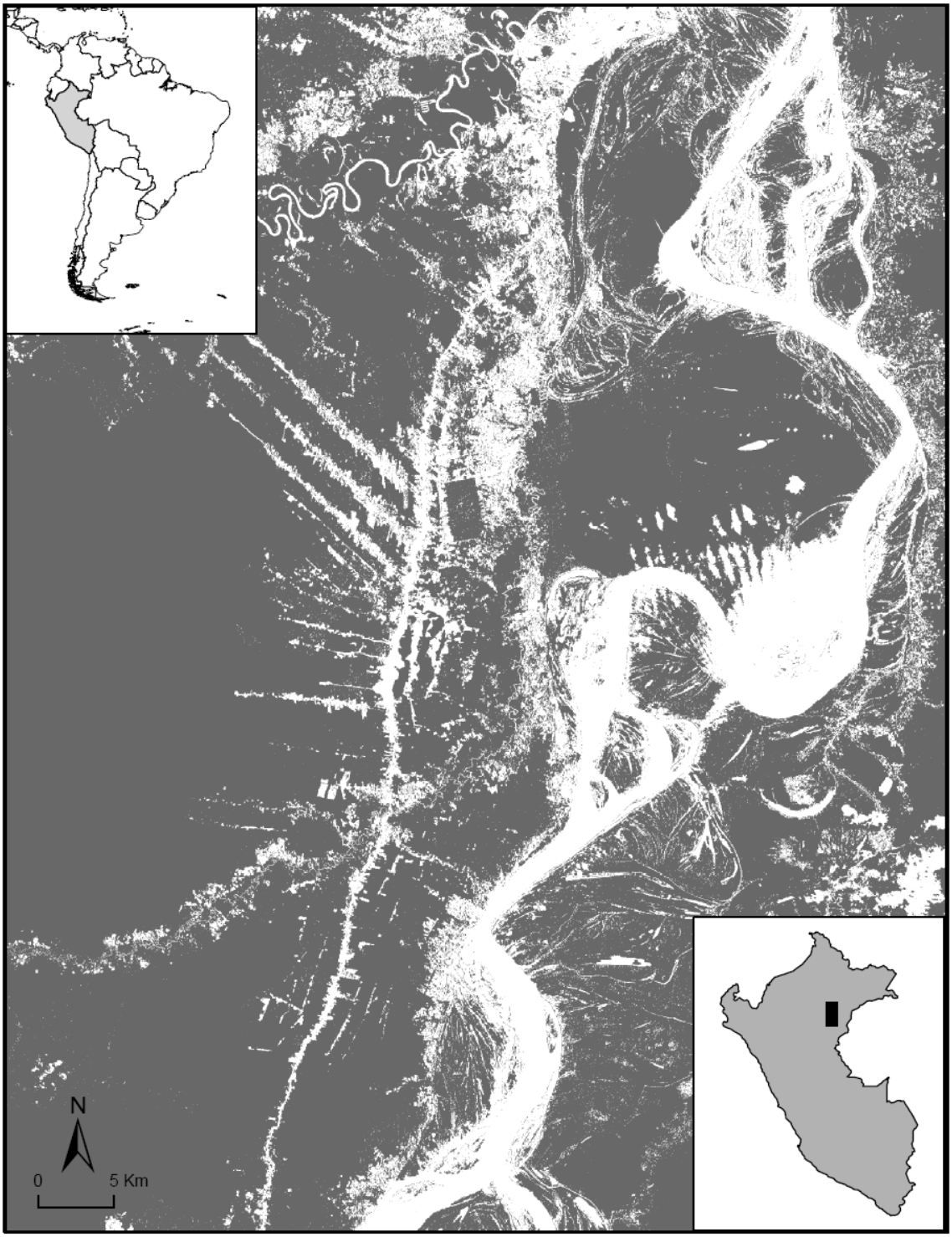

Figure 2.1. Map of study area depicting forest in gray and the combined non-forest class in white. Location of Peru in South America is displayed in the upper-left corner of the map. Image in the bottom-left corner of the map shows the location of the study area in Peru with a black rectangle.

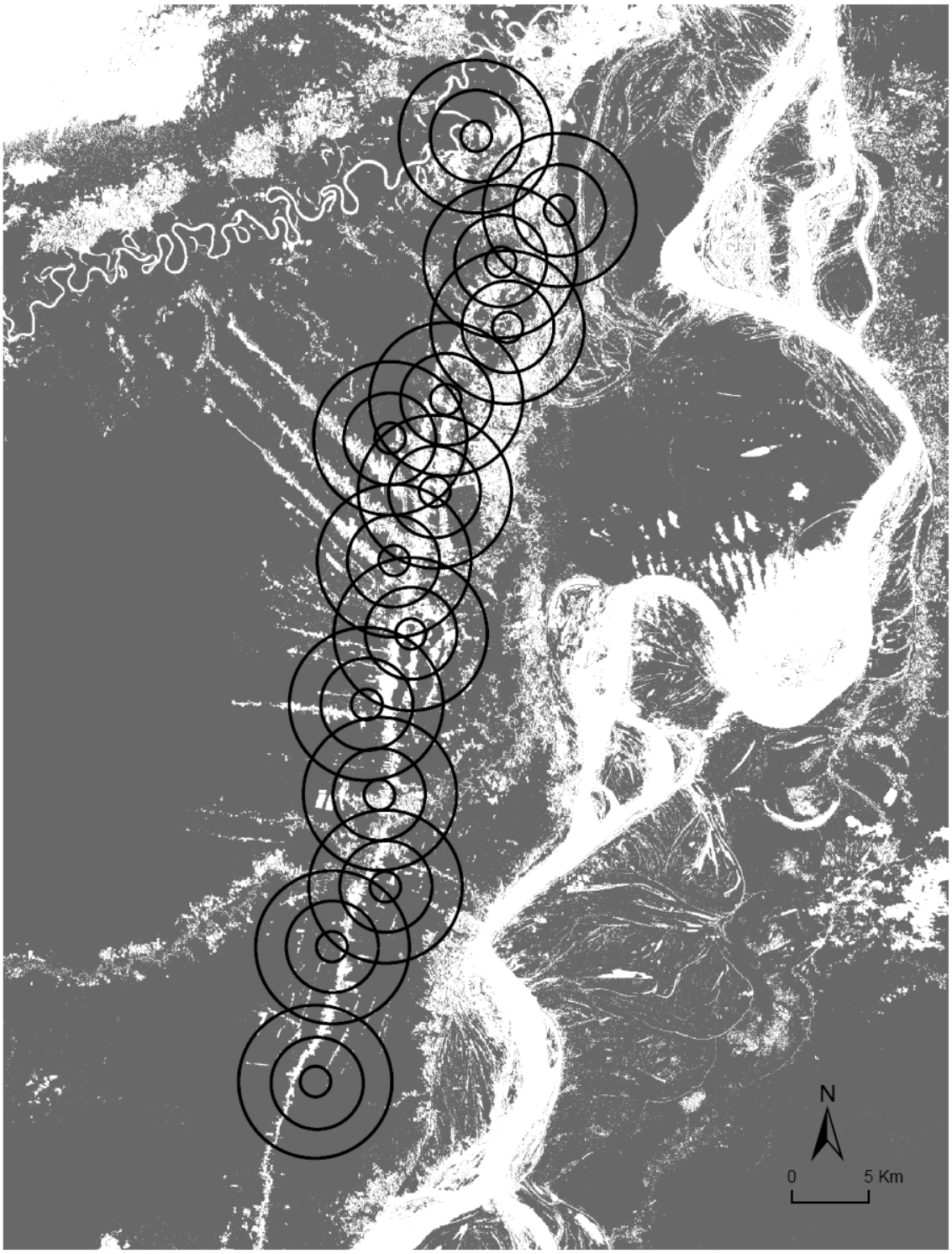

Figure 2.2. Classified image of study area displaying concentric focal scales (1, 3, and 5 km radii) centered on each of the 14 sites. The forest class is displayed in black while the combined class of non-forest is displayed in white. Location of top left corner of image, in decimal degrees, is -3.67255172,-73.55836066.

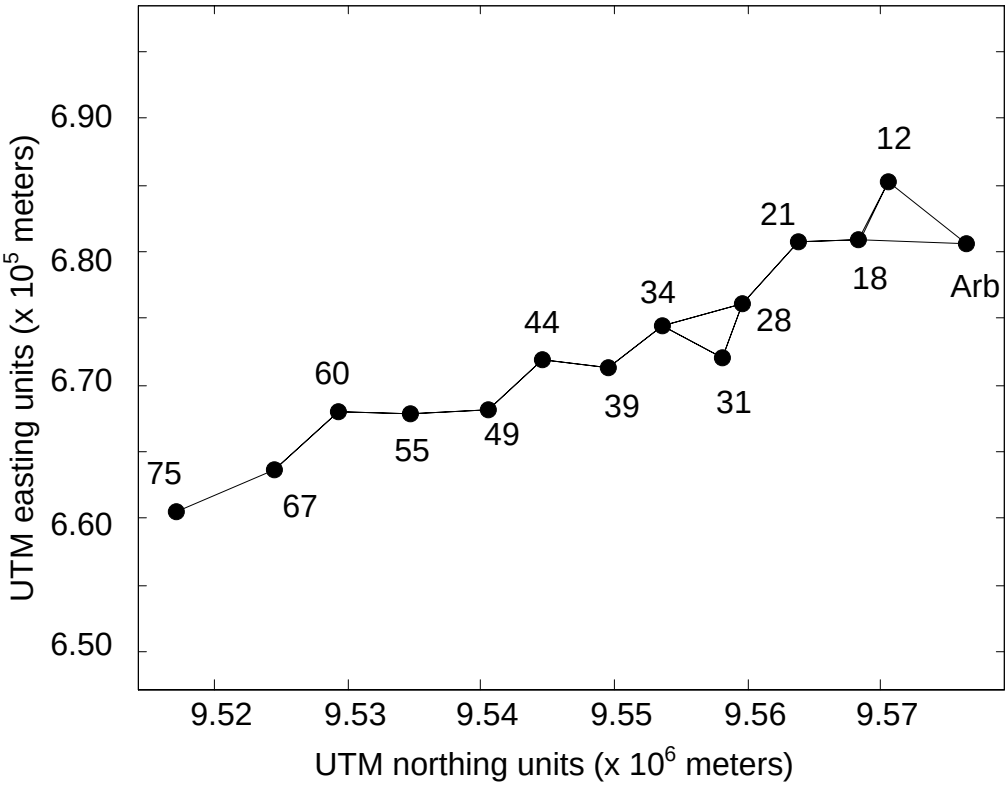

Figure 2.3. Gabriel network (Gabriel and Sokal 1969, Matula and Sokal 1980) of sites (open circles) that was examined for spatial autocorrelation of bat assemblage composition (Renkonen index, Krebs 1989). Paired sites were included in adjusted Gabriel network analysis of spatial autocorrelation if they are connected by 1 or 2 consecutive line segments, whereas sites connected by only one line segment were used in the traditional Gabriel network analysis. For example, site 49 is connected by one line segment to sites 44 and 55, and connected by two line segments to sites 39 and 60. This indicates that geographic and ecological distances between site 49 and sites 39, 44, 55, and 60 will be tested for spatial autocorrelation in adjusted Gabriel network, whereas only geographic and ecological distances between site 49 and sites 44 and 55 were tested in the traditional Gabriel network analysis of spatial autocorrelation.

		Controlled (partialed) characteristics					
		A	B	C	D	E	F
	A	r_{XA}	r_{XA-B}	r_{XA-C}	r_{XA-D}	r_{XA-E}	r_{XA-F}
	B	r_{XB-A}	r_{XB}	r_{XB-C}	r_{XB-D}	r_{XB-E}	r_{XB-F}
Correlated	C	r_{XC-A}	r_{XC-B}	r_{XC}	r_{XC-D}	r_{XC-E}	r_{XC-F}
characteristics	D	r_{XD-A}	r_{XD-B}	r_{XD-C}	r_{XD}	r_{XD-E}	r_{XD-F}
	E	r_{XE-A}	r_{XE-B}	r_{XE-C}	r_{XE-D}	r_{XE}	r_{XE-F}
	F	r_{XF-A}	r_{XF-B}	r_{XF-C}	r_{XF-D}	r_{XF-E}	r_{XF}

Figure 2.4. Illustration of the composite correlation matrix structure for simple and partial correlations between a biotic response characteristic (e.g., species abundance represented by X) and a suite of landscape characteristics represented by letters A through F (modified from Gorresen et al. 2005). Simple correlations are shaded and displayed on the matrix diagonal. Partial correlations between a biotic response characteristic and a landscape characteristic control for the association with one other characteristic. For example, coefficient $\mathbf{r}_{XA-B}$ is the correlation of the abundance of species X to landscape characteristic A while controlling for the effect of landscape characteristic B. A composite matrix of simple and partial correlations summarizes the nature of association between a particular biotic response characteristic and landscape structure at each focal scale (Gorresen et al. 2005).

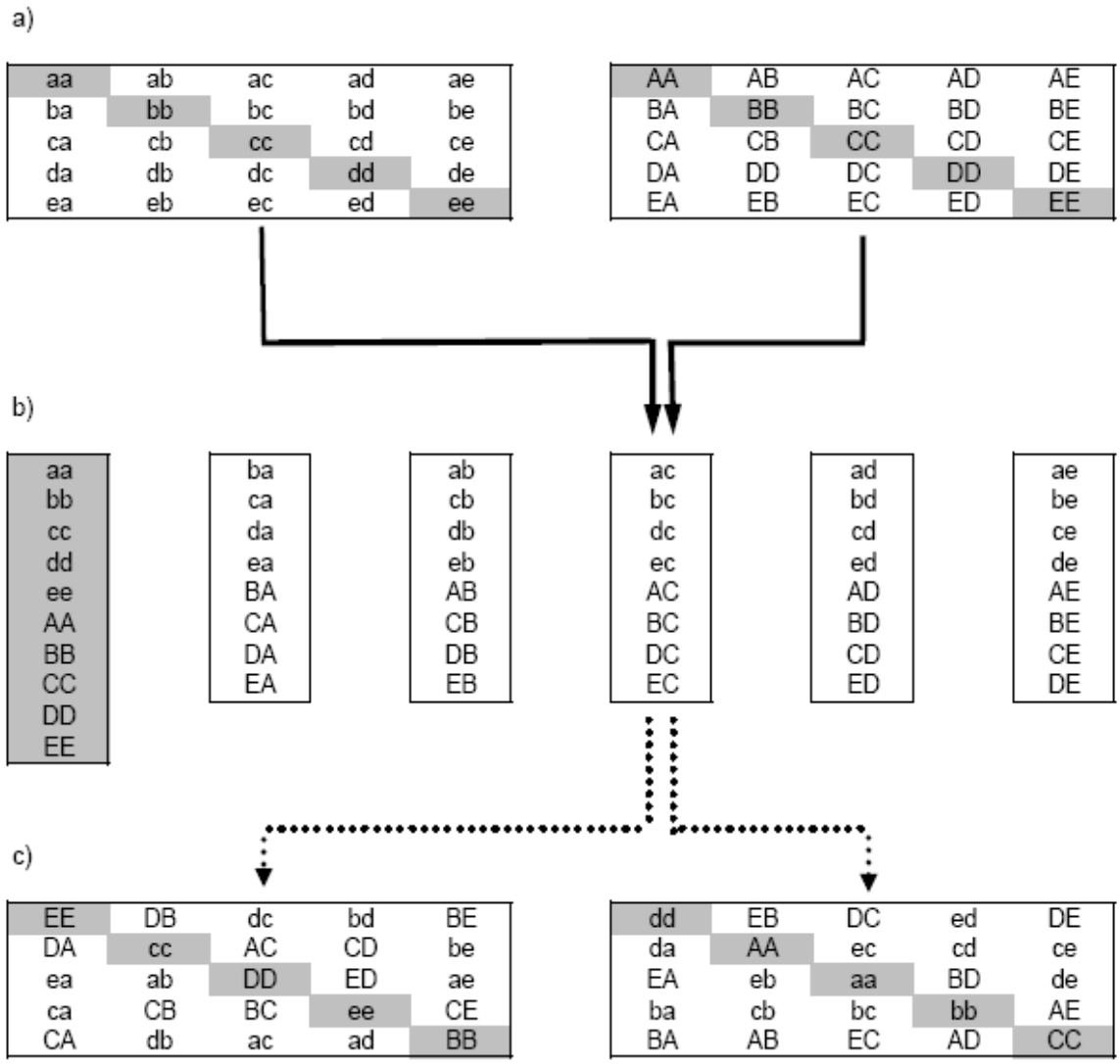

Figure 2.5. Illustrative example of the random permutation method that was used to develop a null model for assessing the similarity between two composite correlation matrices (modified from Gorresen et al. 2005). Elements (pairs of letters designate in order, row and column location) of each empirical matrix are distinguished by upper- and lower-case letters (panel a). Diagonal matrix elements (panel a; shaded) correspond to simple correlation coefficients; all other elements correspond to partial correlation coefficients (see Figure 2.4). Matrix elements from diagonal and each of five columns (excluding diagonal elements) are pooled separately (panel b). Solid arrows portray an example of pooling non-diagonal elements from paired columns (i.e., column 3). Ultimately, elements from each pool are randomly reassigned a new position with respect to the rows in one of two matrices, but the affiliation of an element with its original pool (i.e., column or diagonal location) is retained (panel c). Dashed arrows portray an example of the random re-allocation of off-diagonal elements into original column locations.

a)

		Sign		
		+	-	NS
Magnitude	+	A	B	C
	-	D	E	F
	NS	G	H	I

b)

A

Matrix 1		Matrix 2	
0.9	0.9	0.9	0.9
0.1	0.1	0.1	0.1

B

Matrix 1		Matrix 2	
0.9	0.9	-0.9	-0.9
0.1	0.1	-0.1	-0.1

C

Matrix 1		Matrix 2	
-0.9	0.9	0.9	0.9
-0.1	0.1	-0.1	-0.1

D

Matrix 1		Matrix 2	
0.9	0.9	0.1	0.1
0.1	0.1	0.9	0.9

E

Matrix 1		Matrix 2	
0.9	0.9	-0.1	-0.1
0.1	0.1	-0.9	-0.9

F

Matrix 1		Matrix 2	
-0.9	0.9	0.1	0.1
-0.1	0.1	-0.9	-0.9

G

Matrix 1		Matrix 2	
0.9	0.1	0.1	0.1
0.9	0.1	0.9	0.9

H

Matrix 1		Matrix 2	
0.9	0.1	-0.1	-0.1
0.9	0.1	-0.9	-0.9

I

Matrix 1		Matrix 2	
-0.9	0.1	0.1	0.1
-0.9	0.1	-0.9	-0.9

Figure 2.6. Nine general forms of matrix correspondence (after Gorresen et al. 2005) are possible based on tests of magnitude and sign forms; shaded cells denote scale dependence (panel a). A plus sign indicates a more positive association than expected by chance alone, a negative sign indicates a more negative association than expected to chance alone, and ns (not significant) indicates random associations. Illustrative examples are provided for each possible test outcome to illustrate the nature of matrix correspondence and scale dependence (panel b).

Table 2.1. List of study sites and locational information based on Universal Transverse Mercator projection (Zone 18S) and geographic coordinates.

	Universal Transverse Mercator (m)		Geographic coordinates (degrees)	
Sites	Northing	Easting	Latitude	Longitude
Arboretum	9576331	680662	S 03.83145	W 073.37304
Km 12	9570613	685227	S 03.88308	W 073.33184
Km 18	9568322	680911	S 03.90446	W 073.37066
Km 21	9563739	680828	S 03.94532	W 073.37132
Km 28	9559533	676049	S 03.98344	W 073.41428
Km 31.5	9558127	672123	S 03.99623	W 073.44961
Km 34	9553660	674448	S 04.03658	W 073.42860
Km 39.5	9549537	671303	S 04.07392	W 073.45685
Km 44	9544644	671924	S 04.11816	W 073.45117
Km 49	9540504	668203	S 04.15567	W 073.48462
Km 55	9534681	667830	S 04.20834	W 073.48787
Km 60	9529343	668041	S 04.25661	W 073.48588
Km 66.5	9524455	663602	S 04.30089	W 073.52578
Km 75	9517232	660558	S 04.36627	W 073.55308

Table 2.2. Indices used to characterize landscape structure at 3 focal scales (for a list of possible metrics and definitions, see McGarigal and Marks 1995 or Riitters et al. 1995) for each of 14 study sites (Figure 2.2). Code refers to the residual of the variable after it has been regressed against habitat area,except for forest cover, which is used in its original form.

Index name	Code	Formula	Variables	Description
Composition metrics				
Forest cover	COVER	$P_i = \frac{\sum_{j=1}^{n} a_{ij}}{A}(100)$	P_i, proportion of the focal scale occupied by patch type i (forest); a_{ij},area (m^2) of patch ij; A, total focal scale area (m2).	Percent of the focal scale area that is closed-canopy forest
Patch density	RPDENS	$\frac{n_i}{A}(10{,}000)(100)$	n_i, number off patches in focal scale; A, Area of focal scale.	Number of forest patches per unit area within a focal scale
Mean patch size	RPSIZE	$\frac{\sum_{j=1}^{n} a_{ij}}{n_i}\left(\frac{1}{10{,}000}\right)$	a_{ij}, area (m^2) of patch ij.	Average area of forest patches within a focal scale
Simpson's diversity	RDIV	$1 - \sum_{i=1}^{m} P_i^2$	P_i, proportion of the focal scale occupied by patch type i (forest).	Measures the proportion of focal scale occupied by each patch type.
Configuration metrics				
Edge density	REDGE	$\frac{E}{A}(10{,}000)$	E, total length (m) of edge in focal scale; A, total focal scale area (m^2).	Total length (m) of edge divided by the area of the focal scale
Mean patch shape	RSHAPE	$\frac{p_{ij}}{\min p_{ij}}$	p_{ij}, perimeter of patch ij in terms of number of cell surfaces; min p_{ij}, minimum perimeter of patch ij in terms of number of cell surfaces.	Average of focal patch perimeter divided by the minimum perimeter possible for a maximally compact patch (i.e., a square patch) of the corresponding patch area for all forest patches within the focal scale
Mean proximity index	RPROX	$\sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^2}$	a_{ijs}, area (m^2) of patch ijs within specified neighborhood (m) of patch ij; h_{ijs}, distance (m) between patch ijs and patch ijs, based on patch edge-to-edge distance, computed from cell center to cell center.	An average of the sum of patch area divided by the nearest edge-to-edge distance squared between the patch and the focal patch for all forest patches within the focal scale.
Mean nearest neighboor	RNEAR	$\frac{\sum_{j=1}^{n} h_{ij}}{n_i}$	h_{ij}, distance (m) from patch ij to nearest neighboring patch of the same type (class), based on patch edge-to-edge distance, computed from cell center to cell center; n_i, the number of edge-to edge distances.	Average minimum edge-to-edge distance between all possible pairwise patches of forest in a focal scale.

