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RESEARCH ARTICLE

Influences of scale on bat habitat relationships in a forested landscape in Nicaragua

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Abstract

Context Scale dependence of bat habitat selection is poorly known with few studies evaluating relationships among landscape metrics such as class versus landscape, or metrics that measure composition or configuration. This knowledge can inform conservation approaches to mitigate habitat loss and fragmentation.

Objectives We evaluated scale dependence of habitat associations and scaling patterns of landscape metrics in relation to bat occurrence or capture rate in forests of southwestern Nicaragua.

Methods We captured 1537 bats at 35 locations and measured landscape and class metrics across 10 spatial scales (100–1000 m) surrounding capture locations. We conducted univariate scaling across the 10 scales and identified scales and variables most related to bat occurrence or capture rate.

Results Edge and patch density, at both landscape and class levels, were the most important variables across species. Feeding guilds varied in their response to metrics. Certain landscape and configuration metrics were most influential at fine (100 m) and/or broad (1000 m) spatial scales while most class and composition metrics were influential at intermediate scales.

Conclusions These results provide insight into the scale dependence of habitat associations of bat species and the influence of fine and broad scales on habitat associations. The effects of scale, examined in our study and others from fine (100 m) to broad (5 km) indicate habitat relationships for bats may be more informative at larger scales. Our results suggest there could be general differences in scale relationships for different groups of landscape metrics, which deserves further evaluation in other taxonomic groups.

Keywords Scale-dependent habitat selection · Landscape metrics · Landscape composition · Landscape configuration · Chiroptera · Forest fragmentation · FRAGSTATS · Multi-scale habitat modeling

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Introduction

Species habitat relationships are fundamentally scale dependent. Species select habitat at several levels (Johnson 1980) and within levels species select resources at a range of spatial and temporal scales (Wiens 1989; Levin 1993). Failure to adopt a framework that allows explicit optimization of multi-scale habitat relationships can result in incorrect inferences regarding the nature and strength of habitat selection (Thompson and McGarigal 2002; Grand et al. 2004; Mateo-Sanchez et al. 2014; Shirk et al. 2014). However, despite the importance of multi-scale optimization of habitat relationships models, few papers on habitat ecology published in recent years have conducted any multi-scale optimization (McGarigal et al. 2016, in press). In addition, differences in the scales of strongest relationship with habitat selection among different categories of landscape metrics have rarely been described, despite their importance in clarifying understanding of relationships between landscape metric behavior and ecological relationships (e.g., Neel et al. 2004; Cushman et al. 2008).

Landscape metrics are often measured as class or landscape variables (McGarigal et al. 2002). Class metrics quantify the composition or configuration of patches of a particular class or cover type, while landscape metrics quantify the composition or configuration of the entire multi-class patch mosaic (Cushman et al. 2013b). The relative importance of landscape composition versus landscape configuration in habitat relationships has been widely debated (e.g., Fahrig 1997; With and King 1999; Cushman and McGarigal 2003; Klingbeil and Willig 2009; Cushman et al. 2013a). We know less about the relative importance or predictive value of class versus landscape metrics in describing habitat relationships and differences in the frequency of which class and landscape metrics are associated with species occurrence patterns at broad versus fine scales.

In this paper we evaluate scale dependence of habitat associations of bat species that co-occur in the tropical dry forest of Nicaragua. Tropical dry forests are considered the most threatened of all major lowland tropical forest types (Janzen 1988; Sabogal 1992; Griscom and Ashton 2011). Occurring along the southwestern Pacific coast in Central America, these forests supply ecological and economic benefits to local residents including wood products, pasture, agriculture, watershed protection, and protection of biodiversity (Ryan 1978; Gillespie and Walter 2001; McCrary et al. 2005; González-Rivas et al. 2006; Dent 2010). Originally the most extensive regional forest type, less than 2 % remains. In addition, this forest type has the third highest rate of recent forest cover loss (Hansen et al. 2010; Griscom and Ashton 2011). Currently, tropical dry forest exists primarily as remnant patches of secondary forest that are small and scattered in distribution (Sabogal 1992; Gillespie et al. 2000; Miles et al. 2006).

Previous research documented how human activities in dry forest altered forest structure and composition at multiple scales (Griscom et al. 2005; Romero-Duque et al. 2007; Kodandapani et al. 2008). Fragmentation of forest cover affected wildlife habitat use (e.g., Griscom et al. 2005; Herrerías-Diego et al. 2008). Moderate levels of forest fragmentation increased species diversity for nectarivorous and frugivorous bat species likely because openings created new food sources. However gleaning animalivores (species associated with closed canopy forests) declined (Gorresen and Willig 2004; Clarke et al. 2005; Peters et al. 2006; Bobrowiec and Gribel 2009; Cisneros et al. 2015). Most of these landscape level studies of bats focused on a single, arbitrary scale. Although two studies (Gorresen et al. 2005; Klingbeil and Willig 2009) examined how bat species responded to forest fragmentation and examined effects of landscape composition versus configuration at multiple scales (1, 3, 5 km), these studies occurred in South American humid forests or rainforests.

With 9 families and 61 genera (Medina-Fitoria 2014), Nicaragua is considered a global hotspot for bats (Hutson et al. 2001), with riparian forests harboring the highest species richness, diversity, and abundance (Harvey et al. 2006; Medina et al. 2007). Our goals in this study were to evaluate differences in the: (1) frequency that different landscape metrics are selected in models predicting bat occurrence or capture rate, (2) scale at which variables were selected across bat species and guilds, (3) scale at which landscape and class variables were selected, and (4) scale at which composition and configuration metrics were selected in models predicting occurrence or capture rate of species of bats or guilds in tropical dry forests of Nicaragua.

Only a few papers published about habitat relationships have used multi-scale optimization approaches to identify models predicting multivariate habitat selection, and even fewer have assessed multiple species and the differences in scale of habitat selection among them. McGarigal et al. (2016, in press) identify multi-species studies of scale dependence in habitat selection as a priority for future research. Understanding how and why species inhabiting the same landscapes differ in their scale of habitat selection is critical to developing a fully-fledged science of scale-dependent habitat modeling.

Methods

Study area

Our study area encompassed the Paso del Istmo, the narrow isthmus in the Rivas Province of Nicaragua, bordered east and west by Lake Nicaragua and the Pacific Ocean, respectively (11°12′33″N, 85°44′2″W; Fig. 1). This area contains the highest concentration of Mesoamerican Tropical Dry Forest in Nicaragua (Sesnie et al. 2008) but also is subject to rapid forest loss and fragmentation (Gillespie et al. 2000; Miles et al. 2006; Sesnie et al. 2008). Forest types range from tropical dry deciduous forest at sea level along the Pacific coast to moist broadleaf forest at elevations up to 600 m in the coastal range. Mean annual air temperature is 26.7 °C and annual precipitation averages 1400–2000 mm with <50 mm of rainfall per month during the dry season (December–April; Sesnie et al. 2008). The area is characterized by a mix of land cover types including mature secondary and early successional forest, plantation, pasture, crop lands, urban areas, and wetlands (Sesnie et al. 2008; Rivas et al. 2013).

