



Effects of forest height and vertical complexity on abundance and biodiversity of bats in Amazonia



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ABSTRACT

Anthropogenic activities have accelerated habitat change, loss, and fragmentation, threatening biodiversity over large portions of the tropics. The resulting anthropogenically created landscape mosaics often include forests of different successional stages or that have experienced different levels of anthropogenic use, which affect the physical structure of the forest (e.g., forest height, vertical complexity of vegetation). These physical characteristics of forests may affect the abundance and biodiversity of forest inhabitants, and obscure effects of landscape changes (e.g., percent forest cover) on animal species. Because bats are ecologically diverse and include seed dispersers, pollinators, and top predators, they contribute to the structure and function of forests, and directly affect forest integrity and regeneration. Thus, understanding how variation in the vegetative structure of forests affects the abundance and biodiversity of bats may provide important information to effectively manage and conserve forest fragments. We surveyed bats at 24 sites in the southern Brazilian Amazon, and quantified vegetation structure (density, height, and basal area of trees, density of understory, and canopy openness). Using generalized linear mixed-effects models, we tested simple relationships of each structural characteristic with community- (taxonomic and phylogenetic dimensions of biodiversity), guild-, and population-level attributes of bats. Models for total abundance, taxonomic biodiversity (species diversity and dominance), and phylogenetic diversity were significant, increasing with tree height and basal area, and decreasing with canopy openness. At the population level, abundances of frugivores (*Carollia perspicillata*, *Rhinophylla pumilio*, *Artibeus planirostris*, *A. obscurus*, *A. lituratus*, *Uroderma bilobatum*) and nectarivores (*Lonchopylla thomasi*, *Glossophaga soricina*) were related significantly to vegetation structure. Abundances of some understory frugivores exhibited negative relationships with tree height, choosing younger forests, whereas abundances of canopy frugivores were highest in closed canopy forests. Of the nectarivores, *L. thomasi* was more abundant in older forests (negative relationship with density of trees), whereas *G. soricina* was more abundant in areas with low canopies and low basal area (i.e., earlier successional forest). Consequently, effective management of forest fragments should include consideration of local forest age and vegetation structure, as well as forest connectivity and patch size. In general, protecting areas with large trees and closed canopies enhances the persistence of pollinators and seed dispersers.

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1. Introduction

Fragmentation and loss of natural habitats are the anthropogenic activities that have the greatest negative effects on biological diversity, reducing the abundances of species and increasing

the risk of local extinctions (Laurance et al., 2001). Logging, rearing livestock, and farming, especially in the tropics, have increased habitat loss and fragmentation, thereby threatening biodiversity. In addition to human habitations and areas of active agricultural activities, the complex landscape mosaics typically created by humans include mature forests, secondary forests, and forests in various successional stages (Chazdon et al., 2009; Chazdon, 2014). In addition to landscape-level attributes (e.g., percent forest cover), variation among forest types in physical characteristics (e.g., height, vertical complexity, understory density) can affect animal abundance and diversity (Bradbury et al., 2005; Vierling

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et al., 2008). These responses to forest characteristics may confound attempts to understand effects of landscape composition and configuration, and may be important for informing management and conservation decisions.

The future of tropical biodiversity will depend on the management of large expanses of regenerating secondary forests (Chazdon et al., 2009; Chazdon, 2014), which account for about half of the remaining area of tropical moist forests (Asner et al., 2009). In addition to consideration of the vegetation, effective forest management requires understanding how structural complexity of the vegetation (including primary and secondary forests) provides habitat for the biota (Bradbury et al., 2005; Vierling et al., 2008; Jung et al., 2012), and how it influences the availability of resources (Hayes and Loeb, 2007), exposure to predators (Baxter et al., 2006), and forest microclimates (Chen et al., 1999). In addition, forest structure affects the dispersal of animals (Caras and Korine, 2009), which is especially important for animals that forage within the three-dimensional architecture of forests (i.e., understory, subcanopy, and canopy).