Table 2.3. Untransformed landscape indices for each site at circular focal scales of 1, 3, and 5 km radius. Landscape configuration characteristics are indicated with an asterisk.

Site	COVER	PDENS	PSIZE	SIMPDIV	EDGE*	SHAPE*	NEAR*	PROX*
1 km focal scale								
Arboretum	50.04	9.87	5.07	0.50	120.90	1.41	75.87	87.09
Km 12	58.89	15.28	3.85	0.48	113.24	1.36	71.19	81.41
Km 18	55.40	7.65	7.25	0.49	153.58	1.43	81.70	219.28
Km 21	46.05	13.36	3.45	0.50	137.03	1.35	71.07	102.43
Km 28	43.64	13.70	3.18	0.49	143.59	1.32	79.55	107.37
Km 31.5	83.47	2.23	37.40	0.28	71.56	1.33	69.57	408.51
Km 34	27.65	14.97	1.85	0.40	85.59	1.24	84.33	22.50
Km 39.5	66.84	8.59	7.78	0.44	78.41	1.16	77.40	183.19
Km 44	30.37	6.03	5.04	0.42	58.42	1.31	111.43	27.61
Km 49	69.95	2.23	31.41	0.42	76.14	1.44	76.89	250.55
Km 55	48.91	12.42	3.94	0.50	102.21	1.35	69.40	81.62
Km 60	87.66	0.95	91.86	0.22	51.53	1.47	84.84	229.73
Km 66.5	84.94	1.27	66.85	0.26	46.31	1.37	87.24	104.92
Km 75	99.26	0.32	311.84	0.01	28.30	1.25	0.00	0.00
3 km focal scale								
Arboretum	59.87	5.31	11.28	0.48	78.86	1.34	85.12	495.10
Km 12	51.80	11.28	4.60	0.50	102.62	1.32	76.10	327.33
Km 18	53.40	8.63	6.19	0.50	112.72	1.32	75.34	833.39
Km 21	46.67	11.17	4.18	0.50	111.72	1.31	77.17	428.11
Km 28	58.14	6.72	8.65	0.49	111.06	1.31	75.19	871.25
Km 31.5	67.88	6.36	10.66	0.44	67.81	1.22	75.94	1207.62
Km 34	47.12	10.12	4.66	0.50	84.79	1.27	76.84	250.97
Km 39.5	51.44	7.29	7.06	0.50	93.80	1.27	77.12	660.55
Km 44	50.15	2.94	17.08	0.50	74.71	1.50	80.05	362.43
Km 49	68.47	2.16	31.75	0.43	49.46	1.23	79.56	1835.74
Km 55	65.73	6.36	10.33	0.45	83.56	1.32	70.92	892.43
Km 60	77.49	2.51	30.86	0.35	58.39	1.36	78.12	1498.93
Km 66.5	85.90	1.45	59.23	0.24	36.20	1.27	75.28	1461.78
Km 75	91.04	0.53	171.59	0.16	24.40	1.24	70.18	2628.12
5 km focal scale								
Arboretum	61.71	4.76	12.96	0.47	75.55	1.32	79.38	1307.12
Km 12	59.94	7.92	7.57	0.48	99.20	1.34	72.13	977.95
Km 18	56.71	8.68	6.53	0.49	108.79	1.32	72.35	1419.69
Km 21	49.08	10.92	4.50	0.50	114.15	1.29	75.77	587.55
Km 28	57.70	8.81	6.55	0.49	87.11	1.24	77.50	1038.73
Km 31.5	65.86	6.39	10.31	0.45	71.38	1.26	77.10	1767.48
Km 34	47.42	10.70	4.43	0.50	91.18	1.26	77.90	483.38
Km 39.5	57.50	5.76	9.99	0.49	84.27	1.26	76.92	1465.08
Km 44	64.51	2.25	28.62	0.46	69.11	1.32	74.07	2463.45
Km 49	77.86	1.27	61.15	0.34	40.40	1.21	79.28	6085.17
Km 55	75.88	3.35	22.66	0.37	64.75	1.26	72.54	4115.36
Km 60	81.41	2.24	36.33	0.30	55.59	1.24	76.20	4914.22
Km 66.5	87.89	0.97	90.82	0.21	33.92	1.22	77.52	4714.28
Km 75	92.77	0.34	269.82	0.13	19.10	1.21	82.86	6558.12

Table 2.4. Ecological and geographic distance matrix for all possible pairs of sites. Geographic distances (upper right triangle) are in kilometers and ecological distances are percent dissimilarities (Renkonen index; lower left triangle) of relative abundances of bat species (i.e., species composition).

Site	Arboretum	Km 12	Km 18	Km 21	Km 28	Km 31.5	Km 34	Km 39.5	Km 44	Km 49	Km 55	Km 60	Km 66.5	Km 75
Arboretum		7.32	8.01	12.59	17.42	20.11	23.51	28.38	32.87	37.93	43.58	48.65	54.61	62.42
Km 12	28.03		4.89	8.16	14.39	18.10	20.09	25.26	29.18	34.59	39.92	44.71	50.97	58.81
Km 18	40.55	37.28		4.58	10.04	13.46	16.02	21.10	25.33	30.58	36.09	41.05	47.16	54.99
Km 21	43.39	39.52	26.92		6.37	10.36	11.93	17.10	21.07	26.44	31.83	36.70	42.89	50.73
Km 28	31.77	30.38	31.46	32.24		4.17	6.09	11.07	15.45	20.58	26.18	31.23	37.22	45.05
Km 31.5	40.61	33.33	44.14	50.36	39.72		5.04	8.63	13.48	18.05	23.84	29.07	34.73	42.50
Km 34	21.41	19.73	33.18	31.22	21.88	35.10		5.19	9.36	14.56	20.10	25.15	31.15	38.99
Km 39.5	26.28	20.25	31.83	35.18	22.10	28.91	17.01		4.93	9.55	15.26	20.46	26.24	34.05
Km 44	30.43	30.62	32.58	30.94	23.62	36.31	22.68	19.93		5.57	10.77	15.79	21.84	29.68
Km 49	25.98	26.78	43.44	47.78	35.23	33.33	24.69	21.36	32.73		5.83	11.16	16.70	24.50
Km 55	37.99	27.67	29.33	26.87	30.07	39.24	28.90	21.91	32.42	37.23		5.34	11.07	18.90
Km 60	36.01	30.47	29.73	39.72	29.75	33.83	30.52	19.80	31.30	34.44	21.37		6.60	14.24
Km 66.5	36.62	28.74	39.10	41.52	34.38	30.84	30.06	19.40	29.92	29.52	25.20	25.51		7.84
Km 75	27.56	28.93	30.88	39.64	28.48	28.31	22.73	20.12	30.19	29.61	25.37	22.54	31.47	

Table 2.5. Pearson product moment correlations between original values (i.e., not residuals) of all possible pairs of landscape charateristics (Table 2.2) for sites at each focal scale (1, 3, and 5 km radius) seperately. Bold values indicate significant correlations ($p \leq 0.05$). Landscape configuration characteristics are indicated with an asterisk.

	COVER	PDENS	PSIZE	SIMPDIV	EDGE*	SHAPE*	NEAR*	PROX*
1 km focal scale								
COVER	1							
PDENS	**-0.787**	1						
PSIZE	**0.710**	**-0.608**	1					
SIMPDIV	**-0.781**	**0.758**	**-0.901**	1				
EDGE*	**-0.582**	**0.729**	**-0.629**	**0.816**	1			
SHAPE*	0.140	-0.235	-0.146	0.119	0.219	1		
NEAR*	**-0.561**	0.223	**-0.824**	**0.593**	0.242	0.251	1	
PROX*	0.409	-0.407	-0.192	-0.025	0.029	0.336	0.163	1
3 km focal scale								
COVER	1							
PDENS	**-0.806**	1						
PSIZE	**0.781**	**-0.657**	1					
SIMPDIV	**-0.941**	**0.734**	**-0.901**	1				
EDGE*	**-0.863**	**0.864**	**-0.760**	**0.855**	1			
SHAPE*	-0.360	-0.023	-0.282	0.334	0.265	1		
NEAR*	-0.375	0.020	-0.462	0.449	0.136	0.361	1	
PROX*	**0.897**	**-0.760**	**0.832**	**-0.859**	**-0.793**	-0.478	-0.424	1
5 km focal scale								
COVER	1							
PDENS	**-0.909**	1						
PSIZE	**0.753**	**-0.626**	1					
SIMPDIV	**-0.953**	**0.804**	**-0.865**	1				
EDGE*	**-0.930**	**0.913**	**-0.771**	**0.907**	1			
SHAPE*	**-0.620**	0.471	**-0.549**	**0.687**	**0.720**	1		
NEAR*	0.382	-0.348	**0.642**	-0.499	**-0.605**	**-0.647**	1	
PROX*	**0.942**	**-0.886**	**0.742**	**-0.911**	**-0.911**	**-0.692**	0.417	1

Table 2.6. Pearson Product moment correlations between residual values of all possible pairs of landscape characteristics after removing linear effects of forest area for sites at each focal scale (1, 3, and 5 km radius) seperately. Forest cover was used in its original form (i.e., untransformed). Bold values indicate significant correlations (p≤ .05). Landscape configuration characteristics are indicated with an asterisk.

	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	1							
RPDENS	0.405	1						
RPSIZE	-0.044	-0.110	1					
RDIV	>0.001	0.371	**-0.788**	1				
REDGE*	-0.078	**0.524**	-0.337	**0.711**	1			
RSHAPE*	>0.001	-0.205	-0.351	**0.711**	0.374	1		
RNEAR*	-0.002	-0.428	**-0.732**	0.302	-0.126	0.401	1	
RPROX*	0.001	-0.151	**-0.750**	0.516	0.361	0.309	0.517	1
3 km focal scale								
COVER	1							
RPDENS	>0.001	1						
RPSIZE	>0.001	-0.073	1					
RDIV	>0.001	-0.125	**-0.786**	1				
REDGE*	-0.001	**0.561**	-0.273	0.250	1			
RSHAPE*	>0.001	**-0.568**	-0.001	-0.017	-0.098	1		
RNEAR*	>0.001	-0.517	-0.291	0.303	-0.402	0.261	1	
RPROX*	-0.001	-0.140	0.475	-0.092	-0.085	-0.377	-0.213	1
5 km focal scale								
COVER	1							
RPDENS	-0.034	1						
RPSIZE	-0.014	0.218	1					
RDIV	0.029	**-0.542**	**-0.751**	1				
REDGE*	0.029	0.446	-0.228	-0.051	1			
RSHAPE*	0.034	-0.335	-0.107	0.303	0.426	1		
RNEAR*	-0.028	0.050	**0.559**	-0.432	**-0.725**	**-0.548**	1	
RPROX*	0.002	-0.260	0.087	0.012	-0.177	-0.316	0.099	1

Table 2.7. Residuals (except forest cover) of landscape characteristics after removing the effect of forest area for sites at focal scales of 1, 3, and 5 km radius. Landscape configuration characteristics are indicated with an asterisk.

Site	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
Arboretum	50.04	-0.11	-7.22	0.06	19.12	0.07	-5.12	-26.53
Km 12	58.89	7.09	-32.10	0.09	20.61	0.02	-4.39	-50.48
Km 18	55.40	-1.26	-19.20	0.08	57.28	0.09	3.95	94.73
Km 21	46.05	2.58	1.73	0.03	31.16	0.02	-12.33	-3.03
Km 28	43.64	2.42	8.13	0.02	35.14	-0.01	-5.37	7.05
Km 31.5	83.47	-1.01	-64.17	0.00	4.32	-0.02	8.97	225.97
Km 34	27.65	0.47	49.45	-0.16	-39.36	-0.08	-10.33	-44.90
Km 39.5	66.84	2.01	-49.61	0.09	-5.92	-0.19	6.71	34.75
Km 44	30.37	-7.90	45.05	-0.12	-63.60	-0.02	18.50	-45.64
Km 49	69.95	-3.72	-34.25	0.08	-4.99	0.09	8.09	95.73
Km 55	48.91	2.21	-5.29	0.05	-0.76	0.01	-12.29	-29.64
Km 60	87.66	-1.42	-21.20	-0.03	-11.26	0.11	26.87	38.32
Km 66.5	84.94	-1.63	-39.24	-0.01	-19.18	0.01	27.68	-81.11
Km 75	99.26	0.27	167.93	-0.17	-22.55	-0.11	-50.93	-215.23
3 km focal scale								
Arboretum	59.87	-1.15	-9.28	0.06	-3.53	0.03	8.23	-373.50
Km 12	51.80	3.19	3.58	-0.01	6.53	0.00	-1.58	-196.45
Km 18	53.40	0.87	1.17	0.01	19.43	0.00	-2.18	239.00
Km 21	46.67	2.04	15.58	-0.09	6.91	-0.02	-1.00	123.62
Km 28	58.14	-0.08	-7.79	0.05	25.78	0.00	-1.87	75.43
Km 31.5	67.88	1.54	-29.38	0.09	-0.92	-0.08	-0.18	-4.70
Km 34	47.12	1.07	15.05	-0.08	-19.31	-0.06	-1.29	-71.38
Km 39.5	51.44	-0.88	6.94	-0.02	-2.93	-0.06	-0.59	152.70
Km 44	50.15	-5.49	20.07	-0.04	-24.20	0.17	2.21	-90.49
Km 49	68.47	-2.54	-9.78	0.09	-18.22	-0.07	3.50	597.12
Km 55	65.73	1.10	-24.53	0.08	11.20	0.02	-5.40	-228.58
Km 60	77.49	-0.36	-32.49	0.05	6.02	0.08	2.93	-124.85
Km 66.5	85.90	0.29	-24.52	-0.05	-1.86	0.01	0.91	-522.08
Km 75	91.04	0.41	75.37	-0.13	-4.91	-0.02	-3.70	424.16
5 km focal scale								
Arboretum	61.71	-1.89	-5.95	0.02	-7.68	0.04	3.35	-583.68
Km 12	59.94	0.83	-4.27	0.01	12.50	0.06	-3.74	-650.36
Km 18	56.71	0.81	7.51	0.00	15.81	0.03	-3.22	267.65
Km 21	49.08	1.23	35.22	-0.06	6.59	-0.02	0.88	540.47
Km 28	57.70	1.18	3.61	0.00	-3.95	-0.05	1.84	-258.93
Km 31.5	65.86	0.74	-25.10	0.03	-3.76	-0.01	0.69	-736.61
Km 34	47.42	1.83	21.79	-0.03	-9.83	-0.04	2.70	-60.10
Km 39.5	57.50	-1.92	7.89	0.00	-7.20	-0.03	1.28	198.56
Km 44	64.51	-3.76	-0.82	0.03	-8.96	0.05	-2.20	181.48
Km 49	77.86	-1.46	-21.94	0.03	-11.37	-0.04	1.77	1809.75
Km 55	75.88	0.14	-52.56	0.03	9.12	0.01	-4.79	132.20
Km 60	81.41	0.37	-60.82	0.01	10.71	0.00	-1.63	116.34
Km 66.5	87.89	0.67	-32.09	-0.02	1.67	0.00	-0.91	-1040.56
Km 75	92.77	1.22	127.54	-0.06	-3.65	0.00	3.99	83.79

Table 2.8. Fourteen possible patterns of matrix correpondence are possible (see Fig. 2.6 for illustrative examples of test result combinations) after separate tests for correspondence in magnitude or sign of matrix elements, and Fisher's test of combined probabilities for both tests. Significant pattern similarity (+) in both the magnitude and sign tests, and a significant Fisher's test 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). Additionally, a nonsignificant Fisher's test (ns) with non-significant results in magnitude or sign tests, or both, results in an uncertain correspondence of matrix pattern (pattern U; modified from Gorresen et al. 2005).

Magnitude	Sign	Fisher's test	Scale	Matrix pattern correpondence	Pattern
+	+	*	Independent	magnitude and sign similarity	A
+	-	*	Dependent	magnitude similarity; sign dissimilarity	B
-	+	*	Dependent	magnitude dissimilarity; sign similarity	D
-	-	*	Dependent	magnitude and sign dissimilarity	E
ns	+	*	Inconclusive	sign similarity only	G
ns	-	*	Dependent	sign dissimilarity only	H
+	ns	*	Inconclusive	magnitude similarity only	C
-	ns	*	Dependent	magnitude dissimilarity only	F
ns	ns	*	Inconclusive	uncoupled characters and sign	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
ns	ns	ns	Inconclusive	not significant	I

CHAPTER III
RESULTS

Population and Assemblage Composition

A five month survey with a total of 56,808 mist-net meter hours (n-m h) resulted in the capture of 3024 phyllostomids representing 42 species and 25 genera. Phyllostomids were classified into broad foraging guilds (i.e., frugivores, nectarivores, gleaning animalivores, and sanguinivores; Table 3.1) based on published recommendations (Wilson 1973, Gardner 1977, Willig 1986, Willig et al. 1993). In addition, individuals representing eight species from the families Thyropteridae (*Thyroptera lavali* and *Thyroptera tricolor*), Vespertilionidae (*Myotis nigricans*), and Emballonuridae (*Centronycteris maximiliani*, *Cormura brevirostris*, *Peropteryx leucoptera*, *Saccopteryx bilineata*, and *Saccopteryx leptura*) were encountered in the study area. Three individuals of *Thyroptera lavali*, a species endemic to Peru and listed as vulnerable on the IUCN Red List, were captured in the study area (Chiroptera Specialist Group 1996).

Total abundance (Table 3.1) ranged from 1 capture (e.g., *Lophostoma brasiliense*, *Vampyrum spectrum*, *Chiroderma trinitatum*, and *Chiroderma villosum*) to 1022 captures (e.g., *Carollia perspicillata*). The site at km 31.5 harbored the fewest individuals (105) and the fewest species (14). The site at km 39.5 harbored the most individuals (294) and the site at km 18 harbored the highest richness (28). Measures of diversity and dominance ranged from 1.93 to 2.98 and 2.06 to 4.34, respectively. As is often the case for phyllostomid assemblages in the neotropics (Ascorra et al. 1993, Hice et al. 2004,

Willig et al. in press), the majority of species captured in the study area were rare (35 of the 42 species).

Spatial Autocorrelation

Ecological and geographic distance were not associated significantly for sites linked in the adjusted (Spearman correlation: $r = 0.047$, $p = 0.815$) or traditional (Spearman correlation: $r = 0.1$, $p = 0.714$) Gabriel network. This indicates that spatial autocorrelation is minimal and regression with weighted errors is not necessary as a corrective measure (Legendre 1993).

Response of Population and Assemblage Characteristics to Landscape Structure

A variety of landscape characteristics were associated significantly with biotic response characteristics at each focal scale. Multiple regression and simple correlation analyses identified significant responses to landscape characteristics at the population and assemblage level for each focal scale (Tables 3.2-3.30).

The relationship between abundance and landscape characteristics were species-specific (Table 3.31). Both negative and positive associations were observed for each focal scale. For example, at small and medium focal scales, edge density was associated positively with abundance of *M. crenulatum* (51%, 58%; 1 km, 3 km), *L. thomasi* (28%; 1 km), and *T. saurophila* (37%; 3 km). However, at the largest focal scale (5 km), edge density was associated negatively with the abundance of *C. perspicillata* (38%) and positively with *M. crenulatum* (42%). Forest cover was associated significantly and negatively with the abundances of 3 species (*G. soricina*, *S. lilium*, and *S. tildae*) at each focal scale and with abundances of six species (*C. brevicauda*, *C. perspicillata*, *A. lituratus*, *A. obscurus*, *A. planirostris*, and *U. bilobatum*) at one or two spatial scales.

Forest cover was associated significantly and positively with only 1 species (*V. bidens*) at one focal scale (5 km). *Mimon crenulatum* responded significantly to the most landscape characteristics. Abundance of this species was related positively to edge density and patch density at all three scales, and to mean nearest neighbor distance at the 5 km scale. Three species (*R. fischerae, P. hastatus,* and *D. anderseni*) were not related significantly to any landscape characteristics at any focal scale. Mean patch shape was the only landscape characteristic that was not associated significantly with any biotic response characteristic.

The amount of variation described by multiple regression models differed among species and scales, ranging from an adjusted R^2 of 23% for abundances of *C. perspicillata* and *L. thomasi* at the 1 km scale, to 65% for abundances of *S. lilium* at the 5 km scale (Table 3.31). Assemblage-level indices showed similar variability between focal scales, but responded solely to landscape configuration. Richness (adjusted R^2 = 34%, p = 0.028) was associated negatively with proximity at the smallest focal scale. Based on correlation analyses, dominance was associated positively with edge density at 3 km (31%) and 5 km (55%) scales, and a negative relationship (r = 0.726) to mean nearest neighbor distance at the 5 km scale was identified. Evenness (44%) was associated negatively with mean nearest neighbor distance at the 5 km scale. Species diversity and the number of rare species were not related significantly to any landscape characteristics at any focal scale.