Bat captures

We used single- and triple-high mist nets (38 mm mesh, 2.6 m × 6-, 9-, 12-, or 18-m nets for bats, Avinet, Inc., Dryden, New York, USA) to capture bats along flyways (river and stream corridors, forest trails, and unpaved roads; Kunz and Kurta 1988). We

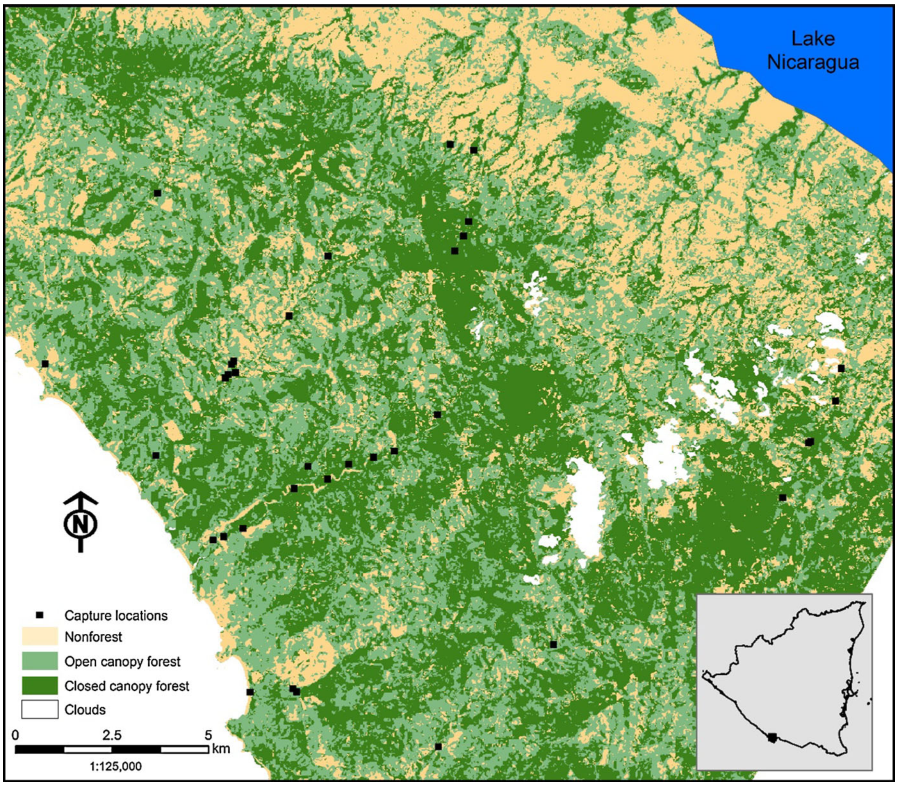


Fig. 1 Study area with capture locations for bats, Paso del Istmo, Nicaragua, December–January, 2010–2012

selected forested sites that were accessible by road and for which we had permission from landowners. We attempted to select sites proportional to availability of three classifications: non-forest, open canopy forest, closed canopy forest. Mist nets were deployed at dusk (~1800) and remained open for up to 7 h. We classified bats to species using a field guide (Reid 2009) and dichotomous key (Timm and LaVal 1998) and weighed bats to nearest 0.5 g. Bats were released $\leq$20 min of capture. Bats were captured and handled under Nicaraguan Permit Autorización No. 015-122011 using guidelines of the American Society of Mammalogists (Sikes et al. 2011) and with approval of the Northern Arizona University Institutional Animal Care and Use Committee.

We standardized captures by calculating a capture rate (1 net hour = one 6-m net open for 1 h) to determine the number of species, individuals, and individuals by species captured per net hour. We also grouped species into 6 guilds following guidance from previous authors (Clarke et al. 2005; Peters et al. 2006; Bobrowiec and Gribel 2009; Klingbeil and Willig 2009): gleaning animalivores (GA), frugivores (FR), nectarivores (NE), sanguinivore (SA), aerial insectivores (AI), and piscivore (PI) (Table 1). Gleaning animalivores included the Phyllostomidae subfamily Phyllostominae associated with closed-canopy forest (Fenton et al. 1992; Clarke et al. 2005). Frugivores, nectarivores, and the sanguinivore were also in the Phyllostomidae family; aerial insectivores included members of the Emballonuridae, Molossidae, Mormoopidae, and Vespertilionidae and the piscivore was a single member of the Noctilionidae. Mist netting at ground level most commonly captures bats in the Phyllostomidae, Mormoopidae, and Noctilionidae. Other families (Emballonuridae, Molossidae, and Vespertilionidae) may fly above the tree canopy or avoid nets and thus bias capture rates (e.g., Bobrowiec and Gribel 2009). Our capture rates for aerial insectivores may therefore be underestimated.

We sampled bats during the dry season at 35 sites (Jan 2010, n = 4; Dec 2011, n = 14; and Jan 2012, n = 17) with capture rates of >1 bat per net hour and >20 net hours. For species (*Carollia perspicillata*, *Artibeus jamaicensis*, *Carollia subrufa*) or guilds (FR, NE, AI) well distributed across sites (captured at >20 of 35 sites), we used capture rate as the response variable. For all others (at $\leq$20 sites), we used occurrence as the response variable.

Vegetation map

The environmental data used to predict occurrence or capture rates of bats were derived from spatial analysis of a vegetation map depicting dominant vegetation types within southwestern Nicaragua (Rivas et al. 2013). The map used supervised classification of SPOT 4 and SPOT 5 imagery based on extensive ground truthing plot surveys. Classification used the first two principal component axes of the spectral bands of SPOT images, a Normalized Difference Vegetation Index and a Soil-adjusted Vegetation index which was based on the red and near-infrared SPOT bands, as well as several topographical predictor variables (elevation, slope, transformed aspect, and Terrain Wetness index) derived from Shuttle Radar Topography Mission (STRM). A ten-fold Classification Rule with the “Quick, Unbiased and Efficient Statistical Tree” (QUEST) algorithm 1.99.1 in RuleGen 1.02 extension of ENVI 4.7 was used as the classification method. Classes mapped included: urban-mixed-agriculture, wetland, young secondary forest, old secondary forest, young regrowth, old regrowth, pasture, crop and plantation, at a 10-m pixel resolution. Classification accuracy was evaluated using an error matrix and kappa statistics, with final classification accuracy of 88 % with an overall Kappa coefficient of 0.86. Classification accuracy for each land class was close to or over 80 % (Rivas et al. 2013). The portion of the Paso del Istmo that comprised our study area was mostly forested (Rivas et al. 2013; Fig. 1) and because we were interested in bat response to forest fragmentation at varying scales, we used vegetation cover types that represented availability of forest or non-forest to bats. Thus for our analysis we reclassified the map into three vegetation cover types, depicting non-forest (urban-mixed-agriculture, plantation, crop, pasture), open canopy forest (young regrowth, old regrowth), and closed canopy forest (old secondary forest, young secondary forest, and wetland dominated by mature, old secondary forest) (Table 2; Rivas et al. 2013).

Landscape metrics

We used FRAGSTATS 4.0 (McGarigal et al. 2013) to analyze the composition and configuration of the landscape as defined by the three land cover classes (non-forest, open-canopy forest, closed-canopy

Table 1 Species of bats captured using mist nets in December 2011, January 2010 and 2012 (1635 net hours), Rivas Isthmus, Nicaragua

Scientific name[a]	Common name	Family/subfamily[b]	Guild	Total
Saccopteryx bilineata[a]	Greater white-lined bat	EMB	AI	11
Rhynchonycteris naso	Proboscis bat	EMB	AI	8
Saccopteryx leptura	Lesser white-lined bat	EMB	AI	3
Molossus pretiosus	Miller's mastiff bat	MOL	AI	17
Cynomops mexicanus	Mexican dog-faced bat	MOL	AI	1
Pteronotus personatus[a]	Lesser mustached bat	MOR	AI	66
Pteronotus gymnonotus[a]	Big naked-backed bat	MOR	AI	23
Pteronotus parnellii[a]	Common mustached bat	MOR	AI	23
Pteronotus davyi	Davy's naked-backed bat	MOR	AI	1
Noctilio leporinus[a]	Greater fishing bat	NOC	PI	61
Noctilio albiventris	Lesser fishing bat	NOC	AI	10
Carollia perspicillata[a]	Seba's short-tailed bat	PHY/Car	FR	281
Carollia subrufa[a]	Gray short-tailed bat	PHY/Car	FR	104
Carollia castanea	Chestnut short-tailed bat	PHY/Car	FR	3
Desmodus rotundus[a]	Common vampire bat	PHY/Des	SA	124
Glossaphaga soricina[a]	Common long-tongued bat	PHY/Glo	NE	45
Glossaphaga commissarisi[a]	Brown long-tongued bat	PHY/Glo	NE	13
Choeroniscus godmani	Godman's long-tongued bat	PHY/Glo	NE	4
Glossaphaga leachi	Gray's long-tongued bat	PHY/Glo	NE	1
Phyllostomus discolor[a]	Pale spear-nosed bat	PHY/Phy	GA	21
Lophostoma brasiliense[a]	Pygmy round-eared bat	PHY/Phy	GA	13
Micronycteris minuta	Tiny big-eared bat	PHY/Phy	GA	9
Tonatia saurophila	Stripe-headed round-eared bat	PHY/Phy	GA	6
Trinycteris nicefori[a]	Niceforo's bat	PHY/Phy	GA	6
Lampronycteris brachyotis	Orange-throated bat	PHY/Phy	GA	4
Micronycteris microtis	Common big-eared bat	PHY/Phy	GA	3
Micronycteris hirsuta	Hairy big-eared bat	PHY/Phy	GA	2
Chrotopterus auritus	Woolly false vampire bat	PHY/Phy	GA	2
Trachops cirrhosus	Fringe-lipped bat	PHY/Phy	GA	2
Lophostoma silvicolum	White-throated round-eared bat	PHY/Phy	GA	1
Phylloderma stenops	Pale-faced bat	PHY/Phy	GA	1
Artibeus jamaicensis[a]	Jamaican fruit-eating bat	PHY/Ste	FR	371
Sturnira parvidens[a]	Little yellow-shouldered bat	PHY/Ste	FR	68
Dermanura phaeotis[a]	Pygmy fruit-eating bat	PHY/Ste	FR	55
Dermanura watsoni[a]	Thomas' fruit-eating bat	PHY/Ste	FR	53
Artibeus intermedius[a]	Intermediate fruit-eating bat	PHY/Ste	FR	26
Artibeus literatus	Great fruit-eating bat	PHY/Ste	FR	20
Centurio senex	Wrinkle-faced bat	PHY/Ste	FR	9
Uroderma bilobatum	Common tent-making bat	PHY/Ste	FR	8
Platyrrhinus helleri	Heller's broad-nosed bat	PHY/Ste	FR	6
Dermanura tolteca	Toltec fruit-eating Bat	PHY/Ste	FR	1
Chiroderma villosum	Hairy big-eyed bat	PHY/Ste	FR	1
Eptesicus furinalis[a]	Argentine brown bat	VES	AI	26
Rhogeessa bickhami[a]	Bickham's little yellow bat	VES	AI	22