Differences in the heterogeneity of forest canopy are among the main determinants of the diversity of understory plants (Getzin et al., 2012), and of the abundances of many animal species (MacArthur and MacArthur, 1961; Bradbury et al., 2005), including invertebrates (Muller and Brandl, 2009) and vertebrates (Clawges et al., 2008; Muller et al., 2009). For bat assemblages, vegetation “clutter” affects the abundance and species composition of as mediated by aerodynamic characteristics and maneuverability of constituent species (Medellín et al., 2000; Bobrowiec et al., 2014; Rainho et al., 2010; Peters et al., 2006; Meyer and Kalko, 2008; Caras and Korine, 2009). Nonetheless, most studies only use coarse qualitative descriptions of such clutter (e.g., edge, open, structurally complex or simple), rather than direct continuous measurements of vegetation structure and density.

Because forest fragments may have different histories of land use (e.g., timber extraction) and represent different successional or regeneration stages, it is important to identify how the abundance and diversity animals are affected by the physical structure of the vegetation. Bats are an ecologically diverse taxon, representing seed dispersers, pollinators, and top predators. In particular, bats pollinate and disperse the seeds of many early successional and understory plants, thereby influencing the structure and functionality of forests, which significantly affects the composition of local communities of plants and animals (Kunz et al., 2011). Indeed, due to their diversity and ecological importance in tropical ecosystems, bats may be a keystone taxon as well as bioindicators of disturbance, as their responses to environmental variation may reflect the responses of other taxa (Jones et al., 2009). The responses of bats to variation in the structure of forests are particularly relevant as they use different habitats for particular ecological functions (e.g., roosts, foraging; Kunz and Fenton, 2006) and respond to characteristics of vegetative structure in species-specific manners (Medellín et al., 2000; Caras and Korine, 2009). In areas of intensive agricultural activity, decreased density of tree species and modification of the physical structure of the vegetation likely influence the composition of bat communities (Willig et al., 2007) due to habitat degradation (Fenton et al., 1992; Medellín et al., 2000; Estrada and Coates-Estrada, 2002; Clarke et al., 2005) and changes in resource availability (Aguirre et al., 2003; Giannini and Kalko, 2004). In Amazonia, *terra firme* forest represents the dominant natural vegetation type, and the abundance of mammal species in this habitat is much greater than in other plant formations, seemingly due to the high heterogeneity and diversity of plant species (Haugaasen and Peres, 2005).

The agriculture and timber industries intersect along the massive Amazonian frontier known as the “arc of deforestation,” and this southern edge of Amazonia faces the highest deforestation

rates in Brazil (Nogueira et al., 2008; Fearnside et al., 2009). Forest loss, fragmentation, and land use associated with the livestock industry are currently the greatest threats to local biodiversity, reducing the extent of available habitats for many animal species. Bats control many herbivorous insects in tropical forests and agricultural systems (Kalka et al., 2008; Williams-Guillén et al., 2008), as well as act as agents of dispersal and pollination for many plants, especially early successional species. Bat assemblages in well-managed forest patches have great potential to enhance recovery to near predisturbance conditions (Clarke et al., 2005; Bobrowiec and Gribel, 2010). Because of the ecosystem services they provide, the persistence of bat community composition is critical for sustainable management of the landscape (Kunz et al., 2011).

Research that is focused only on taxonomic dimension may create a biased view of biodiversity, as taxonomic biodiversity considers that all species to be equally distinct; consequently patterns are not sensitive to ecological or evolutionary variation among species (Cisneros et al., 2014). Phylogenetic biodiversity measures interspecific differences based on the time since divergence from a common ancestor (Faith, 1992). Thus, simultaneous examination of more than one dimension of biodiversity might provide deeper insights into the potential mechanisms underlying patterns of biodiversity and distribution. Moreover, phylogenetic approaches contribute to the understanding of mechanisms that structure communities in response to environmental variation (Stevens et al., 2012). Indeed, phylogenetic biodiversity may be the most sensitive dimension for environmental gradients of Neotropical bats (Stevens and Gavilanez, 2015).