Scale-Dependent Responses of Species and Assemblages to Landscape Structure

Multiple Regression Analysis. The magnitude and direction of association between species abundance and landscape characteristics was scale-dependent (Table

3.31). Five landscape characteristics were associated with fourteen significant responses at the 1 km scale, whereas seven landscape characteristics were associated with twelve significant responses at the 3 and at the 5 km scales. Although the number of responses was similar, the strengths of the association differed greatly among scales. For example, percentage of forest cover accounted for 50% of the variability in abundance of *G. soricina* at the 1 km scale but only 30% at the 5 km scale. Similarly forest cover and mean proximity, together accounted for 54% of the variability in abundance of *A. lituratus* at the 1 km scale but no landscape characteristic significantly accounted for the variability in abundance of *A. lituratus* at the 3 or 5 km scales. Conversely, forest cover accounted for 26% and 36% of the variability in abundance of *C. brevicauda* and *V. bidens* at the 5 km scale, respectively, but no landscape characteristic was a significant predictor of abundance for either species at the 1 and 3 km scales. Abundances of four species (*D. gnoma, R. pumilio, T. saurophila,* and *U. bilobatum*) were associated significantly with landscape characteristics (diversity, nearest neighbor, edge density, and cover) only at the 3 km focal scale

The association of assemblage-level indices with landscape characteristics was dependent on focal scale (Table 3.31). Mean proximity accounted for 34% of the variation in richness at the 1 km scale, but no landscape characteristic was a significant predictor of richness at the 3 or 5 km scales. Mean nearest neighbor distance accounted for 44% of the variation in evenness at the 5 km scale but no landscape characteristic was associated significantly at the 1 or 3 km scales. Dominance was associated with edge density at the 3 and 5 km scales, but the strength of the relationship depended on scale (i.e., 31% for 3 km scale, 55% for 5 km scale).

Correspondence of Correlation matrices. The majority of population-level and assemblage-level characteristics displayed a consistent response to landscape characteristics regardless of scale (pattern A; Table 2.8). Abundance of only one species (*P. elongatus*) and one assemblage-level index (species diversity) exhibited a scale-dependent response to landscape characteristics (Tables 3.32-33). Species diversity exhibited a significant difference in sign and magnitude between small (1 km) and medium (3 km) scales (pattern E). The scale-dependent response (pattern H) of *Phyllostomus elongatus* (1 km vs. 5 km) is a consequence of abundance being associated positively with landscape characteristics at one focal scale and negatively at another focal scale (Gorresen et al. 2005). No significant differences in response for population-level or assemblage-level comparisons were apparent between medium and large focal scales (i.e., 3 km vs. 5 km).

Table 3.1. Population-level (abundance of each phyllostomid species) and assemblage-level (cumulative abundance, richness, Shannon diversity, dominance, evenness and number of rare species) characteristics at each of 14 sites in Iquitos, Peru. Taxa in bold were included in analysis of population-level response to landscape charateristics. All phyllostomids were included in assemblage-level analyses. Bats are classified into broad foraging guilds (F = frugivore, GA = glea animalivore, N = nectarivore, S = sanguinivore) based on published recommendations (Wilson 1973, Gardner 1977, Willig 1986, Willig and Moulton 1989, Stevens et al. 2006).

	Guild	Site Name														Total
		Arboretum	Km 12	Km 18	Km 21	Km 28	Km 31.5	Km 34	Km 39	Km 44	Km 49	Km 55	Km 60	Km 66.5	Km 75	
Population-level																
Carollia brevicauda	F	39	19	62	92	48	17	45	48	32	30	47	24	19	34	556
Carollia benkeithi	F	1	9	8	2	3	2	1	23	2	27	17	8	14	0	117
Carollia perspicillata	F	138	48	66	63	84	38	98	104	79	98	62	40	42	62	1022
Rhinophylla fischerae	F	1	0	1	0	3	0	4	2	1	3	2	4	3	1	25
Rhinophylla pumilio	F	1	6	6	8	7	18	13	15	8	9	16	6	20	9	142
Desmodus rotundus	S	3	0	2	0	0	0	0	0	0	0	0	1	0	0	6
Choeroniscus minor	N	0	0	0	0	0	0	0	1	0	1	0	0	2	0	4
Glossophaga soricina	N	1	4	0	3	2	0	3	1	1	2	1	0	0	0	18
Lonchophylla thomasi	N	1	7	7	4	3	4	0	1	3	1	4	1	0	1	37
Chrotopterus auritus	GA	1	0	0	0	0	0	1	0	1	0	0	0	0	0	3
Glyphonycteris daviesi	GA	1	0	0	0	0	0	0	0	2	0	1	0	0	0	4
Glyphonycteris sylvestris	GA	0	0	0	0	0	0	1	1	0	1	0	1	0	0	4
Lophostoma brasiliense	GA	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Lophostoma silvicolum	GA	0	0	2	2	0	0	2	3	2	0	3	5	2	2	23
Micronycteris minuta	GA	1	0	0	0	3	0	1	0	0	0	0	1	0	0	6
Mimon crenulatum	GA	2	3	19	4	4	1	1	4	0	1	8	5	2	6	60
Phylloderma stenops	GA	1	1	1	0	0	0	0	0	0	0	1	0	0	1	5
Phyllostomus elongatus	GA	15	1	2	1	1	0	1	6	1	1	2	3	1	5	40
Phyllostomus hastatus	GA	7	1	5	1	17	0	3	6	3	1	6	3	0	6	59
Tonatia saurophila	GA	2	0	3	1	1	1	0	2	0	0	1	3	3	1	18
Trachops cirrhosus	GA	1	0	0	0	0	1	0	0	2	2	1	1	0	1	9
Trinycteris nicefori	GA	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2
Vampyrum spectrum	GA	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Artibeus concolor	F	0	0	2	1	1	0	0	0	0	0	0	0	1	0	5
Artibeus lituratus	F	4	0	3	5	18	0	5	7	6	3	1	0	2	1	55
Artibeus obscurus	F	7	4	16	16	25	2	11	13	17	5	13	9	5	4	147
Artibeus planirostris	F	32	16	18	51	23	2	29	27	23	7	46	12	15	11	312
Chiroderma trinitatum	F	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Chiroderma villosum	F	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Dermanura anderseni	F	2	2	0	0	0	0	4	1	0	1	0	1	0	0	11
Dermanura gnoma	F	0	1	6	2	0	3	2	2	1	1	0	4	0	2	24
Mesophylla macconelli	F	3	0	2	1	1	13	2	10	7	3	10	8	5	9	74
Platyrrhinus brachycephalus	F	0	1	1	0	1	0	0	0	0	0	0	0	0	0	3
Platyrrhinus helleri	F	0	0	2	0	0	0	0	0	0	0	1	1	0	1	5
Platyrrhinus sp	F	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Sturnira lilium	F	3	0	17	29	6	1	6	6	19	4	1	0	0	0	92
Sturnira magna	F	1	0	7	3	1	0	3	2	2	0	1	0	1	3	24
Sturnira tildae	F	10	3	19	2	2	0	5	2	3	0	0	0	2	0	48
Uroderma bilobatum	F	0	3	2	0	1	0	4	2	1	2	0	0	0	0	15
Vampyressa bidens	F	0	0	1	0	0	0	0	0	1	5	2	0	2	3	14
Vampyressa brocki	F	3	0	0	0	0	0	0	0	0	0	0	1	0	1	5
Vampyressa thyone	F	1	0	2	1	0	2	0	5	18	2	0	1	2	1	35
Assemblage-level																
Cumulative abundance		282	130	283	292	258	105	245	294	235	210	248	144	143	165	3034
Richness (S)		27	18	28	21	25	14	23	25	24	23	24	24	19	22	42
Diversity (H')		1.93	2.16	2.54	2.02	2.23	1.93	2.09	2.89	2.30	1.96	2.28	2.51	2.29	2.16	2.41
Dominance (D)		2.06	2.71	4.34	3.14	3.07	2.76	2.50	2.83	2.98	2.17	4.07	3.60	3.41	2.66	2.98
Evenness (PIE)		0.73	0.82	0.88	0.81	0.83	0.80	0.79	0.83	0.84	0.75	0.86	0.88	0.86	0.81	0.83
Number of rare species		19	12	21	13	17	6	15	18	16	15	16	17	12	17	35

Table 3.2. Composite correlation matrix at each focal scale between abundance of *Carollia benkeithi* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape characteristics	Controlled (partialled) characteristics							
	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	-0.040	-0.040	-0.066	-0.058	-0.041	-0.041	-0.051	-0.045
RPDENS	0.038	0.038	-0.085	-0.356	-0.066	0.102	0.463	0.122
RPSIZE	**-0.801**	**-0.802**	**-0.800**	-0.544	**-0.806**	**-0.781**	**-0.626**	**-0.777**
RDIV	**0.722**	**0.762**	0.246	**0.722**	**0.864**	**0.693**	**0.726**	**0.637**
REDGE*	0.173	0.181	-0.231	-0.058	0.173	0.077	0.339	0.009
RSHAPE*	0.281	0.295	-0.002	-0.356	0.236	0.280	0.027	0.164
RNEAR*	**0.653**	**0.740**	0.163	-0.544	**0.690**	**0.614**	**0.652**	0.546
RPROX*	0.458	0.470	-0.358	0.144	0.431	0.407	0.186	0.458
3 km focal scale								
COVER	-0.166	-0.166	-0.227	-0.196	-0.168	-0.167	-0.166	-0.167
RPDENS	-0.063	-0.062	-0.153	0.006	-0.166	-0.136	-0.033	-0.077
RPSIZE	**-0.691**	**-0.689**	**-0.681**	-0.503	**-0.676**	**-0.684**	**-0.694**	**-0.723**
RDIV	0.539	0.529	-0.008	0.531	0.519	0.532	0.538	0.527
REDGE*	0.134	0.202	-0.076	0.000	0.133	0.125	0.173	0.125
RSHAPE*	-0.089	-0.150	-0.122	-0.093	-0.076	-0.088	-0.109	-0.137
RNEAR*	0.065	0.038	-0.191	-0.120	0.130	0.091	0.064	0.044
RPROX*	-0.102	-0.110	0.346	-0.061	-0.090	-0.145	-0.089	-0.100
5 km focal scale								
COVER	-0.029	-0.039	-0.060	-0.053	-0.037	-0.027	-0.052	-0.031
RPDENS	-0.252	-0.251	-0.135	0.047	-0.402	-0.290	-0.265	-0.199
RPSIZE	**-0.752**	**-0.737**	**-0.751**	**-0.635**	**-0.737**	**-0.764**	**-0.645**	**-0.800**
RDIV	0.526	0.478	-0.089	0.525	0.551	**0.572**	0.386	0.538
REDGE*	0.225	0.388	0.083	0.295	0.224	0.279	-0.278	0.281
RSHAPE*	-0.064	-0.163	-0.222	-0.276	-0.182	-0.065	-0.505	0.014
RNEAR*	-0.534	-0.538	-0.207	-0.399	**-0.552**	**-0.682**	**-0.533**	**-0.578**
RPROX*	0.248	0.195	0.475	0.283	0.299	0.240	0.356	0.247

Table 3.3. Composite correlation matrix at each focal scale between abundance of *Carollia brevicauda* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	-0.526	-0.534	-0.536	**-0.530**	**-0.571**	-0.529	**-0.568**	-0.528
RPDENS	0.193	0.164	0.190	0.131	-0.057	0.147	0.005	0.155
RPSIZE	0.228	0.216	0.193	0.466	0.396	0.171	-0.125	0.212
RDIV	0.137	0.061	0.445	0.116	-0.244	0.165	0.258	0.180
REDGE*	0.455	0.359	0.505	0.435	0.386	0.458	0.369	0.443
RSHAPE*	-0.115	-0.066	-0.032	-0.152	-0.283	-0.098	0.061	-0.080
RNEAR*	-0.439	-0.339	-0.345	-0.430	-0.354	-0.365	-0.372	-0.392
RPROX*	-0.084	-0.048	0.113	-0.155	-0.246	-0.044	0.152	-0.072
3 km focal scale								
COVER	-0.527	-0.528	**-0.552**	-0.544	-0.549	-0.529	-0.544	**-0.553**
RPDENS	0.082	0.070	0.096	0.040	-0.112	0.024	-0.072	0.119
RPSIZE	0.350	0.304	0.297	0.169	0.406	0.298	0.242	0.183
RDIV	-0.294	-0.243	-0.027	-0.249	-0.345	-0.252	-0.188	-0.233
REDGE*	0.333	0.296	0.397	0.369	0.283	0.277	0.206	0.325
RSHAPE*	-0.104	-0.059	-0.092	-0.096	-0.063	-0.088	-0.024	0.029
RNEAR*	-0.295	-0.252	-0.180	-0.190	-0.156	-0.237	-0.251	-0.200
RPROX*	0.355	0.315	0.191	0.289	0.341	0.291	0.263	0.302
5 km focal scale								
COVER	**-0.548**	-0.548	**-0.575**	**-0.594**	**-0.555**	**-0.555**	-0.549	**-0.601**
RPDENS	0.087	0.092	0.023	-0.188	0.052	0.021	0.086	0.223
RPSIZE	0.375	0.310	0.321	-0.005	0.356	0.307	0.310	0.314
RDIV	-0.497	-0.457	-0.304	-0.432	-0.429	-0.393	-0.425	-0.478
REDGE*	0.141	0.069	0.190	0.089	0.102	0.220	0.274	0.193
RSHAPE*	-0.237	-0.198	-0.194	-0.100	-0.289	-0.217	-0.183	-0.102
RNEAR*	0.123	0.114	-0.078	-0.084	0.280	-0.001	0.118	0.086
RPROX*	0.486	0.446	0.400	0.455	0.433	0.364	0.399	0.405

Table 3.4. Composite correlation matrix at each focal scale between abundance of *Carollia perspicillata* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	**-0.534**	-0.537	-0.541	-0.536	-0.544	-0.544	-0.549	-0.538
RPDENS	-0.122	-0.104	-0.088	-0.139	-0.108	-0.147	-0.229	-0.124
RPSIZE	0.187	0.148	0.158	0.342	0.161	0.102	-0.014	0.106
RDIV	0.079	0.113	0.313	0.066	0.118	0.146	0.146	0.149
REDGE*	-0.026	0.039	0.039	-0.100	-0.023	0.049	-0.054	0.021
RSHAPE*	-0.215	-0.209	-0.137	-0.223	-0.187	-0.182	-0.102	-0.154
RNEAR*	-0.271	-0.304	-0.168	-0.261	-0.233	-0.173	-0.228	-0.197
RPROX*	-0.139	-0.136	0.001	-0.178	-0.118	-0.066	0.000	-0.118
3 km focal scale								
COVER	-0.435	-0.485	-0.450	-0.436	-0.457	-0.437	-0.470	-0.445
RPDENS	-0.491	-0.442	-0.439	-0.441	-0.346	**-0.589**	-0.313	-0.426
RPSIZE	0.278	0.244	0.251	0.452	0.184	0.251	0.405	0.178
RDIV	0.041	-0.021	0.391	0.037	0.121	0.036	-0.086	0.057
REDGE*	-0.334	-0.070	-0.249	-0.320	-0.300	-0.310	-0.176	-0.290
RSHAPE*	-0.081	-0.439	-0.075	-0.072	-0.108	-0.073	-0.191	0.004
RNEAR*	0.415	0.189	0.482	0.381	0.290	0.408	0.374	0.436
RPROX*	0.227	0.160	0.100	0.209	0.188	0.191	0.313	0.204
5 km focal scale								
COVER	-0.400	-0.471	-0.406	-0.402	-0.485	-0.399	-0.446	-0.427
RPDENS	-0.525	-0.467	-0.539	-0.531	-0.273	**-0.554**	**-0.570**	-0.416
RPSIZE	0.229	0.367	0.215	0.370	0.098	0.203	-0.093	0.198
RDIV	0.056	-0.288	0.311	0.039	0.010	0.089	0.329	0.037
REDGE*	**-0.658**	-0.513	**-0.594**	**-0.613**	**-0.614**	**-0.616**	-0.419	**-0.599**
RSHAPE*	-0.147	-0.366	-0.129	-0.168	0.159	-0.148	0.177	-0.043
RNEAR*	0.537	**0.596**	0.473	**0.577**	0.107	0.510	0.503	0.502
RPROX*	0.381	0.266	0.339	0.349	0.309	0.322	0.348	0.349

Table 3.5. Composite correlation matrix at each focal scale between abundance of *Rhinophylla pumilio* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape characteristics	Controlled (partialled) characteristics							
	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	0.223	0.223	0.225	0.226	0.239	0.253	0.225	0.225
RPDENS	-0.032	-0.031	-0.046	0.031	0.200	-0.149	0.029	-0.013
RPSIZE	-0.131	-0.132	-0.128	-0.417	-0.300	-0.356	-0.044	-0.058
RDIV	-0.164	-0.159	-0.426	-0.160	0.137	0.018	-0.212	-0.260
REDGE*	-0.361	-0.397	-0.434	-0.342	-0.351	-0.213	-0.340	-0.426
RSHAPE*	-0.485	-0.490	**-0.558**	-0.451	-0.393	-0.473	**-0.580**	-0.540
RNEAR*	0.138	0.134	0.060	0.193	0.097	0.401	0.134	0.085
RPROX*	0.122	0.116	0.036	0.239	0.282	0.316	0.059	0.119
3 km focal scale								
COVER	0.206	0.209	0.208	0.208	0.208	0.220	0.254	0.206
RPDENS	0.172	0.168	0.161	0.154	0.286	-0.035	-0.191	0.175
RPSIZE	-0.113	-0.100	-0.110	-0.353	-0.149	-0.118	-0.359	-0.145
RDIV	-0.138	-0.117	-0.361	-0.135	-0.110	-0.150	0.053	-0.133
REDGE*	-0.122	-0.261	-0.156	-0.089	-0.119	-0.163	-0.475	-0.117
RSHAPE*	-0.350	-0.305	-0.345	-0.348	-0.359	-0.343	-0.243	-0.356
RNEAR*	**-0.595**	**-0.587**	**-0.646**	**-0.573**	**-0.693**	**-0.543**	**-0.582**	**-0.588**
RPROX*	0.037	0.061	0.101	0.024	0.021	-0.107	-0.111	0.036
5 km focal scale								
COVER	0.206	0.221	0.205	0.210	0.207	0.250	0.204	0.206
RPDENS	0.259	0.246	0.277	0.232	0.300	0.108	0.260	0.244
RPSIZE	-0.105	-0.168	-0.106	-0.270	-0.120	-0.177	-0.006	-0.102
RDIV	-0.104	0.046	-0.267	-0.096	-0.099	0.053	-0.196	-0.096
REDGE*	-0.056	-0.183	-0.076	-0.054	-0.049	0.187	-0.265	-0.057
RSHAPE*	-0.483	-0.419	-0.482	-0.460	-0.492	-0.465	**-0.686**	-0.505
RNEAR*	-0.178	-0.199	-0.147	-0.247	-0.314	**-0.588**	-0.180	-0.177
RPROX*	-0.043	0.023	-0.033	-0.041	-0.052	-0.225	-0.025	-0.042

Table 3.6. Composite correlation matrix at each focal scale between abundance of *Rhinophylla fischerae* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	-0.029	-0.031	-0.030	-0.030	-0.031	-0.029	-0.029	-0.030
RPDENS	-0.385	-0.385	-0.373	-0.329	-0.253	-0.393	-0.351	-0.439
RPSIZE	0.186	0.157	0.186	-0.002	0.066	0.199	0.462	0.010
RDIV	-0.238	-0.111	-0.151	-0.238	0.009	-0.256	-0.308	-0.137
REDGE*	-0.343	-0.174	-0.299	-0.254	-0.342	-0.369	-0.328	-0.283
RSHAPE*	-0.001	-0.089	0.070	0.096	0.146	-0.001	-0.077	0.079
RNEAR*	0.170	0.006	0.456	0.261	0.136	0.186	0.169	0.353
RPROX*	-0.240	-0.326	-0.154	-0.140	-0.132	-0.251	-0.388	-0.239
3 km focal scale								
COVER	0.279	0.320	0.280	0.280	0.282	0.284	0.282	0.279
RPDENS	-0.509	-0.488	-0.496	-0.483	-0.495	-0.472	-0.495	-0.491
RPSIZE	-0.075	-0.124	-0.072	-0.006	-0.118	-0.073	-0.035	-0.090
RDIV	0.090	0.029	0.049	0.086	0.129	0.091	0.049	0.088
REDGE*	-0.154	0.174	-0.175	-0.176	-0.148	-0.133	-0.105	-0.148
RSHAPE*	0.196	-0.124	0.189	0.191	0.177	0.189	0.161	0.210
RNEAR*	0.137	-0.161	0.116	0.111	0.080	0.087	0.132	0.138
RPROX*	0.016	-0.062	0.056	0.023	0.002	0.094	0.044	0.015
5 km focal scale								
COVER	0.319	0.318	0.320	0.317	0.343	0.351	0.326	0.327
RPDENS	-0.190	-0.191	-0.164	-0.182	-0.068	-0.344	-0.201	-0.140
RPSIZE	-0.152	-0.111	-0.148	-0.144	-0.232	-0.198	-0.281	-0.174
RDIV	0.065	-0.039	-0.061	0.071	0.059	0.195	0.151	0.071
REDGE*	-0.323	-0.242	-0.344	-0.295	-0.297	-0.179	-0.280	-0.268
RSHAPE*	-0.370	-0.436	-0.362	-0.380	-0.247	-0.340	-0.313	-0.289
RNEAR*	0.165	0.160	0.280	0.198	-0.104	-0.050	0.147	0.128
RPROX*	0.242	0.190	0.246	0.229	0.188	0.137	0.219	0.230