Table 1 continued

Scientific name[a]	Common name	Family/subfamily[b]	Guild	Total
Myotis nigricans	Black myotis	VES	AI	2
Total				1537

Species grouped into guilds included: *GA* gleaning animalivores, *FR* frugivores, *NE* nectarivores, *SA* sanguinivore, *AI* aerial insectivores, *PI* piscivore

[a] Species used in analysis to evaluate scale dependence of their habitat associations

[b] Families are: *EMB* Emballonuridae; *MOL* Molossidae, *MOR* Mormoopidae, *NOC* Noctilionidae, *PHY* Phyllostomidae, *VES* Vespertilionidae. Subfamilies are: *Car* Carollinae, *Des* Desmodontinae, *Glo* Glossophaginae, *Phy* Phyllostominae, *Ste* Stenodermatinae

Table 2 Reclassification of vegetation cover types for Rivas Isthmus, Nicaragua based categories developed by Rivas et al. (2013)

Reclassification cover type	Cover type (from Rivas et al. 2013)	% of landscape	Class code	Description
Non-forest	Urban-mixed-agriculture	6.1	1	Cities, roads, houses, other human infrastructure, and some agricultural lands such as crop and pasture
	Crop	8.9		All annual crops (e.g., rice, corn, beans, wheat, sugar cane)
	Pasture	19.6		All pastured areas that were grazed by cattle or horses
	Plantation	9.3		All orchards, native and non-native plants that were grown for harvest
Open-canopy forest	Young regrowth	23.1	2	Dense vegetation in age 0–10 with pioneer species and no canopies
	Old regrowth	10.9		Dense vegetation in age 11–25 with some trees reaching maturity and providing open canopies.
Closed-canopy forest	Wetland-mixed-forest	8.4	3	Areas that were along rivers or stream corridors, areas that were near large lakes, and some forested vegetation that was usually along the stream corridors
	Young secondary forest	7.5		Vegetation in age 26–40 with most trees providing mostly closed canopies. No pioneer species were found
	Old secondary forest	6.2		Vegetation in age >40 with fully closed canopies. Most trees were large in diameter and tall

forest). We chose several landscape metrics which quantify the structure of the entire habitat mosaic of the three cover types, as well as several class metrics focusing on the area and configuration of each of the cover types individually, based on past studies of metric behavior (Neel et al. 2004) and parsimony (Cushman et al. 2008).

For landscape metrics we calculated contagion (contag), which quantifies the degree of landscape aggregation and compaction of patch types, contrast weighted edge density (cwed), which quantifies the amount of edge in the landscape weighted by the degree of contrast between adjacent patches, edge density (ed), which measures the total edge among dissimilar patch types without contrast weighting, Simpson's Diversity Index (sidi), which measures the diversity of the landscape mosaic in terms of the combination of the number of patches and extent of each patch type, the perimeter-area fractal dimension (pafrac), which provides a global measure of landscape complexity, patch density (pd), which measures the total density of patches in the landscape across all patch types.

For each cover type, we calculated the following class metrics: percentage of the landscape occupied by each cover type (pland), the patch density of each cover type (pd), the largest patch index of each cover type (lpi), which measures the percentage of the landscape occupied by the largest single patch, the correlation length of each cover type (gyrate_am), which measures the degree to which patches of each cover type extend across the study area providing broad connectivity, edge density of each cover type (ed), disjunct core area density (dcad), which measures the density of core areas (defined as internal patch areas more than 500 m from a patch edge), and core percentage of the landscape (cpland, defined as the extent of the landscape occupied by each cover type that is >500 m from a patch edge). Class variables that described non-forest, open canopy forest, and closed canopy forest were designated with 1, 2, and 3, respectively (e.g., ed_3 represented edge density for closed canopy forest, pd_1 represented patch density of non-forest; Table 2).

We contrasted selection for landscape composition or configuration metrics by bats and guilds. Composition metrics quantify the composition of the landscape without reference to spatial attributes and included percentage of the landscape occupied by each cover type (pland) and Simpson's Diversity Index (sidi). All other variables, requiring spatial information for calculation, were characterized as configuration metrics (McGarigal et al. 2013).

Multi-scale analysis

We conducted a multi-scale analysis of landscape structure, calculating each of the FRAGSTATS metrics listed above at a range of focal scales using a moving window analysis (e.g., McGarigal and Cushman 2005), which quantified local landscape structure surrounding each bat capture site in the landscape at a specified scale. This has a major advantage for habitat analysis given that capture rates for bats at a location are likely driven by the habitat conditions surrounding that location, and that different variables may affect capture rates at different spatial scales (e.g., Grand et al. 2004; Wasserman et al. 2012). Accordingly, for each FRAGSTATS metric we calculated focal moving windows at 10 scales ranging from 100 to 1000 m radius, at 100 m increments. These scales offered examination of fine scale habitat use (e.g., foraging, commuting) without our scales overlapping other capture sites.

Univariate scaling

We used logistic regression for species or guilds recorded as presence versus absence and linear regression for those recorded as capture rate. For each combination of response variable and predictor variable we used univariate scaling (e.g., Grand et al. 2004; Wasserman et al. 2012) to identify the best of the 10 calculated scales for each predictor variable. This was accomplished by running 10 univariate regressions for each predictor variable-response variable combination, one at each scale, and identifying the scale that produced the lowest AICc value. Any predictor variable that did not have any scales at which the *P* value of the univariate regression was less than 0.20 were dropped. We used the 0.20 *P* value cut-off for the univariate analysis given that variables that are individually non-significant may interact significantly in multivariate models.

To determine whether selected scales were influenced by size of the bat species (i.e., did we find more relationships at small scales for bats with small mass but at large scales for large bats), we used Spearman correlation (Myers et al. 2010). We compared the percent of variables selected at each of the 10 calculated scales for each species with mean mass of the species in our study area. We used a *P*-value of 0.05.

To determine if there was a significant difference in frequency among scales considered best for each variable, we conducted a linear mixed effects analysis of variance with scale as the independent variable (factor), individual landscape variables as a random factor, and the response variable being count of number of times (across species) that a variable was included at a given scale. Here, our primary interest was in seeing if some scales were selected more than others across all variables. We ran a Tukey HSD test to evaluate significant differences among scales in frequency of selection using the R package multcomp.

To determine whether there were interactions between frequency that given variables were selected and scale of selection we conducted an analysis of variance in which frequency of significant relationship from univariate scaling was the response variable and the predictor was the interaction between variable and scale. Similarly, we used analysis of variance to test whether there was interaction between scale and whether a variable measured class or landscape attributes and whether a variable measured landscape composition or configuration.