Table 3.7. Composite correlation matrix at each focal scale between abundance of *Glossophaga soricina* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	**-0.736**	**-0.780**	**-0.737**	**-0.753**	**-0.736**	**-0.742**	**-0.747**	**-0.740**
RPDENS	0.485	0.327	0.323	0.276	0.380	0.311	0.288	0.317
RPSIZE	-0.085	-0.023	-0.058	0.175	-0.058	-0.110	-0.265	-0.204
RDIV	0.307	0.098	0.263	0.207	0.283	0.275	0.273	0.305
REDGE*	0.020	-0.206	-0.010	-0.197	0.012	0.064	-0.009	0.053
RSHAPE*	-0.185	-0.063	-0.156	-0.222	-0.140	-0.125	-0.066	-0.099
RNEAR*	-0.245	-0.029	-0.304	-0.244	-0.164	-0.126	-0.165	-0.132
RPROX*	-0.150	-0.056	-0.220	-0.249	-0.114	-0.067	-0.020	-0.102
3 km focal scale								
COVER	**-0.705**	**-0.706**	**-0.708**	**-0.705**	**-0.715**	**-0.707**	**-0.706**	**-0.705**
RPDENS	-0.082	-0.058	-0.052	-0.056	0.040	-0.120	-0.041	-0.055
RPSIZE	0.118	0.080	0.084	0.158	0.042	0.084	0.101	0.083
RDIV	0.025	0.011	0.136	0.018	0.061	0.017	0.005	0.020
REDGE*	-0.228	-0.156	-0.144	-0.171	-0.161	-0.170	-0.157	-0.160
RSHAPE*	-0.101	-0.127	-0.072	-0.071	-0.089	-0.071	-0.086	-0.068
RNEAR*	0.062	0.016	0.071	0.040	-0.024	0.065	0.044	0.050
RPROX*	0.032	0.015	-0.019	0.025	0.009	-0.005	0.033	0.023
5 km focal scale								
COVER	**-0.598**	**-0.619**	**-0.599**	**-0.603**	**-0.615**	**-0.598**	**-0.598**	**-0.624**
RPDENS	-0.283	-0.206	-0.208	-0.195	-0.096	-0.249	-0.210	-0.143
RPSIZE	-0.025	0.035	-0.012	0.072	-0.080	-0.021	-0.058	-0.038
RDIV	0.120	-0.040	0.106	0.079	0.067	0.110	0.119	0.079
REDGE*	-0.323	-0.211	-0.286	-0.273	-0.276	-0.267	-0.333	-0.240
RSHAPE*	-0.079	-0.165	-0.085	-0.113	0.040	-0.083	-0.057	0.006
RNEAR*	0.060	0.077	0.087	0.110	-0.204	0.024	0.065	0.039
RPROX*	0.352	0.241	0.283	0.281	0.245	0.269	0.277	0.281

Table 3.8. Composite correlation matrix at each focal scale between abundance of *Lonchophylla thomasi* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	-0.086	-0.088	-0.087	-0.097	-0.103	-0.089	-0.088	-0.092
RPDENS	0.202	0.201	0.189	0.041	-0.123	0.262	0.153	0.268
RPSIZE	-0.138	-0.118	-0.138	0.396	0.080	-0.060	-0.367	0.173
RDIV	0.453	0.414	**0.562**	0.451	0.117	0.403	0.527	0.348
REDGE*	0.539	0.519	0.528	0.344	**0.536**	0.497	0.528	0.474
RSHAPE*	0.237	0.289	0.203	0.084	0.046	0.236	0.327	0.150
RNEAR*	-0.151	-0.073	-0.371	-0.337	-0.099	-0.275	-0.150	-0.395
RPROX*	0.329	0.370	0.343	0.124	0.170	0.276	0.479	0.328
3 km focal scale								
COVER	-0.303	-0.305	-0.303	-0.322	-0.344	-0.308	-0.309	-0.316
RPDENS	0.099	0.094	0.095	0.147	-0.238	0.236	-0.012	0.141
RPSIZE	0.004	0.011	0.004	0.468	0.158	0.004	-0.059	-0.156
RDIV	0.358	0.358	**0.557**	0.342	0.261	0.350	0.431	0.386
REDGE*	0.499	0.513	0.495	0.429	0.476	0.502	0.440	0.523
RSHAPE*	0.180	0.275	0.172	0.189	0.249	0.172	0.237	0.314
RNEAR*	-0.211	-0.179	-0.209	-0.340	-0.012	-0.259	-0.201	-0.150
RPROX*	0.300	0.303	0.323	0.339	0.372	0.384	0.254	0.286
5 km focal scale								
COVER	-0.214	-0.220	-0.214	-0.238	-0.251	-0.250	-0.248	-0.218
RPDENS	-0.143	-0.132	-0.133	0.063	-0.405	0.007	-0.123	-0.091
RPSIZE	-0.017	0.016	-0.014	0.383	0.097	0.034	0.288	-0.030
RDIV	0.351	0.317	0.493	0.336	0.399	0.243	0.192	0.339
REDGE*	0.452	**0.557**	0.443	0.481	0.435	0.314	0.215	0.481
RSHAPE*	0.431	0.395	0.414	0.347	0.280	0.413	0.245	0.502
RNEAR*	-0.430	-0.411	-0.490	-0.316	-0.159	-0.246	-0.414	-0.440
RPROX*	0.180	0.148	0.178	0.182	0.285	0.355	0.239	0.176

Table 3.9. Composite correlation matrix at each focal scale between abundance of *Lophostoma silvicolum* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	0.033	0.034	0.035	0.036	0.036	0.034	0.033	0.036
RPDENS	-0.193	-0.192	-0.168	-0.059	0.001	-0.254	-0.198	-0.264
RPSIZE	0.296	0.281	0.296	-0.010	0.186	0.233	0.467	0.057
RDIV	-0.382	-0.341	-0.254	-0.382	-0.193	-0.326	-0.411	-0.253
REDGE*	-0.359	-0.309	-0.280	-0.134	-0.359	-0.299	-0.358	-0.267
RSHAPE*	-0.239	-0.290	-0.151	-0.114	-0.121	-0.239	-0.275	-0.148
RNEAR*	0.031	-0.058	0.379	0.166	-0.015	0.143	0.031	0.262
RPROX*	-0.347	-0.388	-0.198	-0.189	-0.250	-0.296	-0.424	-0.347
3 km focal scale								
COVER	0.096	0.096	0.099	0.111	0.096	0.101	0.102	0.096
RPDENS	-0.070	-0.070	-0.055	-0.156	-0.035	0.132	-0.306	-0.080
RPSIZE	0.223	0.218	0.222	-0.332	0.211	0.234	0.136	0.289
RDIV	-0.510	-0.522	**-0.553**	-0.508	-0.507	-0.528	-0.451	-0.517
REDGE*	-0.074	-0.041	-0.014	0.064	-0.073	-0.046	-0.245	-0.080
RSHAPE*	0.307	0.324	0.313	0.344	0.300	0.305	0.435	0.303
RNEAR*	-0.343	-0.442	-0.297	-0.229	-0.406	-0.459	-0.342	-0.365
RPROX*	-0.068	-0.078	-0.201	-0.133	-0.074	0.054	-0.152	-0.067
5 km focal scale								
COVER	0.155	0.157	0.158	0.184	0.153	0.156	0.153	0.156
RPDENS	0.051	0.045	0.023	-0.231	-0.088	0.040	0.059	0.075
RPSIZE	0.110	0.099	0.107	-0.334	0.180	0.105	0.305	0.099
RDIV	-0.420	-0.459	-0.502	-0.410	-0.412	-0.423	-0.591	-0.413
REDGE*	0.270	0.281	0.306	0.275	0.271	0.310	0.138	0.296
RSHAPE*	-0.027	-0.007	-0.010	0.118	-0.158	-0.022	-0.194	0.011
RNEAR*	-0.246	-0.250	-0.373	-0.516	-0.077	-0.310	-0.248	-0.260
RPROX*	0.103	0.118	0.094	0.117	0.159	0.101	0.131	-0.102

Table 3.10. Composite correlation matrix at each focal scale between abundance of *Mimon crenulatum* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	0.317	0.389	0.318	0.345	0.452	0.320	0.335	0.317
RPDENS	**0.611**	**0.579**	**0.578**	0.508	0.331	**0.624**	0.515	**0.587**
RPSIZE	-0.059	0.011	-0.056	0.450	0.329	-0.012	-0.458	-0.076
RDIV	0.415	0.237	**0.569**	0.394	-0.234	0.377	0.547	0.456
REDGE*	**0.754**	**0.588**	**0.751**	**0.673**	**0.715**	**0.726**	**0.719**	**0.764**
RSHAPE*	0.134	0.308	0.115	-0.022	-0.217	0.127	0.298	0.131
RNEAR*	-0.345	-0.108	-0.541	-0.509	-0.342	-0.416	-0.327	-0.387
RPROX*	0.007	0.118	-0.052	-0.249	-0.385	-0.034	0.218	0.007
3 km focal scale								
COVER	0.184	0.243	0.184	0.184	0.285	0.200	0.204	0.186
RPDENS	**0.666**	**0.655**	**0.654**	**0.667**	0.424	**0.570**	**0.558**	**0.692**
RPSIZE	-0.048	0.001	-0.047	-0.014	0.259	-0.052	-0.202	-0.139
RDIV	0.050	0.174	0.019	0.049	-0.227	0.046	0.211	0.064
REDGE*	**0.775**	**0.631**	**0.780**	**0.775**	**0.762**	**0.791**	**0.712**	**0.788**
RSHAPE*	-0.401	-0.034	-0.394	-0.393	-0.495	-0.394	-0.322	-0.366
RNEAR*	-0.443	-0.150	-0.470	-0.473	-0.217	-0.375	-0.435	-0.417
RPROX*	0.158	0.331	0.203	0.161	0.341	0.009	0.072	0.156
5 km focal scale								
COVER	0.062	0.102	0.063	0.073	0.057	0.066	0.059	0.062
RPDENS	**0.596**	**0.592**	**0.589**	0.545	0.445	**0.596**	**0.605**	**0.613**
RPSIZE	0.095	-0.045	0.094	-0.187	0.325	0.084	0.203	0.095
RDIV	-0.286	0.056	-0.323	-0.283	-0.328	-0.266	-0.379	-0.283
REDGE*	**0.647**	0.531	**0.690**	**0.661**	**0.647**	**0.767**	**0.809**	**0.657**
RSHAPE*	-0.104	0.128	-0.092	-0.017	-0.547	-0.102	-0.209	-0.108
RNEAR*	-0.129	-0.199	-0.221	-0.291	**0.646**	-0.223	-0.130	-0.130
RPROX*	-0.003	0.194	-0.012	0.000	0.148	-0.038	0.010	-0.003

Table 3.11. Composite correlation matrix at each focal scale between abundance of *Phyllostomus elongatus* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	-0.043	-0.043	-0.045	-0.043	-0.043	-0.043	-0.045	-0.051
RPDENS	0.098	0.098	0.139	0.085	0.092	0.095	-0.013	0.018
RPSIZE	0.308	0.322	0.308	0.566	0.347	0.321	0.185	-0.188
RDIV	0.052	0.017	0.502	0.052	0.036	0.064	0.139	0.468
REDGE*	0.038	-0.018	0.174	0.001	0.037	0.049	0.006	0.302
RSHAPE*	-0.021	-0.001	0.098	-0.043	-0.038	-0.021	0.091	0.187
RNEAR*	-0.254	-0.236	-0.045	-0.283	-0.251	-0.268	-0.254	0.042
RPROX*	-0.549	-0.543	-0.505	**-0.673**	**-0.603**	**-0.570**	-0.504	**-0.549**
3 km focal scale								
COVER	0.046	0.047	0.048	0.046	0.046	0.047	0.048	0.046
RPDENS	-0.223	-0.222	-0.211	-0.250	-0.278	-0.096	-0.093	-0.233
RPSIZE	0.301	0.292	0.300	0.267	0.316	0.311	0.417	0.372
RDIV	-0.175	-0.210	0.103	-0.175	-0.184	-0.177	-0.285	-0.181
REDGE*	0.014	0.172	0.105	0.061	0.014	0.041	0.146	0.009
RSHAPE*	0.257	0.162	0.270	0.258	0.259	0.257	0.197	0.254
RNEAR*	0.284	0.202	0.406	0.358	0.316	0.232	0.283	0.278
RPROX*	-0.057	-0.091	-0.237	-0.074	-0.056	0.045	0.004	-0.057
5 km focal scale								
COVER	0.101	0.095	0.107	0.108	0.102	0.096	0.109	0.101
RPDENS	-0.301	-0.302	-0.372	-0.481	-0.324	-0.251	-0.320	-0.285
RPSIZE	0.234	0.320	0.231	0.152	0.231	0.262	0.143	0.224
RDIV	-0.181	-0.425	-0.005	-0.177	-0.178	-0.259	-0.099	-0.179
REDGE*	-0.031	0.126	0.026	-0.038	-0.028	-0.134	0.181	-0.008
RSHAPE*	0.210	0.124	0.245	0.284	0.248	0.212	0.398	0.264
RNEAR*	0.210	0.233	0.095	0.147	0.270	0.395	0.206	0.197
RPROX*	0.112	0.036	0.095	0.116	0.109	0.193	0.094	0.112

Table 3.12. Composite correlation matrix at each focal scale between abundance of *Phyllostomus hastatus* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect ofthe landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	-0.406	-0.412	-0.448	-0.407	-0.412	-0.409	-0.451	-0.428
RPDENS	0.175	0.159	0.228	0.188	0.087	0.141	-0.030	0.118
RPSIZE	0.461	0.447	0.421	**0.631**	0.527	0.411	0.174	0.292
RDIV	-0.046	-0.110	0.519	-0.042	-0.225	-0.002	0.102	0.151
REDGE*	0.177	0.091	0.380	0.272	0.161	0.219	0.120	0.312
RSHAPE*	-0.119	-0.079	0.046	-0.101	-0.185	-0.109	0.076	-0.012
RNEAR*	-0.470	-0.404	-0.195	-0.437	-0.417	-0.423	-0.429	-0.326
RPROX*	-0.347	-0.301	-0.003	-0.346	-0.408	-0.300	-0.124	-0.317
3 km focal scale								
COVER	-0.294	-0.300	-0.314	-0.294	-0.303	-0.302	-0.296	-0.304
RPDENS	-0.218	-0.209	-0.196	-0.211	-0.434	-0.093	-0.312	-0.180
RPSIZE	0.371	0.348	0.354	**0.561**	0.453	0.365	0.339	0.271
RDIV	-0.010	-0.036	0.466	-0.009	-0.076	-0.005	0.026	0.016
REDGE*	0.259	0.451	0.383	0.258	0.248	0.280	0.224	0.281
RSHAPE*	0.247	0.146	0.253	0.236	0.270	0.236	0.276	0.374
RNEAR*	-0.115	-0.261	-0.008	-0.113	-0.012	-0.183	-0.110	-0.058
RPROX*	0.274	0.240	0.114	0.262	0.293	0.390	0.246	0.262
5 km focal scale								
COVER	-0.240	-0.248	-0.245	-0.239	-0.239	-0.239	-0.238	-0.252
RPDENS	-0.161	-0.148	-0.222	-0.200	-0.147	-0.161	-0.155	-0.075
RPSIZE	0.282	0.321	0.277	0.378	0.277	0.278	0.256	0.265
RDIV	-0.031	-0.141	0.270	-0.037	-0.039	-0.035	0.017	-0.042
REDGE*	-0.030	0.034	0.030	-0.038	-0.035	-0.034	0.075	0.019
RSHAPE*	-0.003	-0.065	0.019	0.000	0.004	-0.011	0.066	0.094
RNEAR*	0.117	0.129	-0.044	0.116	0.137	0.136	0.120	0.095
RPROX*	0.313	0.278	0.292	0.304	0.302	0.316	0.295	0.303

Table 3.13. Composite correlation matrix at each focal scale between abundance of *Tonatia saurophila* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	0.453	0.456	0.458	0.466	0.503	0.453	0.453	0.454
RPDENS	0.138	0.124	0.109	0.039	-0.148	0.140	0.161	0.139
RPSIZE	-0.175	-0.144	-0.156	0.053	0.011	-0.144	-0.175	-0.136
RDIV	0.267	0.209	0.190	0.239	-0.117	0.233	0.235	0.226
REDGE*	0.492	0.446	0.416	0.395	0.439	0.450	0.450	0.439
RSHAPE*	0.069	0.090	0.008	-0.029	-0.123	0.062	0.045	0.036
RNEAR*	0.058	0.116	-0.094	-0.023	0.119	0.029	0.051	0.006
RPROX*	0.099	0.109	-0.044	-0.042	-0.084	0.073	0.073	0.088
3 km focal scale								
COVER	0.388	0.399	0.399	0.390	0.489	0.388	0.388	0.395
RPDENS	0.262	0.241	0.231	0.258	-0.153	0.268	0.261	0.221
RPSIZE	-0.261	-0.230	-0.240	-0.253	-0.097	-0.241	-0.262	-0.172
RDIV	0.117	0.143	-0.135	0.108	-0.058	0.107	0.125	0.092
REDGE*	**0.661**	**0.590**	**0.582**	**0.605**	**0.609**	**0.609**	**0.650**	**0.606**
RSHAPE*	-0.041	0.125	-0.039	-0.036	0.028	-0.038	-0.029	-0.122
RNEAR*	-0.039	0.107	-0.114	-0.072	0.288	-0.027	-0.036	-0.080
RPROX*	-0.209	-0.166	-0.093	-0.185	-0.179	-0.224	-0.206	-0.193
5 km focal scale								
COVER	0.231	0.245	0.231	0.240	0.237	0.235	0.232	0.245
RPDENS	0.226	0.212	0.233	0.147	0.060	0.198	0.211	0.141
RPSIZE	-0.066	-0.119	-0.067	-0.295	0.017	-0.076	-0.099	-0.042
RDIV	-0.178	-0.063	-0.329	-0.166	-0.159	-0.151	-0.172	-0.172
REDGE*	0.367	0.308	0.359	0.361	0.364	0.439	**0.555**	0.329
RSHAPE*	-0.087	-0.006	-0.085	-0.028	-0.275	-0.077	-0.075	-0.197
RNEAR*	0.033	0.015	0.077	-0.052	0.451	-0.020	0.026	0.061
RPROX*	-0.328	-0.280	-0.315	-0.321	-0.278	-0.363	-0.323	-0.319

Table 3.14. Composite correlation matrix at each focal scale between abundance of *Artibeus lituratus* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	**-0.546**	**-0.557**	**-0.563**	-0.547	-0.546	**-0.567**	**-0.554**	**-0.562**
RPDENS	-0.232	-0.195	-0.174	-0.186	-0.232	-0.264	-0.294	-0.239
RPSIZE	0.286	0.223	0.239	0.312	0.259	0.162	0.184	0.102
RDIV	-0.072	0.013	0.214	-0.060	-0.087	0.042	-0.014	0.071
REDGE*	0.003	0.128	0.102	0.063	0.002	0.113	-0.019	0.094
RSHAPE*	-0.316	-0.318	-0.199	-0.262	-0.286	-0.265	-0.223	-0.209
RNEAR*	-0.189	-0.272	0.026	-0.147	-0.159	-0.058	-0.158	-0.046
RPROX*	-0.276	-0.269	-0.081	-0.234	-0.249	-0.163	-0.177	-0.232
3 km focal scale								
COVER	-0.341	-0.375	-0.358	-0.350	-0.342	-0.342	-0.342	-0.348
RPDENS	-0.442	-0.415	-0.413	-0.458	-0.460	-0.494	-0.473	-0.399
RPSIZE	0.315	0.293	0.296	0.200	0.291	0.296	0.315	0.237
RDIV	-0.238	-0.305	0.016	-0.223	-0.215	-0.223	-0.210	-0.240
REDGE*	-0.067	0.227	0.020	-0.007	-0.062	-0.061	-0.060	-0.047
RSHAPE*	0.016	-0.295	0.016	0.012	0.009	0.015	0.010	0.096
RNEAR*	0.020	-0.251	0.115	0.093	-0.007	0.016	0.019	0.063
RPROX*	0.204	0.149	0.062	0.177	0.188	0.214	0.201	0.192
5 km focal scale								
COVER	-0.334	-0.353	-0.345	-0.339	-0.361	-0.345	-0.348	-0.349
RPDENS	-0.273	-0.245	-0.332	-0.489	-0.050	-0.418	-0.284	-0.185
RPSIZE	0.307	0.368	0.294	0.137	0.219	0.276	0.114	0.282
RDIV	-0.282	-0.502	-0.087	-0.276	-0.338	-0.186	-0.139	-0.291
REDGE*	-0.479	-0.405	-0.423	-0.495	-0.461	-0.363	-0.302	-0.435
RSHAPE*	-0.374	-0.488	-0.350	-0.306	-0.209	-0.364	-0.208	-0.300
RNEAR*	0.382	0.394	0.258	0.289	0.058	0.218	0.369	0.358
RPROX*	0.305	0.239	0.275	0.302	0.236	0.195	0.271	0.287

Table 3.15. Composite correlation matrix at each focal scale between abundance of *Artibeus obscurus* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	**-0.675**	**-0.676**	**-0.677**	**-0.676**	**-0.685**	**-0.676**	**-0.676**	**-0.677**
RPDENS	-0.057	-0.043	-0.035	-0.062	-0.157	-0.049	-0.025	-0.054
RPSIZE	0.101	0.070	0.074	0.171	0.148	0.070	0.162	0.037
RDIV	0.053	0.059	0.159	0.039	-0.110	0.052	0.025	0.086
REDGE*	0.221	0.220	0.206	0.191	0.162	0.185	0.170	0.200
RSHAPE*	-0.033	-0.034	0.002	-0.042	-0.093	-0.025	-0.048	-0.004
RNEAR*	0.065	0.034	0.152	0.039	0.071	0.064	0.049	0.098
RPROX*	-0.089	-0.074	-0.016	-0.101	-0.136	-0.062	-0.107	-0.066
3 km focal scale								
COVER	**-0.547**	**-0.566**	-0.547	-0.548	**-0.576**	**-0.584**	**-0.555**	-0.547
RPDENS	-0.305	-0.255	-0.253	-0.265	-0.551	-0.071	-0.410	-0.253
RPSIZE	0.048	0.022	0.040	-0.013	0.139	0.044	-0.012	0.028
RDIV	-0.073	-0.097	-0.048	-0.061	-0.153	-0.059	-0.008	-0.058
REDGE*	0.378	**0.575**	0.341	0.344	0.317	0.377	0.273	0.321
RSHAPE*	0.420	0.260	0.352	0.351	0.405	0.352	0.418	0.394
RNEAR*	-0.209	-0.371	-0.171	-0.165	-0.055	-0.296	-0.176	-0.172
RPROX*	0.040	-0.002	0.017	0.028	0.064	0.192	-0.004	0.034
5 km focal scale								
COVER	-0.493	-0.502	-0.494	-0.492	-0.497	-0.494	-0.504	-0.509
RPDENS	-0.166	-0.127	-0.124	-0.206	-0.184	-0.188	-0.121	-0.069
RPSIZE	-0.043	-0.003	-0.030	-0.142	-0.012	-0.047	0.070	-0.053
RDIV	-0.080	-0.184	0.162	-0.084	-0.080	-0.043	-0.170	-0.090
REDGE*	0.111	0.157	0.078	0.079	0.083	0.161	-0.046	0.131
RSHAPE*	-0.146	-0.200	-0.148	-0.125	-0.199	-0.144	-0.279	-0.073
RNEAR*	-0.197	-0.152	-0.169	-0.215	-0.141	-0.285	-0.157	-0.187
RPROX*	0.279	0.218	0.245	0.243	0.261	0.209	0.262	0.241

Table 3.16. Composite correlation matrix at each focal scale between abundance of *Artibeus planirostris* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	**-0.586**	**-0.587**	**-0.598**	**-0.587**	**-0.587**	**-0.590**	**-0.596**	**-0.622**
RPDENS	0.054	0.043	0.067	0.059	0.037	0.020	-0.036	-0.008
RPSIZE	0.243	0.203	0.197	0.279	0.221	0.168	0.102	-0.089
RDIV	-0.039	-0.513	0.204	-0.032	-0.067	0.012	0.023	0.176
REDGE*	0.028	-0.001	0.106	0.063	0.022	0.070	0.000	0.163
RSHAPE*	-0.141	-0.108	-0.049	-0.111	-0.132	-0.114	-0.049	-0.012
RNEAR*	-0.218	-0.174	-0.047	-0.174	-0.174	-0.143	-0.176	-0.002
RPROX*	-0.414	-0.334	-0.290	-0.373	-0.369	-0.318	-0.291	-0.336
3 km focal scale								
COVER	-0.499	-0.499	-0.504	-0.517	-0.506	-0.514	-0.503	-0.520
RPDENS	0.037	0.032	0.043	-0.001	-0.076	0.218	-0.046	-0.008
RPSIZE	0.169	0.149	0.147	-0.101	0.203	0.152	0.113	0.331
RDIV	-0.304	-0.261	-0.242	-0.263	-0.320	-0.267	-0.235	-0.302
REDGE*	0.193	0.181	0.218	0.250	0.168	0.199	0.124	0.151
RSHAPE*	0.283	0.320	0.248	0.250	0.267	0.245	0.294	0.157
RNEAR*	-0.158	-0.141	-0.100	-0.062	-0.077	-0.215	-0.137	-0.210
RPROX*	-0.324	-0.279	-0.403	-0.318	-0.271	-0.210	-0.320	-0.281
5 km focal scale								
COVER	-0.432	-0.436	-0.432	-0.441	-0.441	-0.437	-0.439	-0.424
RPDENS	-0.093	-0.069	-0.085	-0.266	-0.149	-0.040	-0.063	-0.057
RPSIZE	0.066	0.082	0.065	-0.217	0.101	0.076	0.163	0.061
RDIV	-0.286	-0.367	-0.336	-0.271	-0.266	-0.314	-0.362	-0.272
REDGE*	0.172	0.194	0.162	0.134	0.143	0.115	0.078	0.155
RSHAPE*	0.118	0.073	0.099	0.189	0.034	0.091	0.029	0.114
RNEAR*	-0.151	-0.121	-0.194	-0.277	-0.029	-0.088	-0.124	-0.130
RPROX*	0.060	0.036	0.048	0.058	0.080	0.087	0.066	0.053

Table 3.17. Composite correlation matrix at each focal scale between abundance of *Dermanura anderseni* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	-0.123	-0.126	-0.125	-0.124	-0.124	-0.123	-0.124	-0.123
RPDENS	0.222	0.220	0.204	0.191	0.343	0.229	0.294	0.225
RPSIZE	-0.186	-0.165	-0.184	-0.150	-0.252	-0.189	-0.160	-0.258
RDIV	0.119	0.040	-0.045	0.118	0.297	0.119	0.091	0.127
REDGE*	-0.126	-0.296	-0.214	-0.300	-0.126	-0.143	-0.114	-0.142
RSHAPE*	0.020	0.068	-0.049	-0.026	0.073	0.020	-0.024	0.015
RNEAR*	0.104	0.224	-0.046	0.072	0.089	0.105	0.104	0.110
RPROX*	0.018	0.053	-0.185	-0.050	0.068	0.012	-0.042	0.018
3 km focal scale								
COVER	-0.253	-0.253	-0.254	-0.254	-0.271	-0.258	-0.285	-0.254
RPDENS	0.010	0.009	0.002	0.022	0.270	-0.127	0.322	0.000
RPSIZE	-0.102	-0.098	-0.098	-0.031	-0.217	-0.101	0.041	-0.076
RDIV	0.104	0.103	0.039	0.101	0.210	0.100	-0.044	0.096
REDGE*	-0.367	-0.436	-0.399	-0.395	-0.355	-0.384	-0.211	-0.363
RSHAPE*	-0.204	-0.233	-0.198	-0.196	-0.249	-0.197	-0.369	-0.241
RNEAR*	0.472	0.539	0.450	0.450	0.367	0.537	0.457	0.454
RPROX*	-0.069	-0.066	-0.023	-0.058	-0.104	-0.155	0.035	-0.067
5 km focal scale								
COVER	-0.238	-0.245	-0.243	-0.246	-0.238	-0.238	-0.238	-0.239
RPDENS	-0.150	-0.137	-0.106	-0.055	-0.042	-0.146	-0.152	-0.114
RPSIZE	-0.170	-0.136	-0.162	-0.054	-0.225	-0.163	-0.356	-0.173
RDIV	0.181	0.113	0.072	0.169	0.161	0.177	0.302	0.168
REDGE*	-0.225	-0.185	-0.273	-0.220	-0.225	-0.249	-0.093	-0.211
RSHAPE*	0.007	-0.050	-0.019	-0.056	0.108	-0.001	0.150	0.035
RNEAR*	0.224	0.234	0.385	0.334	0.092	0.268	0.224	0.216
RPROX*	0.111	0.076	0.124	0.107	0.071	0.113	0.088	0.108

Table 3.18. Composite correlation matrix at each focal scale between abundance of *Dermanura gnoma* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	0.182	0.184	0.183	0.186	0.183	0.184	0.182	0.191
RPDENS	-0.135	-0.133	-0.125	-0.072	-0.126	-0.159	-0.152	-0.093
RPSIZE	0.082	0.067	0.080	-0.102	0.067	0.046	0.108	0.479
RDIV	-0.183	-0.142	-0.190	-0.180	-0.207	-0.152	-0.186	-0.408
REDGE*	-0.051	0.026	-0.021	0.114	-0.049	-0.010	-0.051	-0.176
RSHAPE*	-0.110	-0.140	-0.086	-0.046	-0.097	-0.108	-0.114	-0.220
RNEAR*	-0.010	-0.074	0.072	0.048	-0.016	0.037	-0.010	-0.200
RPROX*	0.302	0.282	0.541	0.463	0.338	0.349	0.353	0.297
3 km focal scale								
COVER	-0.180	-0.180	-0.189	-0.188	-0.184	-0.182	-0.181	-0.214
RPDENS	0.074	0.073	0.101	0.038	0.232	-0.014	0.011	0.181
RPSIZE	0.315	0.317	0.310	0.137	0.270	0.314	0.289	0.068
RDIV	-0.297	-0.286	-0.082	-0.292	-0.254	-0.298	-0.269	-0.290
REDGE*	-0.208	-0.297	-0.131	-0.142	-0.204	-0.223	-0.280	-0.190
RSHAPE*	-0.151	-0.131	-0.156	-0.161	-0.173	-0.149	-0.121	0.074
RNEAR*	-0.125	-0.101	-0.036	-0.038	-0.230	-0.089	-0.123	-0.009
RPROX*	**0.556**	**0.565**	0.478	0.546	0.544	0.537	0.538	**0.547**
5 km focal scale								
COVER	-0.184	-0.182	-0.188	-0.182	-0.191	-0.184	-0.185	-0.198
RPDENS	0.093	0.098	0.041	-0.011	0.037	0.104	0.098	0.210
RPSIZE	0.276	0.260	0.274	0.194	0.320	0.276	0.334	0.261
RDIV	-0.196	-0.173	0.013	-0.198	-0.192	-0.207	-0.221	-0.216
REDGE*	0.155	0.116	0.224	0.140	0.147	0.163	0.209	0.228
RSHAPE*	0.006	0.034	0.030	0.064	-0.071	-0.001	-0.004	0.125
RNEAR*	-0.010	-0.010	-0.198	-0.102	0.150	-0.006	-0.005	-0.042
RPROX*	0.360	0.394	0.344	0.363	0.389	0.372	0.355	0.353

Table 3.19. Composite correlation matrix at each focal scale between abundance of *Mesophylla macconelli* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	0.346	0.422	0.348	0.363	0.385	0.356	0.348	0.349
RPDENS	**-0.610**	**-0.571**	**-0.566**	-0.519	-0.445	**-0.652**	**-0.582**	**-0.562**
RPSIZE	0.117	0.057	-0.110	-0.219	-0.064	0.029	0.286	0.326
RDIV	-0.323	-0.119	-0.353	-0.303	0.010	-0.238	-0.356	-0.441
REDGE*	-0.464	-0.185	-0.427	-0.328	-0.435	-0.384	-0.427	-0.525
RSHAPE*	-0.253	-0.442	-0.214	-0.142	-0.090	-0.237	-0.311	-0.297
RNEAR*	0.122	-0.176	0.287	0.226	0.064	0.235	0.114	0.050
RPROX*	0.146	0.063	0.335	0.360	0.351	0.228	0.093	0.138
3 km focal scale								
COVER	0.447	0.492	0.448	0.451	0.462	0.449	0.447	0.448
RPDENS	-0.468	-0.419	-0.427	-0.409	-0.343	-0.445	-0.463	-0.414
RPSIZE	-0.085	-0.118	-0.076	0.050	-0.158	-0.076	-0.066	-0.127
RDIV	0.152	0.092	0.123	0.136	0.214	0.138	0.128	0.143
REDGE*	-0.288	-0.031	-0.291	-0.304	-0.258	-0.251	-0.263	-0.253
RSHAPE*	0.107	-0.191	0.096	0.099	0.074	0.096	0.087	0.134
RNEAR*	0.050	-0.221	0.024	0.004	-0.067	0.021	0.045	0.062
RPROX*	0.084	0.018	0.126	0.088	0.055	0.120	0.086	0.075
5 km focal scale								
COVER	0.442	0.452	0.442	0.442	0.478	0.468	0.454	0.444
RPDENS	-0.309	-0.292	-0.284	-0.268	-0.172	-0.420	-0.306	-0.279
RPSIZE	-0.075	-0.010	-0.074	0.034	-0.162	-0.107	-0.211	-0.082
RDIV	0.127	-0.039	0.109	0.127	0.117	0.226	0.229	0.127
REDGE*	-0.383	-0.234	-0.358	-0.327	-0.331	-0.249	-0.299	-0.321
RSHAPE*	-0.314	-0.404	-0.276	-0.322	-0.147	-0.266	-0.206	-0.251
RNEAR*	0.211	0.200	0.263	0.258	-0.098	0.038	0.176	0.169
RPROX*	0.103	0.019	0.100	0.092	0.037	0.010	0.077	0.093

Table 3.20. Composite correlation matrix at each focal scale between abundance of *Sturnira lilium* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape characteristics	Controlled (partialled) characteristics							
	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	**-0.722**	**-0.746**	**-0.725**	**-0.729**	**-0.734**	**-0.722**	**-0.722**	**-0.770**
RPDENS	-0.368	-0.256	-0.268	-0.336	-0.425	-0.270	-0.272	-0.219
RPSIZE	-0.128	-0.122	-0.088	0.039	-0.023	-0.110	-0.103	0.279
RDIV	0.206	0.264	0.118	0.142	0.020	0.169	0.141	-0.047
REDGE*	0.262	0.390	0.159	0.114	0.180	0.210	0.185	0.062
RSHAPE*	-0.057	-0.098	-0.076	-0.100	-0.117	-0.040	-0.054	-0.165
RNEAR*	0.034	-0.097	0.059	-0.019	0.048	0.044	0.025	-0.194
RPROX*	0.505	0.325	0.429	0.325	0.309	0.380	0.393	0.349
3 km focal scale								
COVER	**-0.752**	**-0.792**	**-0.754**	**-0.752**	**-0.753**	**-0.752**	**-0.753**	**-0.786**
RPDENS	-0.480	-0.316	-0.312	-0.315	-0.341	-0.383	-0.334	-0.291
RPSIZE	0.116	0.056	0.076	0.167	0.062	0.076	0.098	-0.074
RDIV	0.052	-0.006	0.153	0.034	0.052	0.034	0.017	0.064
REDGE*	-0.095	0.147	-0.043	-0.073	-0.062	-0.063	-0.042	-0.040
RSHAPE*	0.004	-0.227	0.003	0.003	-0.004	0.003	-0.014	0.127
RNEAR*	0.092	-0.127	0.086	0.052	0.038	0.062	0.060	0.131
RPROX*	0.441	0.263	0.291	0.296	0.288	0.316	0.312	0.291
5 km focal scale								
COVER	**-0.722**	**-0.770**	**-0.723**	**-0.723**	**-0.739**	**-0.726**	**-0.723**	**-0.798**
RPDENS	-0.477	-0.305	-0.327	-0.352	-0.223	-0.382	-0.312	-0.223
RPSIZE	0.077	0.140	0.063	0.114	0.006	0.048	0.012	0.030
RDIV	0.054	-0.186	0.097	0.016	0.004	0.066	0.069	0.012
REDGE*	-0.333	-0.135	-0.244	-0.251	-0.251	-0.209	-0.266	-0.198
RSHAPE*	-0.185	-0.284	-0.147	-0.165	-0.052	-0.152	-0.120	-0.021
RNEAR*	0.108	0.116	0.072	0.113	-0.130	0.014	0.095	0.059
RPROX*	**0.614**	0.375	0.421	0.424	0.398	0.401	0.418	0.424

Table 3.21. Composite correlation matrix at each focal scale between abundance of *Sturnira magna* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape characteristics	Controlled (partialled) characteristics							
	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	-0.404	-0.405	-0.458	-0.420	-0.404	-0.436	-0.435	-0.448
RPDENS	-0.073	-0.067	-0.017	0.040	-0.091	-0.159	-0.268	-0.149
RPSIZE	0.515	0.467	0.471	0.425	0.515	0.390	0.317	0.242
RDIV	-0.304	-0.274	0.170	-0.278	-0.414	-0.163	-0.189	-0.070
REDGE*	0.021	0.064	0.239	0.320	0.018	0.184	-0.031	0.209
RSHAPE*	-0.410	-0.398	-0.254	-0.305	-0.412	-0.375	-0.267	-0.281
RNEAR*	-0.404	-0.441	-0.041	-0.311	-0.369	-0.257	-0.369	-0.186
RPROX*	-0.475	-0.452	-0.141	-0.354	-0.474	-0.362	-0.307	-0.435
3 km focal scale								
COVER	-0.245	-0.246	-0.285	-0.296	-0.245	-0.246	-0.256	-0.245
RPDENS	-0.086	-0.083	-0.054	-0.187	-0.152	-0.027	-0.288	-0.082
RPSIZE	0.526	0.507	0.510	0.134	**0.553**	0.513	0.464	**0.569**
RDIV	**-0.580**	**-0.579**	-0.303	**-0.562**	**-0.601**	**-0.563**	-0.529	**-0.563**
REDGE*	0.077	0.148	0.259	0.269	0.075	0.086	-0.050	0.077
RSHAPE*	0.111	0.074	0.126	0.119	0.116	0.108	0.200	0.124
RNEAR*	-0.304	-0.396	-0.178	-0.158	-0.290	-0.336	-0.294	-0.297
RPROX*	0.020	0.008	-0.295	-0.040	0.026	0.065	-0.047	0.019
5 km focal scale								
COVER	-0.278	-0.277	-0.315	-0.314	-0.277	-0.277	-0.277	-0.278
RPDENS	0.017	0.026	-0.102	-0.390	0.053	0.016	0.019	0.021
RPSIZE	0.529	0.519	0.512	0.176	0.515	0.511	0.523	0.516
RDIV	**-0.567**	**-0.641**	-0.296	**-0.552**	**-0.556**	**-0.569**	-0.548	**-0.552**
REDGE*	-0.042	-0.067	0.082	-0.092	-0.048	-0.038	0.087	-0.053
RSHAPE*	-0.025	-0.026	0.026	0.169	-0.014	-0.033	0.058	-0.042
RNEAR*	0.146	0.147	-0.194	-0.120	0.165	0.156	0.148	0.151
RPROX*	-0.023	-0.016	-0.078	-0.019	-0.031	-0.035	-0.038	-0.022

Table 3.22. Composite correlation matrix at each focal scale between abundance of *Sturnira tildae* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	**-0.594**	**-0.596**	**-0.596**	**-0.601**	**-0.619**	**-0.594**	**-0.597**	**-0.596**
RPDENS	0.120	0.096	0.086	0.042	0.070	0.098	0.161	0.083
RPSIZE	-0.122	-0.089	-0.098	0.037	0.009	-0.105	-0.022	-0.258
RDIV	0.191	0.128	0.124	0.154	-0.071	0.165	0.126	0.238
REDGE*	0.353	0.276	0.267	0.250	0.283	0.305	0.302	0.342
RSHAPE*	0.003	0.020	-0.037	-0.062	-0.119	0.000	-0.050	0.031
RNEAR*	0.141	0.173	0.063	0.072	0.158	0.125	0.115	0.192
RPROX*	-0.118	-0.082	-0.257	-0.206	-0.221	-0.100	-0.182	-0.095
3 km focal scale								
COVER	**-0.624**	**-0.624**	**-0.627**	**-0.648**	**-0.628**	**-0.629**	**-0.634**	**-0.652**
RPDENS	-0.002	-0.002	0.006	-0.037	-0.077	0.091	0.108	-0.045
RPSIZE	0.133	0.104	0.104	-0.184	0.140	0.105	0.166	0.289
RDIV	-0.348	-0.274	-0.309	-0.272	-0.311	-0.272	-0.348	-0.314
REDGE*	0.140	0.134	0.145	0.191	0.110	0.125	0.203	0.090
RSHAPE*	0.170	0.161	0.134	0.134	0.146	0.133	0.091	0.026
RNEAR*	0.230	0.209	0.221	0.286	0.246	0.152	0.180	0.126
RPROX*	-0.375	-0.296	-0.391	-0.331	-0.286	-0.264	-0.264	-0.292
5 km focal scale								
COVER	**-0.658**	**-0.664**	**-0.660**	**-0.663**	**-0.661**	**-0.703**	**-0.659**	**-0.684**
RPDENS	-0.149	-0.089	-0.117	-0.221	-0.133	0.016	-0.088	-0.174
RPSIZE	0.134	0.133	0.110	-0.031	0.128	0.151	0.155	0.140
RDIV	-0.204	-0.264	-0.137	-0.173	-0.170	-0.294	-0.207	-0.176
REDGE*	0.112	0.118	0.093	0.057	0.065	-0.078	0.060	0.017
RSHAPE*	0.441	0.298	0.325	0.385	0.312	0.309	0.348	0.243
RNEAR*	-0.069	-0.029	-0.115	-0.121	0.021	0.172	-0.033	-0.006
RPROX*	-0.364	-0.311	-0.288	-0.278	-0.269	-0.197	-0.274	-0.276

Table 3.23. Composite correlation matrix at each focal scale between abundance of *Uroderma bilobatum* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	-0.486	-0.486	-0.488	-0.488	-0.486	-0.494	-0.488	-0.489
RPDENS	0.042	0.036	0.026	-0.003	0.047	-0.001	0.085	0.055
RPSIZE	-0.102	-0.086	-0.089	-0.106	-0.099	0.167	-0.031	0.002
RDIV	0.121	0.099	0.057	0.105	0.156	0.189	0.081	0.050
REDGE*	-0.006	-0.030	-0.043	-0.116	-0.006	0.068	0.006	-0.054
RSHAPE*	-0.208	-0.179	-0.229	-0.239	-0.194	-0.182	-0.241	-0.233
RNEAR*	0.106	0.121	0.042	0.065	0.094	0.185	0.094	0.036
RPROX*	0.139	0.128	0.082	0.079	0.132	0.190	0.085	0.121
3 km focal scale								
COVER	**-0.600**	**-0.609**	**-0.608**	**-0.601**	**-0.609**	**-0.606**	**-0.603**	**-0.636**
RPDENS	-0.210	-0.168	-0.158	-0.176	-0.092	-0.299	-0.256	-0.130
RPSIZE	0.202	0.152	0.161	0.193	0.123	0.163	0.140	0.006
RDIV	-0.067	-0.076	0.120	-0.054	-0.013	-0.056	-0.026	-0.025
REDGE*	-0.207	-0.087	-0.128	-0.157	-0.165	-0.181	-0.224	-0.146
RSHAPE*	-0.168	-0.283	-0.136	-0.136	-0.154	-0.135	-0.114	-0.012
RNEAR*	-0.121	-0.218	-0.053	-0.085	-0.181	-0.065	-0.097	-0.029
RPROX*	0.412	0.314	0.291	0.327	0.321	0.304	0.318	0.330
5 km focal scale								
COVER	-0.511	-0.522	-0.511	-0.520	-0.514	-0.510	-0.515	-0.536
RPDENS	-0.195	-0.150	-0.166	-0.092	-0.078	-0.187	-0.146	-0.078
RPSIZE	0.055	0.090	0.055	0.238	0.014	0.047	0.117	0.030
RDIV	0.175	0.065	0.267	0.135	0.128	0.167	0.114	0.138
REDGE*	-0.193	-0.129	-0.173	-0.176	-0.181	-0.164	-0.343	-0.136
RSHAPE*	-0.069	-0.136	-0.071	-0.125	0.001	-0.077	-0.142	0.021
RNEAR*	-0.105	-0.069	-0.129	-0.020	-0.305	-0.141	-0.076	-0.111
RPROX*	0.352	0.275	0.298	0.302	0.278	0.293	0.311	0.301