Results

Bat capture results

We captured 1537 bats representing 45 species, 29 genera, and 6 families (Table 1). Thirty-six percent of species were infrequently captured (<5 individuals captured) and 4 species represented 57 % of captures (Table 1). We detected sufficient numbers of 20 species captured during 1635 net hours and distributed across our capture sites to evaluate scale dependence of their habitat associations (1412 observations). We restricted all further analyses reported in this paper to those species and guilds (Table 1).

Frequency of variable retention in univariate scaling analyses

The most frequent variables retained in the univariate analysis were class and landscape edge density and patch density (Fig. 2a). Edge density of closed-canopy forest was the most frequently retained variable and was significant at ≥ 1 scale for 71 % of species or guilds analyzed. Landscape patch density, patch density of non-forest and open-canopy forest were the next most frequently retained variables, significant at ≥ 1 scale for 63 % of species or guilds analyzed. The third group of most frequently retained variables was landscape edge density, edge density of non-forest patches, landscape perimeter-area fractal dimension, and patch density of closed-canopy forest, each of which was significant at ≥ 1 scale for 54–58 % of species. Only 1 metric (Simpson's Diversity Index) was never retained in the univariate scaling analysis.

Edge density of closed canopy forest was most frequently positively associated with species or guilds (82 % positive associations; Fig. 2a). Perimeter-area fractal dimension, patch and edge density of open forest, and patch extent of closed canopy forest also tended to be positively associated with occurrence (≥ 75 % of species or guilds with positive associations). Landscape variables edge density and contagion, and class variables patch extent of open canopy forest and percent of landscape in non-forest were negatively associated with 64 % of species or guilds (Fig. 2a).

For gleaning animalivores, 4 of 7 variables retained in univariate analysis included those describing positive associations with closed-canopy forest: edge density, patch extent, percent of landscape, and percent of the landscape comprised by the largest patch (Fig. 2b). Gleaning animalivores were also positively associated with patch density of open-canopy forest and landscape variables for perimeter-area fractal dimension and patch density (Fig. 2b). Negative associations for gleaning animalivores were with non-forest (percent of landscape, percentage of the landscape comprised by the largest patch; Fig. 2c) and some open canopy forest variables (patch extent, percent of landscape, percentage of the landscape comprised by the largest patch; Fig. 2c).

For frugivores, both class and landscape variables were retained in univariate analysis. Those with positive associations included edge and patch density of all cover types, patch extent of closed canopy forest, perimeter-area fractal dimension, and amount of edge in the landscape weighted by degree of contrast between adjacent patches (Fig. 2b). Variables with negative associations included contagion, five measures of open canopy forest (patch extent, percent of landscape, percent of the landscape comprised by the largest patch, percent of the landscape comprised of core area, and number of disjunct core areas) and 2 measures of non-forest (percent of landscape, number of disjunct core areas) (Fig. 2c).

Nectarivores also had both class and landscape variables retained in univariate analysis. Variables with positive associations to capture rate of nectarivores included landscape variables for perimeter-area fractal dimension, patch density, edge density, and amount of edge in the landscape weighted by degree of contrast between adjacent patches (Fig. 2b). Four variables were related to non-forest (edge density, percent of the landscape comprised by the largest patch, patch extent, and percent of landscape); three variables were related to open canopy forest (edge density, percent of the landscape comprised by the largest patch, and patch extent). Only one closed canopy forest variable, patch density, had a positive relationship with nectarivore capture rate (Fig. 2b). Negative associations included three metrics for closed canopy forest (patch extent, percent of landscape, and percent of the landscape comprised by the

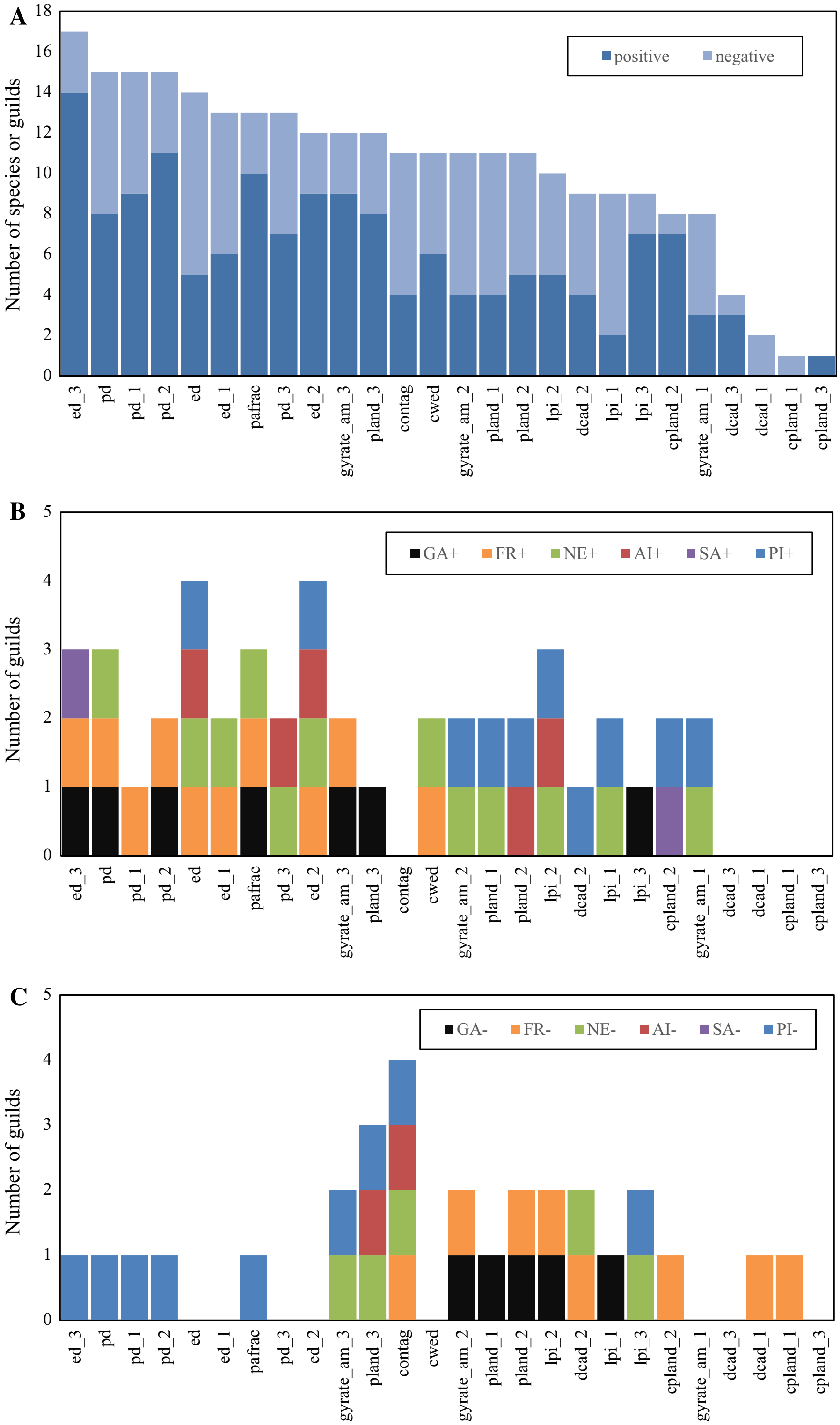


Fig. 2 **a** Number of species and guilds analyzed with significant ($P < 0.2$) univariate regression results for each landscape variable, sorted from highest to lowest and with frequency of positive and negative coefficients for each landscape variable across all species and guild models. Class variables that described non-forest, open canopy forest, and closed canopy forest were designated with 1, 2, and 3, respectively. **b** Guild responses with positive coefficients and **c** negative coefficients. Guilds were gleaning animalivores (GA), frugivores (FR), nectarivores (NE), aerial insectivores (AI), sanguinivore (SA), and piscivore (PI)

largest patch) (Fig. 2c). Nectarivores were also negatively associated with contagion and number of disjunct core areas for open canopy forest (Fig. 2c).