Table 3.24. Composite correlation matrix at each focal scale between abundance of *Vampyressa bidens* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	0.236	0.271	0.248	0.239	0.245	0.239	0.237	0.246
RPDENS	-0.500	-0.485	-0.477	-0.472	-0.424	-0.470	**-0.581**	-0.553
RPSIZE	0.310	0.285	0.302	0.319	0.227	0.381	0.349	0.155
RDIV	-0.140	0.054	0.173	-0.136	0.073	-0.207	-0.115	0.004
REDGE*	-0.269	-0.001	-0.167	-0.236	-0.261	-0.345	-0.276	-0.182
RSHAPE*	0.151	0.055	0.283	0.214	0.273	0.147	0.200	0.251
RNEAR*	-0.091	-0.375	0.203	-0.050	-0.127	-0.163	-0.089	0.062
RPROX*	-0.279	-0.398	-0.070	-0.236	-0.196	-0.336	-0.264	-0.270
3 km focal scale								
COVER	0.488	0.523	0.499	0.489	0.502	0.494	0.496	0.511
RPDENS	-0.411	-0.359	-0.352	-0.370	-0.281	-0.332	-0.535	-0.336
RPSIZE	0.242	0.198	0.211	0.266	0.157	0.214	0.169	0.087
RDIV	-0.068	-0.113	0.176	-0.060	-0.001	-0.058	-0.006	-0.034
REDGE*	-0.270	-0.045	-0.190	-0.229	-0.236	-0.225	-0.342	-0.222
RSHAPE*	0.179	-0.062	0.160	0.156	0.138	0.156	0.214	0.300
RNEAR*	-0.204	-0.455	-0.124	-0.168	-0.307	-0.229	-0.178	-0.124
RPROX*	0.333	0.260	0.221	0.287	0.279	0.382	0.263	0.290
5 km focal scale								
COVER	**0.643**	**0.649**	**0.649**	**0.643**	**0.644**	**0.643**	**0.650**	**0.697**
RPDENS	-0.225	-0.195	-0.226	-0.228	-0.203	-0.177	-0.189	-0.105
RPSIZE	0.158	0.161	0.112	0.175	0.108	0.122	0.268	0.085
RDIV	-0.018	-0.122	0.136	0.005	0.004	-0.021	-0.086	0.008
REDGE*	-0.062	0.066	-0.004	-0.029	-0.029	-0.072	-0.246	0.044
RSHAPE*	0.081	0.020	0.097	0.087	0.107	0.084	-0.024	0.237
RNEAR*	-0.224	-0.184	-0.306	-0.208	-0.306	-0.173	-0.190	-0.249
RPROX*	0.506	0.357	0.383	0.389	0.390	0.440	0.417	0.389

Table 3.25. Composite correlation matrix at each focal scale between abundance of *Vampyressa thyone* and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between abundance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	0.245	0.361	0.246	0.246	0.258	0.245	0.267	0.249
RPDENS	**-0.754**	**-0.730**	**-0.742**	**-0.762**	**-0.707**	**-0.750**	**-0.677**	**-0.723**
RPSIZE	-0.058	-0.202	-0.056	-0.175	-0.191	-0.067	0.368	0.120
RDIV	-0.068	0.324	-0.178	-0.065	0.222	-0.063	-0.209	-0.187
REDGE*	-0.311	0.159	-0.348	-0.362	-0.301	-0.317	-0.276	-0.398
RSHAPE*	-0.019	-0.251	-0.040	0.007	0.107	-0.018	-0.208	-0.078
RNEAR*	0.405	0.129	0.515	0.433	0.374	0.436	0.392	0.355
RPROX*	0.185	0.102	0.208	0.249	0.324	0.194	-0.030	0.179
3 km focal scale								
COVER	0.114	0.149	0.114	0.114	0.126	0.120	0.127	0.116
RPDENS	**-0.655**	**-0.651**	**-0.648**	**-0.672**	-0.545	**-0.595**	-0.549	**-0.642**
RPSIZE	0.116	0.089	0.115	0.055	-0.005	0.123	0.285	0.032
RDIV	-0.104	-0.246	-0.021	-0.104	0.006	-0.104	-0.279	-0.089
REDGE*	-0.439	-0.113	-0.424	-0.426	-0.436	-0.430	-0.314	-0.429
RSHAPE*	0.334	-0.061	0.334	0.332	0.323	0.332	0.249	0.440
RNEAR*	0.447	0.166	0.503	0.502	0.326	0.393	0.444	0.504
RPROX*	0.186	0.124	0.149	0.177	0.165	0.354	0.319	0.185
5 km focal scale								
COVER	0.199	0.234	0.200	0.198	0.215	0.196	0.203	0.203
RPDENS	**-0.662**	**-0.655**	**-0.685**	**-0.732**	**-0.621**	**-0.641**	**-0.663**	**-0.636**
RPSIZE	0.059	0.269	0.055	0.172	-0.006	0.077	0.009	0.039
RDIV	0.072	-0.438	0.179	0.077	0.066	0.023	0.127	0.076
REDGE*	-0.278	0.038	-0.261	-0.264	-0.267	-0.387	-0.298	-0.239
RSHAPE*	0.178	-0.054	0.188	0.166	0.338	0.181	0.274	0.265
RNEAR*	0.093	0.157	0.066	0.132	-0.162	0.225	0.086	0.067
RPROX*	0.210	0.050	0.203	0.206	0.168	0.283	0.200	2.060

Table 3.26. Composite correlation matrix at each focal scale between species richness and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between richness and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	-0.387	-0.393	-0.394	-0.389	-0.392	-0.392	-0.388	-0.393
RPDENS	-0.197	-0.182	-0.165	-0.232	-0.321	-0.156	-0.231	-0.213
RPSIZE	0.208	0.175	0.191	0.424	0.275	0.265	0.215	0.099
RDIV	0.095	0.169	0.394	0.087	-0.037	0.034	0.111	0.207
REDGE*	0.173	0.310	0.254	0.138	0.159	0.111	0.153	0.239
RSHAPE*	0.165	0.119	0.238	0.129	0.101	0.152	0.193	0.218
RNEAR*	-0.068	-0.157	0.117	-0.093	-0.043	-0.136	-0.062	0.030
RPROX*	-0.183	-0.202	-0.040	-0.251	-0.246	-0.230	-0.161	-0.169
3 km focal scale								
COVER	-0.243	-0.267	-0.245	-0.243	-0.245	-0.257	-0.247	-0.246
RPDENS	-0.427	-0.414	-0.409	-0.410	**-0.602**	-0.296	-0.385	-0.402
RPSIZE	0.130	0.106	0.126	0.293	0.173	0.134	0.188	0.064
RDIV	0.071	0.019	0.275	0.069	0.036	0.079	0.018	0.084
REDGE*	0.145	0.495	0.183	0.127	0.140	0.183	0.233	0.155
RSHAPE*	0.334	0.118	0.327	0.326	0.342	0.324	0.293	0.415
RNEAR*	0.179	-0.052	0.222	0.161	0.254	0.098	0.174	0.213
RPROX*	0.154	0.102	0.103	0.157	0.164	0.310	0.194	0.150
5 km focal scale								
COVER	-0.277	-0.292	-0.277	-0.283	-0.295	-0.320	-0.293	-0.282
RPDENS	-0.241	-0.222	-0.233	-0.188	-0.393	-0.097	-0.216	-0.186
RPSIZE	0.023	0.079	0.026	0.176	0.092	0.078	0.201	0.012
RDIV	0.132	-0.001	0.210	0.119	0.138	-0.007	0.017	0.119
REDGE*	0.283	0.416	0.277	0.272	0.264	0.107	0.132	0.303
RSHAPE*	0.440	0.368	0.418	0.398	0.344	0.413	0.345	0.500
RNEAR*	-0.260	-0.237	-0.310	-0.213	-0.077	-0.021	-0.242	-0.264
RPROX*	0.179	0.121	0.170	0.171	0.230	0.350	0.202	0.171

Table 3.27. Composite correlation matrix at each focal scale between species diversity and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between diversity and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape characteristics	Controlled (partialled) characteristics							
	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	0.099	0.989	0.100	0.100	0.099	0.104	0.104	0.099
RPDENS	0.015	0.015	-0.002	-0.043	0.027	-0.049	0.160	0.012
RPSIZE	-0.147	-0.145	-0.146	-0.049	-0.164	-0.279	0.100	-0.242
RDIV	0.148	0.153	0.053	0.147	0.224	0.289	0.066	0.183
REDGE*	-0.015	-0.027	-0.076	-0.172	-0.015	0.108	0.023	-0.009
RSHAPE*	-0.297	-0.299	-0.375	-0.381	-0.313	-0.296	-0.469	-0.305
RNEAR*	0.290	0.326	0.270	0.259	0.289	0.465	0.289	0.349
RPROX*	-0.019	-0.017	-0.196	-0.112	-0.015	0.079	-0.206	-0.019
3 km focal scale								
COVER	-0.069	-0.069	-0.069	-0.069	-0.070	-0.070	-0.071	-0.069
RPDENS	-0.132	-0.132	-0.134	-0.146	-0.331	-0.023	-0.310	-0.132
RPSIZE	-0.022	-0.032	-0.022	-0.164	0.047	-0.022	-0.100	-0.031
RDIV	-0.101	-0.119	-0.191	-0.101	-0.171	-0.099	-0.029	-0.100
REDGE*	0.239	0.381	0.242	0.274	0.239	0.265	0.159	0.241
RSHAPE*	0.200	0.153	0.200	0.199	0.231	0.200	0.281	0.220
RNEAR*	-0.244	-0.367	-0.261	-0.224	-0.165	-0.312	-0.243	-0.246
RPROX*	0.011	-0.008	0.024	0.001	0.032	0.095	-0.043	0.011
5 km focal scale								
COVER	0.006	0.000	0.005	0.005	-0.002	0.006	-0.004	0.006
RPDENS	-0.185	-0.185	-0.166	-0.206	-0.359	-0.196	-0.179	-0.187
RPSIZE	-0.113	-0.075	-0.113	-0.145	-0.053	-0.113	0.102	-0.115
RDIV	0.023	-0.094	-0.094	0.023	0.039	0.023	-0.148	0.023
REDGE*	0.276	0.408	0.259	0.278	0.276	0.304	0.042	0.284
RSHAPE*	0.002	-0.064	-0.010	-0.005	-0.133	0.003	-0.237	0.009
RNEAR*	-0.340	-0.340	-0.340	-0.370	-0.217	-0.409	-0.343	-0.347
RPROX*	0.019	-0.031	0.029	0.019	0.072	0.021	0.056	0.019

Table 3.28. Composite correlation matrix at each focal sclae between species evenness and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between evenness and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	0.134	0.134	0.134	0.134	0.134	0.134	0.141	0.134
RPDENS	-0.002	-0.002	-0.010	0.010	-0.024	0.007	0.151	-0.008
RPSIZE	-0.077	-0.077	-0.077	-0.162	-0.069	-0.067	0.228	-0.160
RDIV	-0.030	-0.031	-0.146	-0.029	-0.077	-0.048	-0.135	-0.011
REDGE*	0.034	0.042	0.006	0.078	0.034	0.021	0.077	0.052
RSHAPE*	0.041	0.041	0.015	0.056	0.030	0.041	-0.095	0.055
RNEAR*	0.310	0.339	0.369	0.332	0.314	0.318	0.307	0.382
RPROX*	-0.039	-0.039	-0.146	-0.027	-0.055	-0.054	-0.242	-0.039
3 km focal scale								
COVER	0.129	0.131	0.131	0.130	0.147	0.140	0.151	0.132
RPDENS	0.132	0.131	0.121	0.119	-0.178	0.457	-0.185	0.106
RPSIZE	-0.171	-0.162	-0.169	-0.411	-0.050	-0.183	-0.390	-0.088
RDIV	-0.107	-0.091	-0.392	-0.106	-0.260	-0.107	0.062	-0.127
REDGE*	0.470	0.478	0.442	0.511	0.466	0.547	0.329	0.460
RSHAPE*	0.384	**0.559**	0.386	0.381	0.484	0.381	**0.624**	0.338
RNEAR*	-0.520	-0.528	**-0.599**	-0.510	-0.405	**-0.689**	-0.516	**-0.582**
RPROX*	-0.199	-0.183	-0.135	-0.210	-0.179	-0.063	-0.367	-0.198
5 km focal scale								
COVER	0.129	0.150	0.129	0.136	0.127	0.144	0.130	0.131
RPDENS	0.343	0.336	0.349	0.296	0.215	0.270	0.401	0.399
RPSIZE	-0.017	-0.100	-0.019	-0.223	0.067	-0.050	0.313	-0.034
RDIV	-0.173	0.018	-0.276	-0.168	-0.160	-0.093	-0.448	-0.173
REDGE*	0.349	0.237	0.355	0.347	0.350	0.535	0.040	0.391
RSHAPE*	-0.279	-0.180	-0.276	-0.236	-0.497	-0.272	**-0.693**	-0.234
RNEAR*	-0.449	-0.494	-0.528	**-0.586**	-0.302	**-0.743**	-0.448	-0.474
RPROX*	0.169	0.281	0.170	0.173	0.249	0.090	0.239	0.168

Table 3.29. Composite correlation matrix at each focal scale between species dominance and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between dominance and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape	Controlled (partialled) characteristics							
characteristics	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019
RPDENS	0.019	0.019	0.002	-0.044	-0.167	0.074	0.123	0.033
RPSIZE	-0.149	-0.148	-0.149	-0.038	-0.046	-0.067	0.009	-0.118
RDIV	0.159	0.164	0.069	0.159	-0.065	0.075	0.103	0.130
REDGE*	0.286	0.327	0.251	0.248	0.286	0.214	0.322	0.271
RSHAPE*	0.250	0.259	0.214	0.208	0.161	0.250	0.185	0.233
RNEAR*	0.211	0.242	0.152	0.173	0.260	0.125	0.211	0.190
RPROX*	0.095	0.099	-0.026	0.014	-0.010	0.019	-0.018	0.095
3 km focal scale								
COVER	0.056	0.057	0.058	0.056	0.070	0.058	0.065	0.056
RPDENS	0.221	0.221	0.209	0.232	-0.174	0.479	-0.063	0.203
RPSIZE	-0.273	-0.264	-0.273	-0.354	-0.142	-0.284	-0.517	-0.227
RDIV	0.069	0.100	-0.244	0.069	-0.104	0.077	0.280	0.055
REDGE*	**0.600**	**0.589**	**0.567**	**0.602**	**0.599**	**0.655**	0.499	**0.595**
RSHAPE*	0.278	0.503	0.288	0.280	0.422	0.278	0.500	0.238
RNEAR*	-0.518	-0.483	**-0.648**	**-0.566**	-0.376	**-0.636**	-0.517	**-0.571**
RPROX*	-0.160	-0.134	-0.036	-0.155	-0.137	-0.062	-0.323	-0.160
5 km focal scale								
COVER	0.090	0.103	0.090	0.089	0.105	0.085	0.101	0.090
RPDENS	0.268	0.264	0.353	0.323	-0.133	0.344	0.437	0.254
RPSIZE	-0.298	-0.377	-0.298	-0.434	-0.197	-0.285	0.190	-0.293
RDIV	0.012	0.194	-0.332	0.014	0.083	-0.039	-0.482	0.015
REDGE*	**0.765**	**0.748**	**0.749**	**0.766**	**0.764**	**0.777**	0.501	**0.765**
RSHAPE*	0.164	0.280	0.142	0.170	-0.273	0.166	-0.403	0.152
RNEAR*	**-0.726**	**-0.767**	**-0.707**	**-0.798**	-0.387	**-0.770**	**-0.726**	**-0.724**
RPROX*	-0.072	-0.004	-0.048	-0.072	0.100	-0.021	0.000	-0.072

Table 3.30. Composite correlation matrix at each focal scale between the number of rare species and each of a suite of landscape characteristics. Simple correlations are on the diagonal. Partial correlations (elements in columns other than the diagonal) between the number of rare species and a landscape characteristic control for the effect of the landscape characteristic in the column heading. Significance ($p \leq 0.05$) of a correlation is indicated in bold. Landscape configuration characteristics are indicated with an asterisk.

Landscape characteristics	Controlled (partialled) characteristics							
	COVER	RPDENS	RPSIZE	RDIV	REDGE*	RSHAPE*	RNEAR*	RPROX*
1 km focal scale								
COVER	-0.233	-0.234	-0.245	-0.233	-0.236	-0.234	-0.237	-0.245
RPDENS	-0.108	-0.106	-0.076	-0.128	-0.227	-0.090	-0.197	-0.161
RPSIZE	0.312	0.295	0.303	0.537	0.395	0.357	0.273	0.117
RDIV	0.036	0.081	0.467	0.035	-0.108	0.004	0.090	0.237
REDGE*	0.161	0.253	0.305	0.185	0.155	0.134	0.138	0.299
RSHAPE*	0.088	0.066	0.215	0.078	0.030	0.086	0.167	0.199
RNEAR*	-0.168	-0.232	0.090	-0.183	-0.147	-0.216	-0.163	-0.006
RPROX*	-0.314	-0.327	-0.124	-0.378	-0.392	-0.350	-0.262	-0.305
3 km focal scale								
COVER	-0.123	-0.131	-0.127	-0.123	-0.124	-0.129	-0.123	-0.125
RPDENS	-0.343	-0.341	-0.334	-0.352	-0.533	-0.207	-0.343	-0.323
RPSIZE	0.267	0.256	0.265	0.354	0.328	0.280	0.307	0.201
RDIV	-0.060	-0.110	0.250	-0.060	-0.107	-0.057	-0.093	-0.043
REDGE*	0.170	0.462	0.260	0.190	0.168	0.211	0.226	0.189
RSHAPE*	0.318	0.158	0.328	0.315	0.339	0.316	0.303	0.428
RNEAR*	0.094	-0.103	0.185	0.117	0.178	0.012	0.093	0.140
RPROX*	0.195	0.156	0.079	0.189	0.211	0.355	0.219	0.193
5 km focal scale								
COVER	-0.056	-0.068	-0.055	-0.055	-0.058	-0.061	-0.055	-0.060
RPDENS	-0.264	-0.262	-0.314	-0.360	-0.323	-0.238	-0.264	-0.195
RPSIZE	0.182	0.254	0.182	0.193	0.202	0.197	0.193	0.164
RDIV	-0.072	-0.266	0.097	-0.074	-0.071	-0.115	-0.063	-0.082
REDGE*	0.063	0.206	0.107	0.058	0.061	0.013	0.130	0.127
RSHAPE*	0.119	0.032	0.139	0.146	0.100	0.117	0.165	0.243
RNEAR*	0.038	0.055	-0.077	0.009	0.122	0.125	0.040	0.008
RPROX*	0.323	0.273	0.313	0.324	0.339	0.381	0.320	0.322

Table 3.31. Results from multiple regression and correlation analysis of population-level (species abundances; double square root transformed) and assemblage-level (richness, diversity, evenness, dominance, and number of rare species) characteristics as a function of a suite of landscape characteristics for focal scales of 1, 3 and 5 km radius, seperately. Coefficients of multiple determination (model R2) are adjusted for the number of variables selected in each model. The individual contribution of the variables to the model is listed as ΔR2. Significant regression models or parametrs and correlation coefficients ($p \leq 0.05$) are indicated in bold. Symbols in the sign column refer to the sign of the regression parameter estimates (Gorresen and Willig 2004).

	1 Km focal scale					3 Km focal scale					5 Km focal scale				
	Multiple regression			Correlation		Multiple regression			Correlation		Multiple regression			Correlation	
	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p
Carollia benkeithi															
COVER				-0.040	0.893				-0.166	0.570				-0.029	0.921
RPDENSE				0.038	0.897				-0.062	0.834				-0.251	0.387
RPSIZE	**64**	**0.01**	**-**	**-0.800**	**0.001**	**47**	**0.007**	**-**	**-0.681**	**0.007**	**56**	**0.002**	**-**	**-0.751**	**0.002**
RDIV				0.722	0.004				0.531	0.051				0.525	0.054
REDGE				0.173	0.554				0.133	0.651				0.224	0.441
RSHAPE				0.280	0.332				-0.088	0.765				-0.065	0.825
RNEAR				**0.652**	**0.011**				0.064	0.827				**-0.533**	**0.050**
RPROX				0.458	0.100				-0.100	0.733				0.247	0.394
Model R^2	**61**	**0.01**				**42**	**0.007**				**53**	**0.002**			
Carollia brevicauda															
COVER				-0.526	0.054				-0.527	0.053	**30**	**0.043**	**-**	**-0.548**	**0.042**
RPDENSE				0.164	0.576				0.070	0.812				0.092	0.756
RPSIZE				0.193	0.498				0.297	0.303				0.321	0.263
RDIV				0.116	0.701				-0.249	0.390				-0.432	0.123
REDGE				0.386	0.175				0.283	0.327				0.102	0.729
RSHAPE				-0.098	0.730				-0.088	0.764				-0.217	0.457
RNEAR				-0.372	0.185				-0.251	0.387				0.118	0.687
RPROX				-0.072	0.803				0.302	0.294				0.405	0.150
Model R^2											**26**	**0.043**			
Carollia perspicillata															
COVER	**29**	**0.049**	**-**	**-0.534**	**0.049**				-0.435	0.120				-0.400	0.157
RPDENSE				-0.104	0.724				-0.442	0.114				-0.467	0.092
RPSIZE				0.158	0.590				0.251	0.388				0.215	0.460
RDIV				0.066	0.822				0.037	0.900				0.039	0.894
REDGE				-0.023	0.937				-0.300	0.297	**38**	**0.02**	**-**	**-0.614**	**0.019**
RSHAPE				-0.182	0.533				-0.073	0.804				-0.148	0.613
RNEAR				-0.228	0.432				0.374	0.188				0.503	0.067
RPROX				-0.118	0.688				0.204	0.484				0.349	0.222
Model R^2	**23**	**0.049**									**32**	**0.02**			
Rhinophylla fischerae															
COVER				-0.029	0.921				0.279	0.334				0.319	0.267
RPDENSE				-0.385	0.174				-0.488	0.076				-0.191	0.513
RPSIZE				0.186	0.524				-0.072	0.807				-0.148	0.613
RDIV				-0.238	0.413				0.086	0.769				0.071	0.808
REDGE				-0.342	0.231				-0.148	0.613				-0.297	0.302
RSHAPE				-0.001	0.997				0.189	0.518				-0.340	0.235
RNEAR				0.169	0.563				0.132	0.653				0.147	0.616
RPROX				-0.239	0.410				0.015	0.960				0.230	0.430
Model R^2															

Table 3.31. (Continued)

	1 Km focal scale					3 Km focal scale					5 Km focal scale				
	Multiple regression			Correlation		Multiple regression			Correlation		Multiple regression			Correlation	
	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p
Rhinophylla pumilio															
COVER				0.223	0.443				0.206	0.479				0.206	0.481
RPDENSE				-0.031	0.916				0.168	0.566				0.246	0.397
RPSIZE				-0.128	0.663				-0.110	0.708				-0.106	0.719
RDIV				-0.160	0.586				-0.135	0.645				-0.096	0.744
REDGE				-0.351	0.219				-0.119	0.685				-0.049	0.868
RSHAPE				-0.473	0.088				-0.343	0.230				-0.465	0.094
RNEAR				0.134	0.648	**34**	**0.03**	-	**-0.582**	**0.029**				-0.180	0.537
RPROX				0.119	0.684				0.036	0.903				-0.042	0.886
Model R^2						**28**	**0.03**								
Glossophaga soricina															
COVER	**54**	**0.003**	-	**-0.736**	**0.003**	**50**	**0.005**	-	**-0.705**	**0.005**	**36**	**0.024**	-	**-0.598**	**0.024**
RPDENSE				0.327	0.253				-0.058	0.844				-0.206	0.480
RPSIZE				-0.058	0.844				0.084	0.776				-0.012	0.969
RDIV				0.207	0.477				0.018	0.951				0.079	0.789
REDGE				0.012	0.967				-0.161	0.582				-0.276	0.339
RSHAPE				-0.125	0.669				-0.071	0.808				-0.083	0.777
RNEAR				-0.165	0.574				0.044	0.882				0.065	0.825
RPROX				-0.102	0.729				0.023	0.938				0.281	0.330
Model R^2	**50**	**0.003**				**46**	**0.005**				**30**	**0.024**			
Lonchophylla thomasi															
COVER				-0.086	0.769				-0.303	0.292				-0.214	0.463
RPDENSE				0.201	0.491				0.094	0.749				-0.132	0.652
RPSIZE				-0.138	0.639				0.004	0.990				-0.014	0.963
RDIV				0.451	0.106				0.342	0.232				0.336	0.240
REDGE	**28**	**0.048**	+	**0.536**	**0.048**				0.476	0.086				0.435	0.120
RSHAPE				0.236	0.416				0.172	0.558				0.413	0.142
RNEAR				-0.150	0.608				-0.201	0.490				-0.414	0.141
RPROX				0.328	0.253				0.286	0.322				0.176	0.548
Model R^2	**23**	**0.048**													
Lophostoma silvicolum															
COVER				0.033	0.911				0.096	0.744				0.155	0.596
RPDENSE				-0.192	0.510				-0.070	0.812				0.045	0.878
RPSIZE				0.296	0.305				0.222	0.446				0.107	0.717
RDIV				-0.382	0.178				-0.508	0.064				-0.410	0.146
REDGE				-0.359	0.207				-0.073	0.803				0.271	0.348
RSHAPE				-0.239	0.410				0.305	0.289				-0.022	0.942
RNEAR				0.031	0.917				-0.342	0.232				-0.248	0.393
RPROX				-0.347	0.224				-0.067	0.819				0.102	0.728
Model R^2															
Mimon crenulatum															
COVER				0.317	0.269				0.184	0.529				0.062	0.834
RPDENSE				**0.579**	**0.030**				**0.655**	**0.011**				**0.592**	**0.026**
RPSIZE				-0.056	0.850				-0.047	0.873				0.094	0.750
RDIV				0.394	0.163				0.049	0.869				-0.283	0.327
REDGE	**51**	**0.04**	+	**0.715**	**0.004**	**58**	**0.001**	+	**0.762**	**0.002**	**42**	**0.001**	+	**0.647**	**0.012**
RSHAPE				0.127	0.666				-0.394	0.164				-0.102	0.730
RNEAR				-0.327	0.253				-0.435	0.120	**24**	**0.018**	+	-0.130	0.658
RPROX				0.007	0.980				0.156	0.595				-0.003	0.991
Model R^2	**47**	**0.04**				**55**	**0.001**				**60**	**0.003**			

Table 3.31. (Continued)

	1 Km focal scale					3 Km focal scale					5 Km focal scale				
	Multiple regression			Correlation		Multiple regression			Correlation		Multiple regression			Correlation	
	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p
Phyllostomus elongatus															
COVER				-0.043	0.884				0.046	0.877				0.101	0.732
RPDENSE				0.098	0.740				-0.222	0.445				-0.302	0.293
RPSIZE				0.308	0.285				0.300	0.297				0.231	0.426
RDIV				0.052	0.860				-0.175	0.550				-0.177	0.546
REDGE				0.037	0.899				0.014	0.963				-0.028	0.925
RSHAPE				-0.021	0.943				0.257	0.376				0.212	0.466
RNEAR				-0.254	0.381				0.283	0.326				0.206	0.479
RPROX	**30**	**0.042**	**-**	**-0.549**	**0.042**				-0.057	0.847				0.112	0.703
Model R^2	**24**	**0.042**													
Phyllostomus hastatus															
COVER				-0.406	0.149				-0.294	0.308				-0.240	0.409
RPDENSE				0.159	0.587				-0.209	0.474				-0.148	0.614
RPSIZE				0.421	0.134				0.354	0.214				0.277	0.337
RDIV				-0.042	0.887				-0.009	0.975				-0.037	0.901
REDGE				0.161	0.582				0.248	0.393				-0.035	0.904
RSHAPE				-0.109	0.711				0.236	0.416				-0.011	0.970
RNEAR				-0.429	0.126				-0.110	0.707				0.120	0.683
RPROX				-0.317	0.269				0.262	0.366				0.303	0.292
Model R^2															
Tonatia saurophila															
COVER				0.453	0.104				0.388	0.171				0.231	0.426
RPDENSE				0.124	0.673				0.241	0.406				0.212	0.467
RPSIZE				-0.156	0.594				-0.240	0.408				-0.067	0.819
RDIV				0.239	0.411				0.108	0.714				-0.166	0.570
REDGE				0.439	0.116	**37**	**0.021**	+	**0.609**	**0.021**				0.364	0.201
RSHAPE				0.062	0.834				-0.038	0.898				-0.077	0.795
RNEAR				0.051	0.863				-0.036	0.903				0.026	0.931
RPROX				0.088	0.764				-0.193	0.508				-0.319	0.266
Model R^2						**31**	**0.021**								
Artibeus lituratus															
COVER	**29**	**0.044**	**-**	**-0.546**	**0.043**				-0.341	0.232				-0.334	0.244
RPDENSE				-0.195	0.505				-0.415	0.140				-0.245	0.398
RPSIZE				0.239	0.410				0.296	0.304				0.294	0.307
RDIV				-0.060	0.838				-0.223	0.443				-0.276	0.340
REDGE				0.002	0.996				-0.062	0.833				-0.461	0.097
RSHAPE				-0.265	0.360				0.015	0.959				-0.364	0.201
RNEAR				-0.158	0.590				0.019	0.949				0.369	0.194
RPROX				-0.232	0.426				0.192	0.510				0.287	0.319
Model R^2	**24**	**0.044**													
Artibeus obscurus															
COVER	**46**	**0.08**	**-**	**-0.675**	**0.008**	**30**	**0.042**	**-**	**-0.547**	**0.043**				-0.493	0.073
RPDENSE				-0.043	0.883				-0.255	0.379				-0.127	0.665
RPSIZE				0.074	0.801				0.040	0.891				-0.030	0.918
RDIV				0.039	0.895				-0.061	0.836				-0.084	0.775
REDGE				0.162	0.580				0.317	0.270				0.083	0.779
RSHAPE				-0.025	0.934				0.352	0.218				-0.144	0.624
RNEAR				0.049	0.867				-0.176	0.548				-0.157	0.592
RPROX				-0.066	0.822				0.034	0.909				0.241	0.406
Model R^2	**41**	**0.08**				**24**	**0.042**								

Table 3.31. (Continued)

	1 Km focal scale					3 Km focal scale					5 Km focal scale				
	Multiple regression			Correlation		Multiple regression			Correlation		Multiple regression			Correlation	
	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p
Artibeus planirostris															
COVER	**43**	**0.005**	-	**-0.586**	**0.028**				-0.499	0.069				-0.432	0.123
RPDENSE				0.043	0.884				0.032	0.914				-0.069	0.816
RPSIZE				0.197	0.500				0.147	0.617				0.065	0.825
RDIV				-0.032	0.915				-0.263	0.364				-0.271	0.349
REDGE				0.022	0.941				0.168	0.566				0.143	0.626
RSHAPE				-0.114	0.697				0.245	0.398				0.091	0.756
RNEAR				-0.176	0.548				-0.137	0.641				-0.124	0.674
RPROX	**18**	**0.043**	-	-0.336	0.240				-0.281	0.331				0.053	0.858
Model R^2	**54**	**0.005**													
Dermanura anderseni															
COVER				-0.123	0.675				-0.253	0.383				-0.238	0.413
RPDENSE				0.220	0.450				0.009	0.974				-0.137	0.641
RPSIZE				-0.184	0.529				-0.098	0.738				-0.162	0.581
RDIV				0.118	0.689				0.101	0.731				0.169	0.564
REDGE				-0.126	0.669				-0.355	0.213				-0.225	0.439
RSHAPE				0.020	0.947				-0.197	0.499				-0.001	0.997
RNEAR				0.104	0.724				0.457	0.101				0.224	0.441
RPROX				0.018	0.952				-0.067	0.820				0.108	0.714
Model R^2															
Dermanura gnoma															
COVER				0.182	0.533				-0.180	0.539				-0.184	0.528
RPDENSE				-0.133	0.651				0.073	0.805				0.098	0.739
RPSIZE				0.080	0.785				0.310	0.280				0.274	0.343
RDIV				-0.180	0.538				-0.292	0.311				-0.198	0.498
REDGE				-0.049	0.867				-0.204	0.483				0.147	0.616
RSHAPE				-0.108	0.712				-0.149	0.612				-0.001	0.998
RNEAR				-0.010	0.974				-0.123	0.674				-0.005	0.988
RPROX				0.297	0.303	**30**	**0.043**	+	**0.547**	**0.043**				0.353	0.216
Model R^2						**24**	**0.043**								
Mesophylla macconelli															
COVER				0.346	0.226				0.447	0.109				0.442	0.114
RPDENSE	**33**	**0.033**	-	**-0.571**	**0.033**				-0.419	0.136				-0.292	0.310
RPSIZE				0.110	0.708				-0.076	0.797				-0.074	0.803
RDIV				-0.303	0.293				0.136	0.644				0.127	0.665
REDGE				-0.435	0.120				-0.258	0.373				-0.331	0.248
RSHAPE				-0.237	0.414				0.096	0.744				-0.266	0.358
RNEAR				0.114	0.698				0.045	0.879				0.176	0.547
RPROX				0.138	0.639				0.075	0.800				0.093	0.752
Model R^2	**27**	**0.033**													
Sturnira lilium															
COVER	**52**	**0.04**	-	**-0.722**	**0.004**	**56**	**0.002**	-	**-0.752**	**0.002**	**52**	**0.001**	-	**-0.722**	**0.004**
RPDENSE				-0.256	0.377				-0.316	0.271				-0.305	0.289
RPSIZE				-0.088	0.764				0.076	0.795				0.063	0.830
RDIV				0.142	0.628				0.034	0.907				0.016	0.956
REDGE				0.180	0.538				-0.062	0.832				-0.251	0.386
RSHAPE				-0.040	0.893				0.003	0.993				-0.152	0.603
RNEAR				0.025	0.933				0.060	0.838				0.095	0.746
RPROX				0.349	0.222				0.291	0.312	**18**	**0.025**	+	0.424	0.131
Model R^2	**48**	**0.04**				**53**	**0.002**				**65**	**0.001**			

Table 3.31. (Continued)

	1 Km focal scale					3 Km focal scale					5 Km focal scale				
	Multiple regression			Correlation		Multiple regression			Correlation		Multiple regression			Correlation	
	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p
Sturnira magna															
COVER				-0.404	0.152				-0.245	0.399				-0.278	0.337
RPDENSE				-0.067	0.819				-0.083	0.777				0.026	0.930
RPSIZE				0.471	0.089				0.510	0.062				0.512	0.061
RDIV				-0.278	0.335	**31**	**0.037**	**-**	**-0.562**	**0.037**	**30**	**0.041**	**-**	**-0.552**	**0.041**
REDGE				0.018	0.951				0.075	0.799				-0.048	0.870
RSHAPE				-0.375	0.187				0.108	0.714				-0.033	0.911
RNEAR				-0.369	0.195				-0.294	0.307				0.148	0.613
RPROX				-0.435	0.120				0.019	0.948				-0.022	0.940
Model R^2						**26**	**0.037**				**25**	**0.041**			
Sturnia tildae															
COVER	**35**	**0.025**	**-**	**-0.594**	**0.025**	**39**	**0.017**	**-**	**-0.624**	**0.017**	**43**	**0.011**	**-**	**-0.658**	**0.011**
RPDENSE				0.096	0.745				-0.002	0.995				-0.089	0.761
RPSIZE				-0.098	0.738				0.104	0.723				0.110	0.709
RDIV				0.154	0.600				-0.272	0.347				-0.173	0.555
REDGE				0.283	0.327				0.110	0.708				0.065	0.825
RSHAPE				0.000	0.999				0.133	0.650				0.309	0.282
RNEAR				0.115	0.697				0.180	0.538				-0.033	0.911
RPROX				-0.095	0.746				-0.292	0.310				-0.276	0.340
Model R^2	**30**	**0.025**				**34**	**0.017**				**39**	**0.011**			
Uroderma bilobatum															
COVER				-0.486	0.078	**36**	**0.023**	**-**	**-0.600**	**0.023**				-0.511	0.062
RPDENSE				0.036	0.903				-0.168	0.567				-0.150	0.610
RPSIZE				-0.089	0.761				0.161	0.582				0.055	0.853
RDIV				0.105	0.721				-0.054	0.856				0.135	0.645
REDGE				-0.006	0.983				-0.165	0.572				-0.181	0.536
RSHAPE				-0.182	0.533				-0.135	0.646				-0.077	0.795
RNEAR				0.094	0.750				-0.097	0.741				-0.076	0.797
RPROX				0.121	0.680				0.330	0.250				0.301	0.295
Model R^2						**31**	**0.023**								
Vampyressa bidens															
COVER				0.236	0.416				0.488	0.077	**41**	**0.013**	**+**	**0.643**	**0.013**
RPDENSE				-0.485	0.079				-0.359	0.208				-0.195	0.505
RPSIZE				0.302	0.295				0.211	0.469				0.112	0.704
RDIV				-0.136	0.643				-0.060	0.840				0.005	0.985
REDGE				-0.261	0.367				-0.236	0.416				-0.029	0.922
RSHAPE				0.147	0.617				0.156	0.594				0.084	0.775
RNEAR				-0.089	0.763				-0.178	0.543				-0.190	0.516
RPROX				-0.270	0.350				0.290	0.314				0.389	0.169
Model R^2											**36**	**0.013**			
Vampyressa thyone															
COVER				0.245	0.398				0.114	0.699				0.199	0.495
RPDENSE	**53**	**0.003**	**-**	**-0.730**	**0.003**	**42**	**0.12**	**-**	**-0.651**	**0.012**	**43**	**0.011**	**-**	**-0.655**	**0.011**
RPSIZE				-0.056	0.849				0.115	0.695				0.055	0.851
RDIV				-0.065	0.824				-0.104	0.724				0.077	0.794
REDGE				-0.301	0.296				-0.436	0.119				-0.267	0.357
RSHAPE				-0.018	0.951				0.332	0.247				0.181	0.536
RNEAR				0.392	0.166				0.444	0.112				0.086	0.771
RPROX				0.179	0.540				0.185	0.528				0.206	0.479
Model R^2	**50**	**0.003**				**38**	**0.012**				**38**	**0.011**			

Table 3.31. (Continued)

	1 Km focal scale					3 Km focal scale					5 Km focal scale				
	Multiple regression			Correlation		Multiple regression			Correlation		Multiple regression			Correlation	
	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p	ΔR^2 (%)	p	Sign	r	p
Richness (S)															
COVER				-0.387	0.172				-0.243	0.403				-0.277	0.337
RPDENSE				-0.182	0.533				-0.414	0.141				-0.220	0.446
RPSIZE				0.191	0.512				0.126	0.667				0.026	0.929
RDIV				0.087	0.767				0.069	0.814				0.119	0.685
REDGE				0.159	0.588				0.140	0.632				0.264	0.362
RSHAPE				0.152	0.604				0.324	0.259				0.413	0.143
RNEAR				-0.062	0.834				0.174	0.553				-0.242	0.404
RPROX	**40**	**0.028**	-	-0.169	0.563				0.150	0.610				0.171	0.558
Model R^2	**34**	**0.028**													
Diversity (H')															
COVER				0.099	0.736				-0.069	0.816				0.006	0.984
RPDENSE				0.015	0.960				-0.132	0.654				-0.185	0.526
RPSIZE				-0.146	0.618				-0.022	0.941				-0.113	0.701
RDIV				0.147	0.616				-0.101	0.732				0.023	0.938
REDGE				-0.015	0.960				0.239	0.411				0.276	0.339
RSHAPE				-0.296	0.305				0.200	0.494				0.003	0.993
RNEAR				0.289	0.317				-0.243	0.403				-0.343	0.229
RPROX				-0.019	0.948				0.011	0.971				0.019	0.949
Model R^2															
Evenness (PIE)															
COVER				0.134	0.648				0.129	0.659				0.129	0.660
RPDENSE				-0.002	0.995				0.131	0.655				0.336	0.240
RPSIZE				-0.007	0.794				-0.169	0.563				-0.019	0.949
RDIV				-0.029	0.920				-0.106	0.719				-0.168	0.566
REDGE				0.034	0.908				0.466	0.093				0.350	0.220
RSHAPE				0.041	0.890				0.381	0.179				-0.272	0.347
RNEAR				0.307	0.286				-0.516	0.059	**48**	**0.006**	-	-0.448	0.108
RPROX				-0.039	0.896				-0.198	0.498				0.168	0.566
Model R^2											**44**	**0.006**			
Dominance (D)															
COVER				0.019	0.950				0.056	0.850				0.090	0.760
RPDENSE				0.019	0.950				0.221	0.448				0.264	0.362
RPSIZE				-0.149	0.612				-0.273	0.345				-0.298	0.302
RDIV				0.159	0.586				0.069	0.814				0.014	0.961
REDGE				0.286	0.322	**36**	**0.024**	+	**0.599**	**0.024**	**58**	**0.001**	+	**0.764**	**0.001**
RSHAPE				0.250	0.389				0.278	0.336				0.166	0.570
RNEAR				0.211	0.469				-0.517	0.058				**-0.726**	**0.003**
RPROX				0.095	0.748				-0.160	0.584				-0.072	0.807
Model R^2						**31**	**0.024**				**55**	**0.001**			
# of Rare Species															
COVER				-0.233	0.422				-0.123	0.676				-0.056	0.848
RPDENSE				-0.106	0.719				-0.341	0.233				-0.262	0.366
RPSIZE				0.303	0.292				0.265	0.359				0.182	0.533
RDIV				0.035	0.905				-0.060	0.840				-0.074	0.802
REDGE				0.155	0.596				0.168	0.565				0.061	0.836
RSHAPE				0.086	0.771				0.316	0.271				0.117	0.692
RNEAR				-0.163	0.577				0.093	0.751				0.040	0.893
RPROX				-0.305	0.288				0.193	0.508				0.322	0.261
Model R^2															

Table 3.32. Levels of significance from tests of similarity in response of species-level or assemblage-level characteristics to a suite of landscape characteristics at each of three focal scales. Fisher's test of combined probabilities was used to assess the consistency in magnitude or direction of responses. Comparison-wise error rates for the three pairwise contrasts of focal scale for a particular population-level or assemblage-level characteristic were adjusted to 0.035 to hold experiment-wise errorrate constant at 0.10 via the Dunn-Sida´k 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 results are shown in bold.

		Scale comparison								
		1 km - 3 km			1 km - 5 km			3 km - 5 km		
		Magnitude	Sign	Fisher's test	Magnitude	Sign	Fisher's test	Magnitude	Sign	Fisher's test
Population-level	Guild									
Carollia brevicauda	F	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.021**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Carollia castanea	F	**<0.001**	**0.072**	**0.001**	**<0.001**	**0.070**	**<0.001**	**0.002**	**<0.001**	**<0.001**
Carollia perspicillata	F	**<0.001**	**0.017**	**<0.001**	**0.020**	**0.006**	**0.001**	**<0.001**	**<0.001**	**<0.001**
Rhinophylla fischerae	F	**<0.001**	0.669	**0.006**	0.222	0.453	0.330	**<0.001**	**<0.001**	**<0.001**
Rhinophylla pumilio	F	**0.004**	**<0.001**	**<0.001**	**<0.001**	**0.054**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Glossophaga soricina	N	**<0.001**	0.890	**0.007**	**<0.001**	0.908	**0.007**	**<0.001**	**<0.001**	**<0.001**
Lonchophylla thomasi	N	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Lophostoma silvicolum	GA	**0.024**	**<0.001**	**<0.001**	0.396	0.660	0.613	**<0.001**	**<0.001**	**<0.001**
Mimon crenulatum	GA	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.056**	**<0.001**	**<0.001**	**0.001**	**<0.001**
Phyllostomus elongatus	GA	0.273	0.089	0.114	0.278	**<0.001**	**0.002**	**<0.001**	**<0.001**	**<0.001**
Phyllostomus hastatus	GA	**<0.001**	**0.004**	**<0.001**	**0.037**	0.418	0.080	**<0.001**	**<0.001**	**<0.001**
Tonatia saurophila	GA	**<0.001**	**0.004**	**<0.001**	**<0.001**	**0.024**	**<0.001**	**<0.001**	**0.004**	**<0.001**
Artibeus lituratus	F	**<0.001**	0.392	**0.004**	**0.008**	0.344	**0.020**	**<0.001**	**<0.001**	**<0.001**
Artibeus obscurus	F	**<0.001**	0.506	**0.004**	**<0.001**	0.975	**0.008**	**<0.001**	**0.002**	**<0.001**
Artibeus planirostris	F	**<0.001**	**0.002**	**<0.001**	**<0.001**	0.593	**0.005**	**<0.001**	**<0.001**	**<0.001**
Dermanura anderseni	F	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.004**	**<0.001**
Dermanura gnoma	F	**<0.001**	**0.014**	**<0.001**	**<0.001**	0.828	**0.007**	**<0.001**	**<0.001**	**<0.001**
Mesophylla macconelli	F	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.003**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Sturnira lilium	F	**<0.001**	**0.020**	**<0.001**	**<0.001**	**0.002**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Sturnira magna	F	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.160	**0.002**	**<0.001**	0.442	**0.004**
Sturnira tildae	F	**<0.001**	**0.031**	**<0.001**	**<0.001**	0.964	**0.008**	**<0.001**	**<0.001**	**<0.001**
Uroderma bilobatum	F	**<0.001**	0.515	**0.004**	**<0.001**	**0.036**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Vampyressa bidens	F	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Vampyressa thyone	F	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Assemblage-level										
Richness (S)		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Diversity (H')		**<0.001**	**<0.001**	**<0.001**	0.093	0.584	0.212	**<0.001**	**0.002**	**<0.001**
Dominance (D)		**0.005**	**0.004**	**<0.001**	0.091	**0.052**	**0.030**	**<0.001**	**<0.001**	**<0.001**
Evenness (PIE)		0.274	**<0.001**	**0.003**	0.112	0.546	0.208	**0.001**	**0.007**	**<0.001**
Number of rare species		**<0.001**	**0.001**	**<0.001**	0.078	**0.006**	**0.004**	**<0.001**	**<0.001**	**<0.001**

Table 3.33. Symbolic representation of matrix corespondence between focal scales for population-level and assemblage-level attributes. Symbols indicate that the response was more similar (+) or dissimilar (-) than expected due to chance; ns indicates nonsignificance. Letters A–I represent the type of similarity or dissimilarity between focal scales as a result of separate tests of correspondence in magnitude and sign of matrix elements, and Fisher's test of combined probabilities for both tests. The letter I designates an uncertain result (see Table 3.4; Gorresen et al. 2005).