Variables retained in univariate analysis for aerial insectivores included landscape variables edge density (positive relationship; Fig. 2b) and contagion (negative relationship; Fig. 2c). Aerial insectivores were positively associated with variables for open canopy forest including edge density, percent of landscape, and percent of the landscape comprised by the largest patch (Fig. 2b). They were positively associated with patch density of closed canopy forest (Fig. 2b) but negatively associated with percent of the landscape in closed canopy forest (Fig. 2c).

We captured only 1 sanguinivorous species. Both edge density of closed canopy forest and percent of the landscape comprised of core area of open canopy forest were positive associations for this species (Fig. 2b). We also captured only 1 piscivorous species (*Noctilio leporinus*). Both landscape and class variables were retained in univariate analysis for this species. The greater fishing bat was positively associated with edge density (Fig. 2b) and negatively associated with patch density, landscape complexity, and contagion (Fig. 2c). All positive class univariate relationships related to non-forest and open canopy forest (Fig. 2b). Class univariate relationships that were negative were mostly for closed canopy forest although patch density for non-forest and open canopy forest were also negative relationships (Fig. 2c).

Univariate scaling results

There was a significant difference in frequency among scales considered best for each variable (ANOVA, $P < 4.267\text{–}10$). The Tukey HSD shows that across variables, scale 100 was selected statistically significantly more frequently than scales 400–900, but not more than 200, 300, or 1000. Scale 200 was selected significantly more frequently than 400–900, but not more than 100, 200, 300, or 1000. Scale 300 was selected significantly more frequently than 400, 700, or 800, but not more than 100, 200, 300, 500, 600, 900, or 1000. Scale 1000 was selected significantly more frequently than scale 400, 600, 700, 800, or 900, but not more than 100, 200, 300 or 500. Overall, variables were most frequently selected at the broadest scale (1000 m focal radius) with a second mode of relatively high frequency of selection at the finest scales (100, 200, 300 m; Fig. 3a). We found no relationship between size of the bat species and scales selected (Spearman correlation coefficient, Rho $= -0.32$ to 0.44, $n = 20$, $P \geq 0.05$).

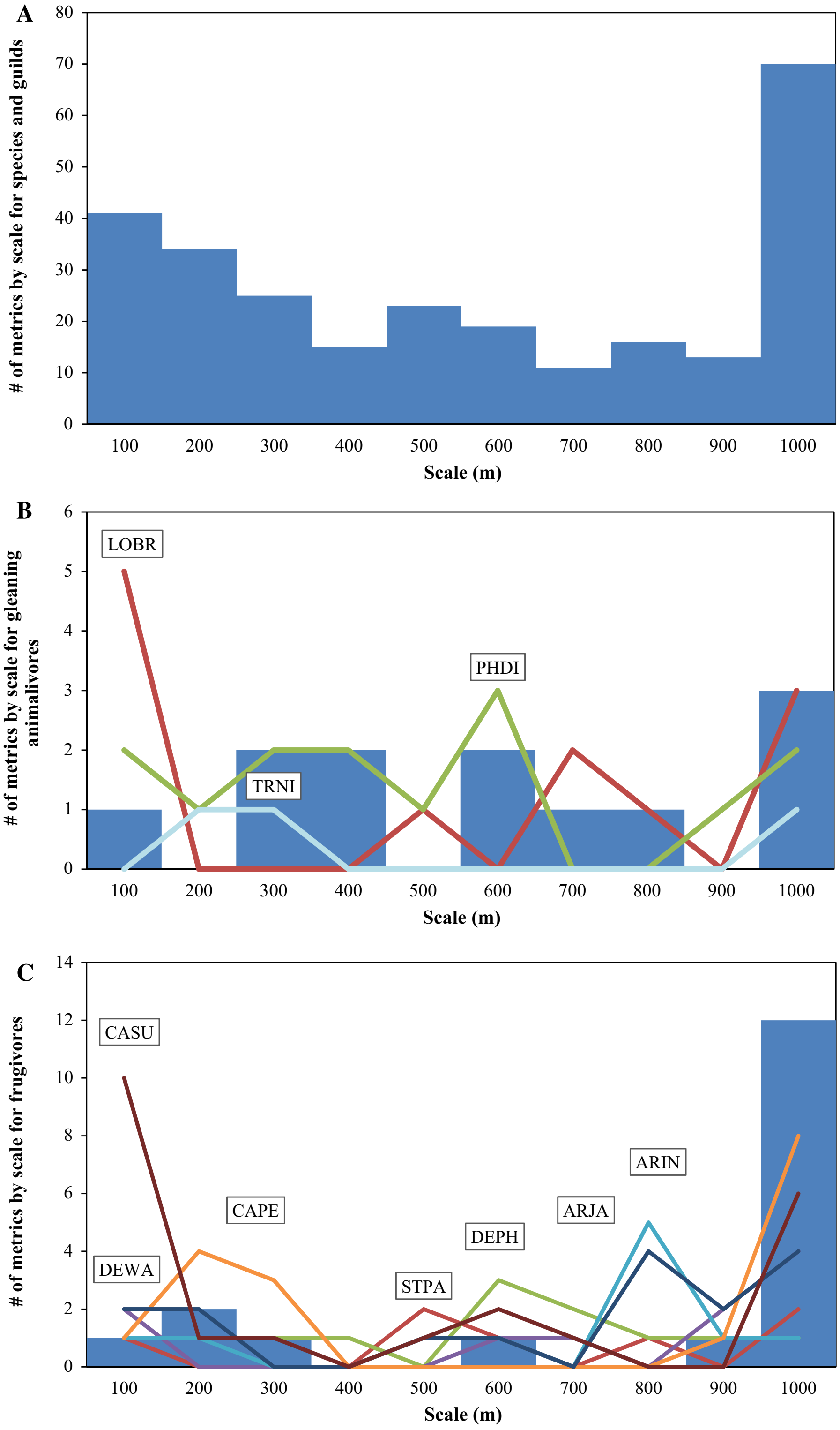
Variables most frequently associated with gleaning animalivores were distributed across all scales (Fig. 3b). Variables for frugivores were dominant at the broadest scale (1000 m) for the group as a whole and for many species regardless of body mass (Fig. 3c). Variables for the nectarivore guild were associated most with the broadest scale (1000 m; Fig. 3d); however both species in this group [GLSO: *Glossaphaga soricina* (10 g) and GLCO: *Glossaphaga commissarisi* (10 g)] had strong selection for fine scales ($\leq$600 m; Fig. 3d). Scales for aerial insectivores were bimodal with most selected at 200 and 300 or 900 and 1000 m (Fig. 3e). Only 2 variables for the sanguinivore were selected; one each at the 200 and 1000 m scale. In contrast, variables for the piscivore were selected at all but the 600 and 700 m scale (Fig. 3f).

There was a marginally significant interaction between variable and scale indicating that some variables were more frequently associated with particular scales across species and guilds (ANOVA $P < 0.142$). Eight variables were most frequently associated with both fine and broad scales (i.e., $\leq$300 and $\geq$800 m focal radius; Fig. 4a). These included class and landscape edge density and patch density. Five variables were most frequently associated with broad scales ($\geq$700 m focal radius; Fig. 4b), which included mostly landscape level measures of habitat heterogeneity.

There was also a marginally significant interaction between scale and whether a variable was important at the class or landscape level (ANOVA $P < 0.065$), indicating that there were differences in the scale at which class and landscape variables were most frequently selected. There were bimodal distributions for both class and landscape variables, with both selected most frequently at fine or broad scales, and less frequently selected at intermediate scales (e.g., 300–700 m). This bimodality was stronger for landscape metrics than for class metrics, which were more frequently selected at intermediate scales (Fig. 5).

There was also a marginally significant interaction between scale at which a variable was selected and whether it measured landscape composition or landscape configuration ($P < 0.072$). Similar to the results above on landscape versus class metrics,

Fig. 3 Number of times each scale was selected as the best scale ($P < 0.2$) in univariate regression analysis across all variables for **a** all species and guilds, **b** gleaning animalivores, **c** frugivores, **d** nectarivores, **e** aerial insectivores, and **f** piscivore. Scales for individual species associated with guilds are depicted by *lines* and *acronyms*



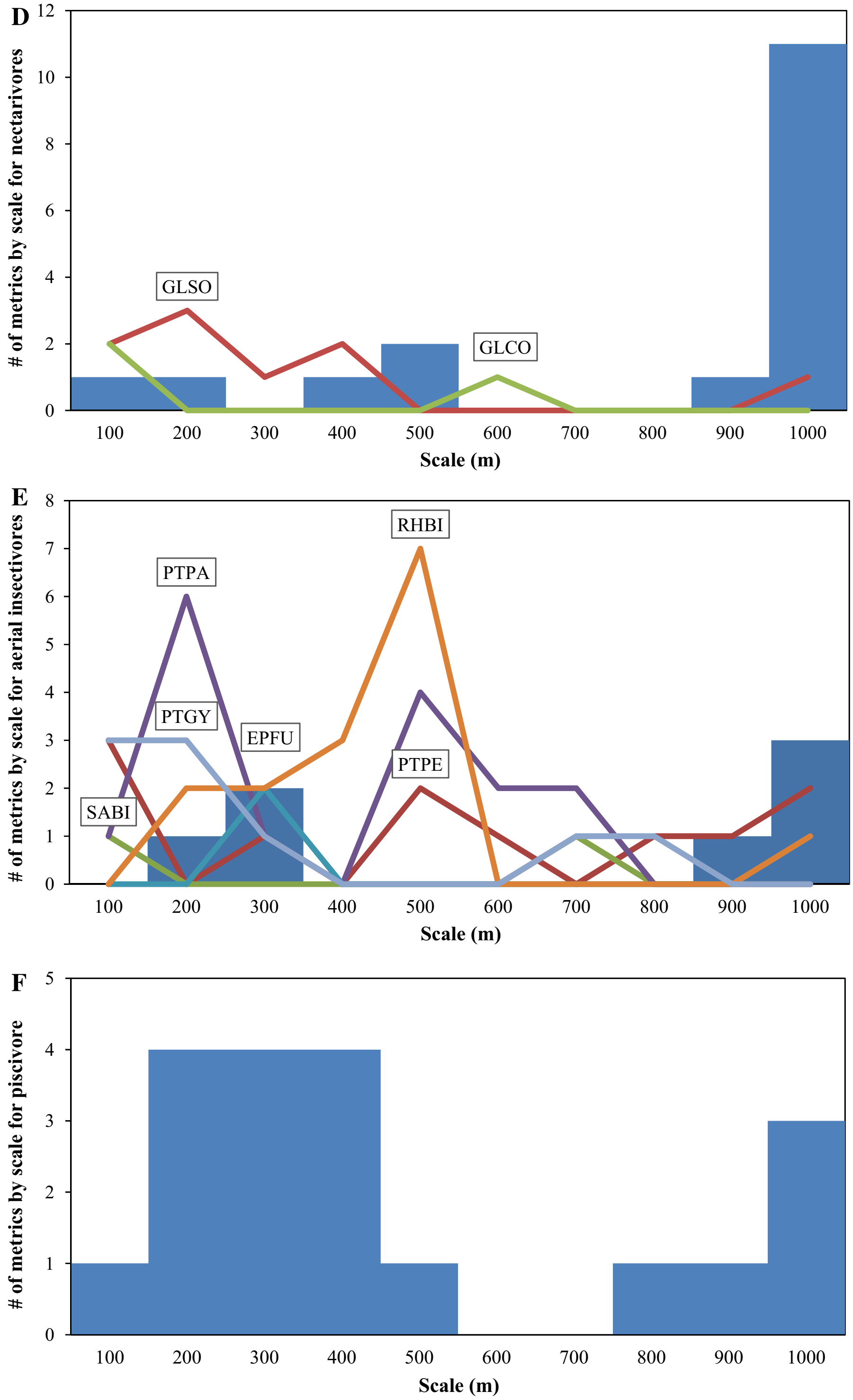
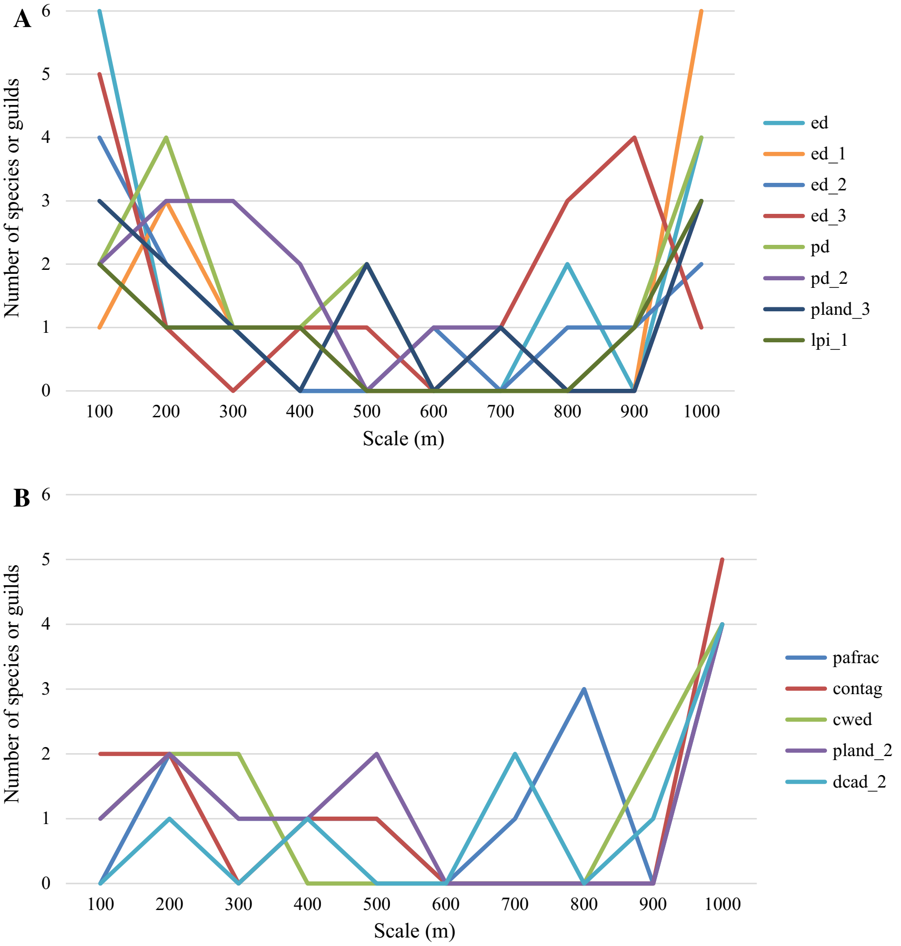


Fig. 3 continued

there was a bimodal pattern of selection for both composition and configuration metrics, with fine and broad scales selected more than intermediate scales (Fig. 6). The bimodal pattern of scale of selection seemed to be stronger for configuration metrics than for composition metrics, which were more

Fig. 4 Frequency of selection for each landscape variable across all 10 scales for variables with **a** a bimodal trend (highest at low and high scales) and **b** selection at highest scale (1000 m). *Acronyms followed by a number* indicate class variables, while *acronyms without numbers* indicate landscape variables. Classes are *1* non-forest, *2* open canopy forest, *3* closed canopy forest



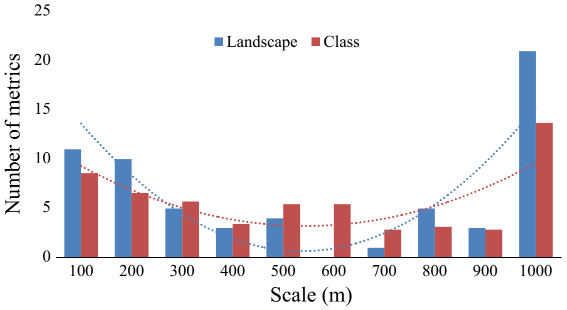


Fig. 5 Frequency of association with each scale as best for species or guilds of bats for class (n = 21) and landscape (n = 6) metrics. *Trend lines* (2 polynomial) indicate selection across scales. Class variables were rescaled to be comparable to landscape level variables (21:6; class variables divided by 3.5)

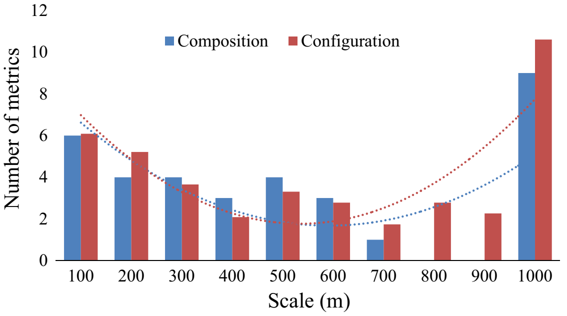


Fig. 6 Frequency of association with each scale as best for species or guilds of bats for landscape composition (n = 23) and landscape configuration (n = 4). *Trend lines* (2 polynomial) indicate selection across scales. Composition variables were rescaled to be comparable to configuration variables (23:4; class variables divided by 5.75)

frequently selected at intermediate scales (300–600 m; Fig. 6).