		Scale comparison											
		1 km - 3 km				1 km - 5 km				3 km - 5 km			
		Magnitude	Sign	Fisher's Test	Type	Magnitude	Sign	Fisher's Test	Type	Magnitude	Sign	Fisher's Test	Type
Population-level	Guild												
Carollia brevicauda	F	+	+	*	A	+	+	*	A	+	+	*	A
Carollia castanea	F	+	+	*	A	+	+	*	A	+	+	*	A
Carollia perspicillata	F	+	+	*	A	+	+	*	A	+	+	*	A
Rhinophylla fischerae	F	+	ns	*	C	ns	ns	ns	I	+	+	*	A
Rhinophylla pumilio	F	+	+	*	A	+	+	*	A	+	+	*	A
Glossophaga soricina	N	+	ns	*	C	+	ns	*	C	+	+	*	A
Lonchophylla thomasi	N	+	+	*	A	+	+	*	A	+	+	*	A
Lophostoma silvicolum	GA	+	+	*	A	ns	ns	ns	I	+	+	*	A
Mimon crenulatum	GA	+	+	*	A	+	+	*	A	+	+	*	A
Phyllostomus elongatus	GA	ns	ns	ns	I	ns	-	*	**H**	+	+	*	A
Phyllostomus hastatus	GA	+	+	*	A	+	ns	ns	I	+	+	*	A
Tonatia saurophila	GA	+	+	*	A	+	+	*	A	+	+	*	A
Artibeus lituratus	F	+	ns	*	C	+	ns	*	C	+	+	*	A
Artibeus obscurus	F	+	ns	*	C	+	ns	*	C	+	+	*	A
Artibeus planirostris	F	+	+	*	A	+	ns	*	C	+	+	*	A
Dermanura anderseni	F	+	+	*	A	+	+	*	A	+	+	*	A
Dermanura gnoma	F	+	+	*	A	+	ns	*	C	+	+	*	A
Mesophylla macconelli	F	+	+	*	A	+	+	*	A	+	+	*	A
Sturnira lilium	F	+	+	*	A	+	+	*	A	+	+	*	A
Sturnira magna	F	+	+	*	A	+	ns	*	C	+	ns	*	C
Sturnira tildae	F	+	+	*	A	+	ns	*	C	+	+	*	A
Uroderma bilobatum	F	+	ns	*	C	+	+	*	A	+	+	*	A
Vampyressa bidens	F	+	+	*	A	+	+	*	A	+	+	*	A
Vampyressa thyrone	F	+	+	*	A	+	+	*	A	+	+	*	A
Assemblage-level													
Richness (S)		+	+	*	A	+	+	*	A	+	+	*	A
Diversity (H')		-	-	*	**E**	ns	ns	ns	I	+	+	*	A
Dominance (D)		+	+	*	A	ns	+	*	G	+	+	*	A
Evenness (PIE)		ns	+	*	G	ns	ns	ns	I	+	+	*	A
Number of rare species		+	+	*	A	ns	+	*	G	+	+	*	A

CHAPTER IV
DISCUSSION

Landscape Characteristics

Ecological patterns in this study (Table 3.31) depended on focal scale, as in other studies (e.g., Allen and Starr 1982, Lyons and Willig 1999, Waide et al. 1999, Gross et al. 2000, Willig 2003, Gorresen and Willig 2004, Gorresen et al. 2005). The majority of empirical studies of fragmentation evaluate the response of particular species to the spatial structure of habitat at a single, patch-based scale (McGarigal and Cushman 2002, Fahrig 2003). However, as evidenced by this study, the effects of fragmentation operate at multiple spatial scales, depend on species-specific behavioral and life-history characteristics (Fahrig and Paloheimo 1988a, 1988b; Kareiva 1990), and result from patterns and processes that operate simultaneously across a range of scales (McGarigal and Cushman 2002). Regional and local species densities are linked by the dispersal of individuals across habitats and among populations (e.g., Pulliam 1988, Rolstad 1991). Consequently, a species' ability to utilize the matrix within which habitat patches are located will significantly alter the effects of habitat loss and fragmentation (Wiens et al. 1993). Accordingly, large-scale (regional) conditions indirectly determine local abundance by the movement of individuals among sites (Gorresen and Willig 2004). The home ranges of smaller bat species that occur in the study area (e.g., *Glossophaga soricina* and *Vampyressa bidens*), as well as home ranges of gleaning insectivores that forage short distances from their roosts (e.g., *Lophostoma silvicolum*; Lemke 1984, Arita et al. 1997, Kalko et al. 1999), are likely less than 3 km in radius. However, abundances

of these species were associated significantly with landscape characteristics at the 5 km focal scale, suggesting that local abundance reflects a collection of factors (e.g., prey densities, roost availability, plant distributions) operating at multiple scales.

In general, studies that have identified the independent effects of composition and configuration demonstrate landscape composition has a greater impact on the occurrence or incidence of species in habitat mosaics than does spatial configuration (McGarigal and McComb 1995, Trzcinski et al. 1999, Villard et al. 1999, Gorresen and Willig 2004). This pattern of association of species with landscape structure was similar for bats in fragmented Amazonian rain forest in the environs of Iquitos (Table 3.31). However, this pattern may be due to the dominance of frugivores in the assemblage (Table 3.1). Abundances of frugivorous species responded significantly to characteristics of landscape composition more than to characteristics of landscape configuration. However, abundances of gleaning animalivores responded significantly to characteristics of landscape configuration only (Figure 4.1). In addition, assemblage characteristics only were associated with characteristics of landscape configuration (Table 3.31).

Differences in response to landscape structure demonstrated by gleaning animalivores and frugivores may be a consequence of changes in food availability or foraging strategies. Abundances of frugivores were associated primarily with changes in forest cover and are likely responding to changes in fruit availability, capitalizing on the influx of succesional fruits while still exploiting dispersed patches of fruit available in forests. Frugivores that specialize on canopy fruits (i.e., *Artibeus*) can travel long distances in search of fruits, minimizing the influence of landscape configuration on foraging behavior. Moreover, understory frugivores (i.e., *Carollia* and *Rhinophylla*)

often roost close to multiple feeding areas (Heithaus and Flemming 1978), and food is available in forest as well as other habitats (i.e., secondary forest, active and abandoned agricultural fields). Consequently, the identity of the matrix habitat may influence abundance more than the arrangement of forest patches, explaining why frugivores respond more to the landscape composition than to configuration. Abundances of gleaning animalivores were associated primarily with edge density. This may be the result of changes in abundances of insect or small vertebrate species or the introduction of new prey species adapted to edge habitat (Laurance et al. 2002). Differences in vegetation structure (e.g., relative heights of plants, increased number of dead trees and leaf litter) and microclimatic characteristics (e.g., light permeability, reduced humidity) of edges may provide higher visibility or better quality foraging for bats that hunt from perches or by trawling. Moreover, edges may be convenient flyways between resource patches. The association of trophic guilds with particular characteristics of landscape structure remains an unexplored area in ecology and conservation biology, but may provide valuable information regarding responses to fragmentation by groups of species that exploit similar resources.

Population and Assemblage Responses

In general, the abundances and richness of species were higher in fragmented forest than in continuous forest. These results are more consistent with studies concerning the response of bats to selective logging (e.g., Ochoa 2000, Clarke et al. 2005a, 2005b; Peters et al. 2006) than to the response of bats to deforestation (Fenton et al. 1992, Brosset et al. 1996, Cosson et al. 1999). Iquitos is in the early stages of forest exploitation. Percent of closed canopy forest for sites at the smallest focal scale (27%-

99%) was more variable than at the largest focal scale (47%-92%), corroborating the contention that deforestation occurs at a relatively small scale (i.e., 1 to 4 ha patches) in this region. Such small scale forest conversion and the lack of completely deforested sites may explain why the effects of anthropogenic activities manifest primarily as changes in abundance (e.g., *C. perspicillata*, *C. brevicauda, A. obscurus*, and *R. pumilio*) rather than by alterations in the presence of species (Gorresen and Willig 2004; Clarke et al. 2005a, 2005b; Gorresen et al. 2005, Willig et al. in press).

Contrary to results from Atlantic Forest of Paraguay using an equivalent experimental design, the majority of phyllostomids (e.g., *C. perspicillata*, *A. lituratus*, *S. lilium*) captured in Iquitos responded negatively to forest cover and positively to characteristics indicative of fragmentation (e.g., edge density). Although a number of species had higher abundances in moderately fragmented Atlantic Forest, species responded positively to forest cover and patch density, and negatively to edge density. In Iquitos, nine species responded negatively to forest cover and four species responded positively to edge density at a number of scales (Table 3.31). These observations are consistent with a number of interpretations. Many of the species captured in Paraguay are at the edge of their geographic ranges, and population dynamics often are regulated by different factors at edges (e.g., climatic, decreased food and roost availability) than at centers (e.g., competition, predator-prey interactions) of geographic ranges (Brown et al. 1996, Willig et al. 2000). This may explain why abundances of species that are present in both locations were disparate (e.g., *C. perspicillata*: 163 in Paraguay and 1022 in Iquitos; Gorresen and Willig 2004, Table 3.1), especially considering that the sampling effort in Paraguay was almost three times that of the current study. Furthermore, forest

conversion occurs at a relatively small scale in Iquitos, and the openings caused by anthropogenic disturbances may mimic the characteristics of natural disturbances, which often increase the abundances of some species in fragmented areas (Willig et al. in press). In contrast, eastern Paraguay has experienced deforestation rates twice that of the Amazon basin and has less than 20% of its forest remaining (Keel et al. 1993), causing species to show responses typical of those associated with habitat loss rather than with natural disturbances (Gorresen and Willig 2004, Gorresen et al. 2005).

Similar to other studies in the Neotropics (Brosset et al. 1996; Hice et al. 2004; Clarke et al. 2005a, 2005b; Willig et al. in press), the most abundant bat species in Iquitos are generalist frugivores from the genus *Carollia* (i.e., *C. perspicillata* and *C. brevicada*). In fact, the eight most abundant species in the study area were frugivores (Table 3.1) and likely account for the positive relationship between dominance and edge density at the 3 and 5 km focal scales. For birds and forest-interior bats, insectivores are especially vulnerable to fragmentation, whereas many frugivores and nectarivores remain stable or increase in abundance in fragments (Bierregaard and Stouffer 1997, Kalko 1998, Sampaio 2000, Gorresen and Willig 2004, Wunderle et al. 2005, Peters et al. 2006, Willig et al. in press). This pattern of response by bat populations to anthropogenic disturbance may be related to species-specific aspects of their foraging ecology (Schulze et al. 2000; Gorresen and Willig 2004; Clarke et al. 2005a, 2005b; Willig et al. in press). The most common frugivores (i.e., *Carollia*, *Artibeus*, and *Sturnira*) and nectarivores (i.e., *G. soricina* and *L. thomasi*) have higher abundances in moderately fragmented sites than in sites characterized by large amounts of continuous closed canopy forest (Table 3.1). Frugivores and nectarivores often exploit food resources after forest conversion to

agriculture and during secondary succession, following abandonment of agriculture. This transpires because many fruit bearing plants (e.g., *Cecropia*, *Piper*, and *Solanum*) on which bats feed are early- or mid-successional species (Fleming 1988, Marinho-Filho 1991, Gorchov et al. 1993). Consequently, a matrix of mature forest with patches of secondary forest and agriculture may provide a more desirable landscape for frugivores and nectarivores than do extensive, intact forests (Clarke 2005a, Willig et al. in press), at least when deforestation and fragmentation are small compared to the size of the regional landscape.

Changes in land use, specifically conversion of forest habitat, are likely to enhance vulnerability of bats with specialized ecological requirements. For Neotropical bats, roosting habitat is more abundant in forests because bats roost in dense vegetation to avoid terrestrial predators (Kunz and Lumsden 2003). Consequently, species that rely on forest habitat for food as well as for roosts may be affected disproportionately by fragmentation. For example, gleaning animalivores, in particular *L. silvicolum* (which roost only in active termite nests of *N. corniger*; Kalko et al. 2006), are very rare or even absent in small (1 ha) fragments in Brazil (Sampaio et al. 2003) and are less than half as abundant in secondary forest or agricultural areas than in closed canopy forest in Iquitos (Willig et al. in press). In this study, 4 of the 5 gleaning animalivores (*L. silvicoulm*, *M. crenulatum*, *P. elongatus*, and *T. saurophilla*) occurred in each of the three sites (i.e., Km 60, Km 66.5, and Km 75) characterized by large amounts of continuous forest, and the fifth species (*P. hastatus*) was captured in two of the three sites (Table 3.1). Specialized roost requirements do not appear to be a feature of many species of gleaning animalivores outside the genus *Lophostoma* (Kalko et al. 2006). However, gleaning animalivores were

present in only some of the fragmented sites, and although specialized roosting requirements cannot be discounted, a specialized diet may be a more important factor in sensitivity to forest disturbance. Members of this guild glean large arthropods and occasionally small vertebrates from vegetative surfaces (Gardner 1977, Bonaccorso 1978). Although suitable prey are not absent from disturbed forests, densities of prey or prey types may be low (LaVal and Fitch 1977). Consequently, even moderate amounts of fragmentation can affect local populations of more specialized bat species and may thereby alter the structure of assemblages.

Conservation Implications

This study represents the first attempt to identify the response of phyllostomids to spatially explicit landscape characteristics measured at multiple focal scales in fragmented, lowland Amazonian forest. Populations and assemblages responded to a variety of landscape characteristics at multiple focal scales, some smaller and some larger than particular species home ranges. Because organisms are cognizant of resources and habitat features at a number of scales (Kotliar and Wiens 1990), they may respond to both local and regional characteristics of a landscape. Consequently, multiscale approaches likely are critical to the success of management and conservation strategies.

Disturbed habitats may provide higher numbers and quality of resources for some taxa (e.g., *G. soricina*, *C. perspicillata*, and *S. lilium*) that feed on fruits and flowers of early successional plants (Fleming 1988, Marinho-Filho 1991, Gorchov et al. 1993) or for particular phyllostomids (e.g., *Phyllostomus hastatus*) that opportunistically supplement their animalivorous diet with fruit (Willig et al. 1993, Voss and Emmons 1996, Simmons and Voss 1998). In the current study, richness and abundances of phyllostomids were

higher in moderately fragmented forest, demonstrating that maintenance of large areas of continuous forest with a mix of successional habitat and human land uses may be able to sustain biodiversity with little negative impact. This has been documented previously for bats in Trinidad (Clarke et al. 2005a, 2005b), Paraguay (Gorresen and Willig 2004), and in the context of a non-manipulative experiment in Iquitos examining forest, succesional forest, and agricultural areas (Willig et al. in press). Small-scale deforestation may not diminish the tendency for bats to traverse open or disturbed areas (Gorchov et al. 1993) and many Neotropical species cross open areas of 0.5 km or greater (Bernard and Fenton 2003). For example, *Carollia perspicillata* used 320 ha in five nights of tracking, encompassing multiple forest fragments separated by savannas in Brazil (Bernard and Fenton 2003). However, as the size and frequency of deforested areas increases, fewer frugivores may be able to traverse these large open areas. As a result, patterns of seed dispersal may be altered appreciably. This could adversely affect tropical ecosystem function and regeneration of forest, because bats play a critical role in dispersing seeds of successional plants.

Bat biodiversity can be maintained in fragmented tropical forests as long as the deforestation occurs at small scales (relative to the organism) and large areas of unfragmented forest at the regional scale are pervasive. However, anthropogenic effects already may have altered the abundance and composition of bat species in forested habitats that are in close proximity to areas of human land use in Iquitos, creating a biased view of assemblages and underestimating the severity of anthropogenic effects (Willig et al. in press). Bats respond to spatially explicit characteristics of landscapes and

future research that fails to account for this scale-dependent behavior may lead to spurious conclusions regarding fragmentation.

Trophic guilds, assemblages, and species do not respond in the same manner to landscape structure. Particular attention needs to be directed towards understanding the autecology, life histories, and response to forest fragmentation by rare bat species as well as by guilds or families underrepresented by mist netting (e.g., gleaning animalivores and aerial insectivores: Emballonuridae, Vespertillionidae, and Mollosidae). Continued long-term research, employing multiple sampling methods (i.e., mist netting, roost searching, and acoustic monitoring), in areas such as Iquitos could provide critical knowledge to land managers and policy makers to guide sustainable use of tropical habitats.

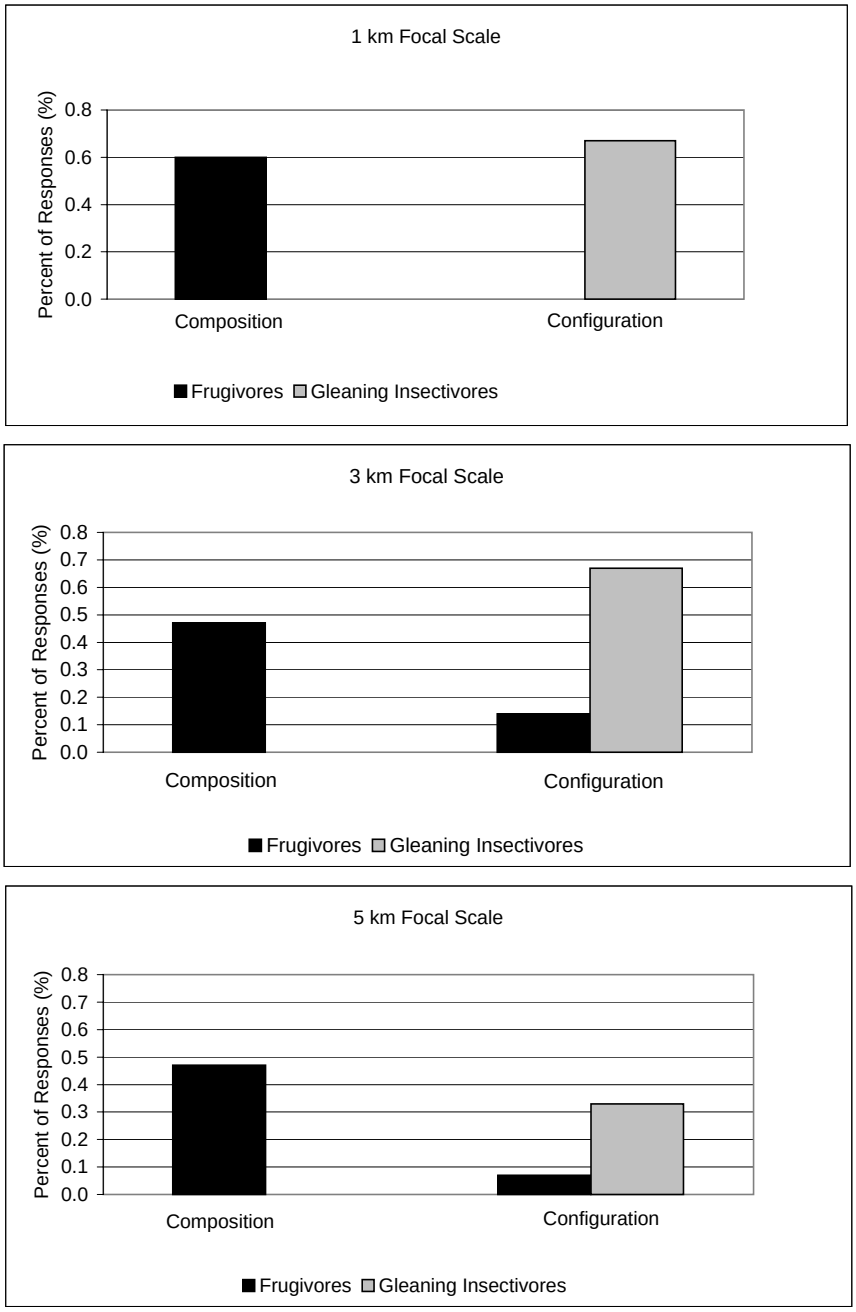

Figure 4.1. Comparison of the response of frugivores (black bars) and gleaning animalivores (gray bars) to compositional versus configurational aspects of the landscape at each of 3 focal scales, based on species with significant responses to landscape characteristics at any scale. Fifteen species of frugivores and three species of gleaning animalivores responded to landscape characteristics at at least one scale. Because a species may not respond to lanscape characteristics at all 3 focal scales, percentages do not sum to 100%.

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