Discussion

Species habitat relationships are fundamentally scale dependent, and many studies have demonstrated the importance of using approaches that allow explicit optimization of multi-scale habitat relationships (Thompson and McGarigal 2002; Grand et al. 2004; Mateo-Sanchez et al. 2014; Shirk et al. 2014). However, despite the importance of multi-scale optimization of habitat relationships models, only a small fraction of papers on habitat ecology published in recent years have conducted any multi-scale optimization (McGarigal et al. 2016, in press). Most of these assessed multi-scale habitat relationships for terrestrial vertebrates, with only a handful of studies assessing multi-scale habitat relationships in bats (e.g., Gorresen et al. 2005; Klingbeil and Willig 2009; Lacki et al. 2010; Razgour et al. 2011; Akasaka et al. 2012; de Boer et al. 2013). Our results provide some insight into the relative performance of different landscape metrics driving captures of bats in a Central American tropical dry forest.

First, we observed a consistent dominance of configuration metrics associated with patch density and edge density over other metrics in predicting bat capture rates and occurrence across multiple species. The fact that patch density and edge density out performed all other configuration metrics suggests that these simple and intuitive measures of landscape configuration may be of general utility in predicting habitat relationships. This is useful, as many configuration metrics are much more complicated and difficult to interpret (Neel et al. 2004; Cushman et al. 2008). Similarly high performance of patch density and edge density has also been observed in multi-scale analyses of other species, such as American marten (*Martes americana*; e.g., Wasserman et al. 2012; Shirk et al. 2014), and in the prediction of fragmentation effects on gene flow (e.g., Cushman et al. 2013a). Grand et al. (2004) evaluated multi-scale habitat selection for a large number of bird and moth species, and found that patch density, along with mean patch size (not evaluated in our study but directly related to patch density) were the most frequently retained configuration variables (they did not evaluate class level edge density).

In addition, our results showed that composition and configuration metrics were selected similarly [e.g., correlation length of a patch type (gyrate_am) was similar in selection to percentage of the landscape in that patch type (pland)]. Most studies have suggested that habitat area is more influential than habitat fragmentation (e.g., Fahrig 1997), and thus that habitat composition should be more important as a predictor of species occurrence than habitat configuration. This expectation has been found to be true for a wide range of taxa, ranging from moths (Grand et al. 2004), forest breeding birds (Villard et al. 1999; Cushman and McGarigal 2002; Grand et al. 2004), to brown bears (*Ursus arctos*; Mateo-Sanchez et al. 2014). For example, Grand et al. (2004), in a multi-scale optimization study of a large number of bird and moth species found that percentage of the landscape (a composition metric) was by far the most frequently retained variable, and much more frequently retained than configurational alternatives measuring habitat extensiveness (such as correlation length). Despite the high mobility of volant taxa such as bats, our results suggest that landscape configuration may be as important as composition.

Although our bat assemblage represented a taxonomically diverse group with tremendous variation in diets and foraging strategies, most of these species rely on forests for at least one or more key life history functions (e.g., roosts, food; Reid 2009; Medina-Fitoria 2014). Our strongest relationship across species and guilds was a positive one with edge density of closed canopy forest. Many of the species we captured use open canopy or fragmented forests (Wilson et al. 1996; Estrada and Coates-Estrada 2002; Montiel et al. 2006). In our study area, our bat assemblage likely represents species adapted to or tolerating the mixture of small agricultural fields, pastures, and forest patches present. This is similar to observations of high bat species richness in fragmented forests or heterogeneous human-modified landscapes of forest and agricultural systems by Gorresen and Willig (2004) and Montiel et al. (2006) and explains the high number of positive relationships we found with patch density of open canopy forest (pd_1) and our measure of landscape complexity (pafrac) relative to other metrics. However, patches of closed canopy forest remained important to our assemblage. Positive associations between species diversity and landscape habitat diversity have also been reported for forest birds (e.g., Cushman and McGarigal 2003).

Species guilds differed in terms of which landscape metrics were selected. For example, metrics selected for gleaning animalivores suggested that they were sensitive to extent and pattern of closed canopy forest. We noted positive relationships for percent of the landscape, extensiveness, and length of the longest patch of closed canopy forest. The importance of closed canopy forest to gleaning animalivores was also suggested by their negative associations with non-forest and open forest metrics including percent of the landscape, habitat extensiveness, and length of the longest patch. Surprisingly, we noted a positive association with edge density of closed canopy forest and gleaning animalivore occurrence (Medellín et al. 2000; Meyer et al. 2008). Klingbeil and Willig (2009) noted a similar positive relationship. In both studies, many species were positively associated with edge density, thus prey for gleaning animalivores may be more abundant and easier to capture along forest edges.

In contrast, the frugivore guild was positively associated with many open forest and non-forest metrics. Klingbeil and Willig (2009) found negative relationships between frugivores and percent forest cover at three scales (1, 3, and 5 km) and suspected frugivores were responding to higher fruit availability in open areas. Our frugivore guild included species that can travel long distances for fruit and feed in closed canopy forest (e.g., *Artibeus*) or those that feed more locally (e.g., *Carollia*) (Heithaus and Fleming 1978; Klingbeil and Willig 2009) and thus the patchy nature of our study area appeared to have a positive impact on these species.

Similar to frugivores, nectarivores in our study responded positively to many metrics of non-forest or open canopy forest, including extensiveness and length of longest patches, edge density, and percent of the landscape in non-forest. Nectarivores were also positively associated with patch density of closed canopy forest although not extensive patches. Higher overall landscape complexity, combining closed canopy, open canopy, and non-forest, seems to improve habitat quality for nectarivores, as was also noted by Clarke et al. (2005) and Willig et al. (2007).

Aerial insectivores also responded positively to landscape heterogeneity, and were more frequently captured in areas with high patch and edge density of open canopy forest and less abundant in portions of the landscape with extensive closed canopy forest. Estrada-Villegas et al. (2010) found that forest fragmentation did not negatively affect forest-associated aerial insectivores and concluded small forest fragments could be of great conservation value. Our results support this conclusion.

We found only two positive associations for our sanguinivore, the common vampire bat. Our results suggested that these bats are found most frequently in open canopy forest patches that are near closed canopy forest. This species is often associated with altered forest landscapes (logged or farmed) and have been identified as the best single indicator of disturbance associated with domestic livestock (Wilson et al. 1996). Livestock were present throughout much of our landscape at large commercial ranches or small subsistence holdings. In contrast, many of the positive associations for the piscivorous greater fishing bat related to metrics for non- or open canopy forest. These large bats generally roost in hollow trees or caves and forage over water for fish and insects (Hood and Knox Jones 1984). In our study area, many of the larger streams and rivers were close to human developments embedded in a forest matrix. Fishing bats roosted along rivers, often close to or in small towns, explaining their association with open canopy landscapes with little forest cover.

Little is known about how landscape variables relate to species occurrence across scale. An early exploration found that habitat selection for bald eagles (*Haliaeetus leucocephalus*) varied in spatial scale across several orders of magnitude, with variables associated with human disturbance affecting occurrence at broad spatial scales, while micro-habitat features such as perch locations and foraging were selected at fine spatial scales (Thompson and McGarigal 2002). Similarly, Wasserman et al. (2012) found that American marten habitat selection was affected by variables across a range of scales, with marten avoiding landscapes that were fragmented by anthropogenic impacts such as clear-cut logging and road building at broad spatial scales and selecting habitats for foraging at fine spatial scales within unfragmented landscapes. Elliot et al. (2014) found similar patterns of broad scale avoidance by African lions (*Panthera leo*) of anthropogenic risk and fine scale selection of optimal vegetation types. Similarly, Mateo-Sanchez et al. (2014) found brown bears avoided anthropogenic landscape features at broad spatial scales and responded to habitat configuration of natural features at relatively fine spatial scales. Our results indicate that bats in Mesoamerican forest landscapes have complex, multi-scale associations with habitat composition and configuration that cannot be simply described as broad scale avoidance of disturbance and fine scale selection of optimal foraging. Rather, the picture that emerges from our results is that many bat species seem to occur most frequently in landscapes of intermediate heterogeneity and a mixture of closed canopy, open canopy and non-forested habitat types, with differences among guilds in terms of the strength of association with different landscape metrics and the scales at which each is most influential.

Most studies that assessed multi-scale optimization of habitat selection were species-focused, and often found a mixture of fine and coarse scales at which variables maximally influenced habitat selection. Many of these studies found that relatively coarse scales, beyond the extent of the home range of the focal species, were the most influential on patterns of occurrence (e.g., Grand et al. 2004; Wasserman et al. 2012; Mateo-Sanchez et al. 2014; Shirk et al. 2014) and movement (e.g., Elliot et al. 2014; Zeller et al. 2014). Our study evaluated a relatively large number of scales (10), but these were limited to a 1000 m maximum radius to avoid spatial overlap of sampling windows to improve statistical independence of observations. However, given that many past studies have found scales of selection often are larger than the size of home ranges, and the fact that our largest analyzed scale is smaller than the home range of the species with the smallest home range in our study area, it is likely that for many species or guilds stronger relationships may exist at broader scales than we analyzed.

Several researchers have investigated multi-scale habitat selection in bats. For example, de Boer et al. (2013) evaluated the effects of external or ''contextual'' predictors that capture the spatial configuration of the landscape and found that bats responded to landscape composition at scales ranging from 500 m to 32 km, with more land cover variables associated with bat response at the finest two scales evaluated. Similarly, Akasaka et al. (2012) evaluated how changing the grain of spatial analysis of land cover variables affected prediction of bat occurrence and found that for two of three species studied the finest grain of analysis provided the strongest prediction. Klingbeil and Willig (2009) examined responses of species and guilds to landscape structure at three scales (1, 3, 5 km) and found both composition and configuration influenced abundance (for species) or measures of diversity (for guilds). These associations often occurred at all three scales, particularly the largest focal scale (5 km). Gorresen et al. (2005) also used species and guilds to examine responses to landscape characteristics at three scales (1, 3, 5 km) and found most significant responses were at the 5-km scale.

Our results provide some insight into the frequency of different scales being identified as the driving scales in habitat analysis of bat occurrence patterns. We found a clear pattern of highest frequency of variables being identified at the broadest scale (1000 m radius). However, we also observed high frequency of selection at the finest spatial scale analyzed (100 m) with decreasing frequency up to 300 m indicating a bimodal pattern wherein most variables seemed to be selected at broad scales while some were selected at fine scales, and a few selected at intermediate scales. Similar bimodal patterns of scale selection have been observed in carnivores (e.g. Wasserman et al. 2012; Elliot et al. 2014; Shirk et al. 2014), but further research is needed to demonstrate this as a general trend for bats. Our results suggest the possibility that in the Central American tropical dry forest, bats generally respond to broad scale habitat patterns similar to that reported for bats elsewhere (e.g., Gorresen et al. 2005) and proportionally finer scale relative to mobility than most reported results for terrestrial mammals (e.g., Wasserman et al. 2012; Mateo-Sanchez et al. 2014; Shirk et al. 2014).

Although our guilds appeared to vary in frequency of scale selection (i.e., gleaning animalivores across most scales, frugivores dominant at 1000 m scale), we detected no difference in scale selection for guilds or species. Size (i.e., mass) of the species likewise did not affect scale selection. Although size of an animal generally influences its home range and movement (e.g., McNab 1963; Harestad and Bunnel 1979; Tucker et al. 2014), size may not be as strong an influence for highly volant species such as bats (e.g., Corbett et al. 2008; Chambers et al. 2011). Alternatively, the scales we examined may have been well within home ranges of our species and thus did not present difficulty for commuting or foraging. During our study, we observed movements of 220–2610 m for seven radio tagged bats (C Chambers, unpublished data), and others observed home ranges or movements of small to mid-sized bats (e.g., *Glossophaga*, *Carollia*) of 1450 m to 20 ha (Heithaus and Fleming 1978; Gorresen et al. 2005; Albrecht et al. 2007) Although home ranges are not well established for many tropical bat species, Gorresen et al. (2005) found more significant responses to landscape characteristics at larger (5 km) than smaller scales (1, 3 km). Thus we suspect many have home ranges larger than the broadest scale we used.

We believe this is also the first formal effort to explore scales at which different categories of landscape metrics are most associated with species capture rate or occurrence. In our case, landscape metrics, which quantify the structure of the entire multi-class patch mosaic, were most frequently selected at fine or broad spatial scales, while class metrics, which quantify the structure of a particular focal cover class, were more evenly distributed across spatial scales. Simultaneously, we found that metrics measuring landscape configuration tended to be selected at the finest or broadest spatial scales while those measuring landscape composition were selected more evenly across spatial scales. Mateo-Sanchez et al. (2014) found that most landscape composition metrics for brown bears were selected at the two broadest scales, while landscape configuration metrics were selected across a broad range, with most selected at relatively fine scales. Gorresen and Willig (2004) found that overall, landscape composition had greater impact than configuration on bat species abundance and frugivores in particular in a fragmented forest in Paraguay, particularly at the largest scale (5 km). However, landscape configuration had stronger effects on abundance of gleaning animalivores (Klingbeil and Willig 2009). A re-analysis of the results presented by Grand et al. (2004) provides one of the best published comparisons of class and landscape variables across scale for multiple species. Results for birds revealed that the average optimal scale of landscape variables was less than that of class variables, and the average optimal scale of configuration variables was less than composition variables. However, results for moths showed the opposite pattern, with a higher average scale for configuration and landscape variables than for composition and class variables (Grand et al. 2004). In our case most of our composition metrics were class, while our configuration metrics were relatively evenly distributed across class and landscapes. We found a bimodal relationship in both cases, with most variables selected either at fine spatial scales or broad spatial scales, especially for landscape and configuration metrics. One possible explanation of this pattern could be that habitat selection and activity patterns of bats are primarily driven by two levels (sensu Johnson 1980), corresponding to home range (second order) and foraging site (third order). Home range selection probably occurs at scales at or above our largest scale (1000 m) such that variables related to that order of selection would be most influential at the broadest scales we measured. Foraging site selection is probably governed by microhabitat and fine-scale vegetation conditions at scales at or below our finest scale (100 m pixel), such that variables related to that order of selection would be most influential at the finest scales we measured.

Conclusion

This study provides one of the first evaluations of scale dependence of bat habitat selection, and is the first to evaluate patterns of scale relationships among different categories of landscape metrics, including class versus landscape metrics and landscape composition versus landscape configuration metrics. We found that edge density and patch density were the most important variables across bat species. Given that these metrics have also been found to be particularly important in several previous publications on habitat relationships modeling we suggest they may have general utility for habitat modeling studies. With consideration to scale, strongest selection was at the broadest scale for the largest number of variables. Our analysis was constrained to 1000 m because of our study area and capture locations but other studies examined scales to 5000 m. Examining relationships at large scales may yield additional patterns. A second mode of high selection was seen at 100 m scale (finest scale). We suspect these two scales may be related to orders of habitat selection (sensu Johnson 1980) with many variables related to home range scale habitat selection (second order), corresponding to the broadest scales we measured, and others related to foraging site selection (third order), corresponding to the finest scales we measured, with few variables strongly selected at intermediate scales. Landscape and configuration metrics appear to be more strongly bimodal in scale than class and composition metrics, though all were most frequently selected at fine or broad spatial scales. This may vary with guilds and across other ecosystem types; thus further work is needed to evaluate this across replicated studies. Overall, our results provide insight into the scale dependence of the habitat associations of multiple bat species and suggest the possibility that there could be general differences in scale relationships for groups of landscape metrics.

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