The aim of this study was to assess how variation in the physical structure of forests affects the abundance, taxonomic biodiversity, and phylogenetic biodiversity of phyllostomid bats and each of two broadly defined foraging guilds (i.e., herbivores and animalivores) in a highly fragmented region of the southern Amazon. We expected that populations of understory frugivores (e.g., *Carollia* spp., *Rhinophylla* spp.) and nectarivores (e.g., *Lonchophylla thomasi*, *Glossophaga soricina*) would be more abundant in forests with a lower canopy, greater tree density, and greater understory clutter, as such physiognomies typically are rich in resources for these taxa (Norberg and Rayner, 1987; Willig et al., 2007; Marciente et al., 2015). In contrast, we expected canopy frugivores (e.g., *Artibeus* spp.) and gleaning animalivores (e.g., *Phyllostomus elongatus*, *Lophostoma silvicolium*) to be more abundant in taller forests with closed canopies and less clutter (Fenton et al., 1992; Clarke et al., 2005; Willig et al., 2007). We expected taxonomic and phylogenetic biodiversity to be greatest in tall, vertically complex forests with relatively low understory clutter. Such forests provide resources and for all guilds of bats and should harbor more species, a more even distribution of individuals, and multiple species from each phyllostomid clade. In contrast, we expect shorter forests with dense understories to be dominated by understory frugivores, which are members of the same clade (i.e., carollines), and to harbor relatively few animalivorous phyllostomines, resulting in low taxonomic and phylogenetic biodiversity.

2. Materials and methods

2.1. Study area

Field work was conducted in the Municipality of Alta Floresta (09°53'S, 56°28'W), in the north of the State of Mato Grosso. The municipality is within the Amazonian Biome and the dominant plant formation is *terra firme* forest. Currently, only 46% of the native vegetation remains in this area, with this municipality being one of the most deforested in Amazonia. The anthropogenic matrix

comprises extensive rural properties devoted to livestock, thus constituting a relatively homogeneous landscape of pasture (Michalski et al., 2008).

We sampled 24 sites from nine forest fragments that range in size from 0.5 km² to 545 km² (Fig. 1). Six sites were in the largest fragment (545.4 km², sites 3, 4, 19–21 in Fig. 1), four sites were in the northernmost large fragment (234 km², sites 15–18 in Fig. 1), two sites were in a medium size fragment (98 km², sites 1–2 in Fig. 1) and each of the remaining six smaller fragments (0.5–5.1 km², sites 5–10, 11–14, 23–24 in Fig. 1) contained two sites each.

We chose these sites to represent the diversity of fragment sizes and variation in landscape configurations that characterize forest in the study area. Due to the hierarchical spatial arrangement, some sites were in the same fragment; this sampling design was incorporated into the generalized linear mixed-effects models used to analyze data.

2.2. Bat surveys

Bats were captured at each site following identical protocols: 12 mist nets (12 × 2.6 m) placed along understory tracks (open trails), opened for six hours per night for 4 nights (288 net-hour/site), resulting in a total effort of 6912 net-hours. For logistical reasons, two sites within a subset (e.g., 19 and 20 or 13 and 14) were always sampled on the same night. All 24 sites were sampled once in a

field survey and 4 surveys were completed; two during each season (Dry, April to July 2013; and Wet, October 2013 to January 2014). During the rainy season, sampling was suspended if heavy rain persisted for ≥2 h; in such cases, surveys were repeated the following night. In case of heavy rain that lasted <2 h, survey time was added to the end of night to ensure that effort was the same at each site during each season (i.e., 144 net-hours).

Species identification followed Lim and Engstrom (2001), Gardner (2007) and Díaz et al. (2011). Species identifications were verified via collection of a reference series deposited in the Coleção de Mamíferos da Universidade de Brasília. Collections and captures were authorized by a permit from ICMBIO (SISBIO 36201-2).

2.3. Community-level characteristics

During each season, we characterized each site with regard to total abundance, taxonomic biodiversity, and phylogenetic biodiversity. Metrics of taxonomic biodiversity included species richness (number of species captured), Berger-Parker dominance, rarity (number of species whose relative abundance was less than 1/S, where S = richness), and Shannon diversity (Berger and Parker, 1970; Faith, 1992). To enable comparisons between assemblages or dimensions, each metric was converted to its effective number of species or Hill number (Jost, 2006). This transformation ensures that higher metric values indicate higher diversity (e.g., high Hill numbers for dominance indicate low dominance). Each metric

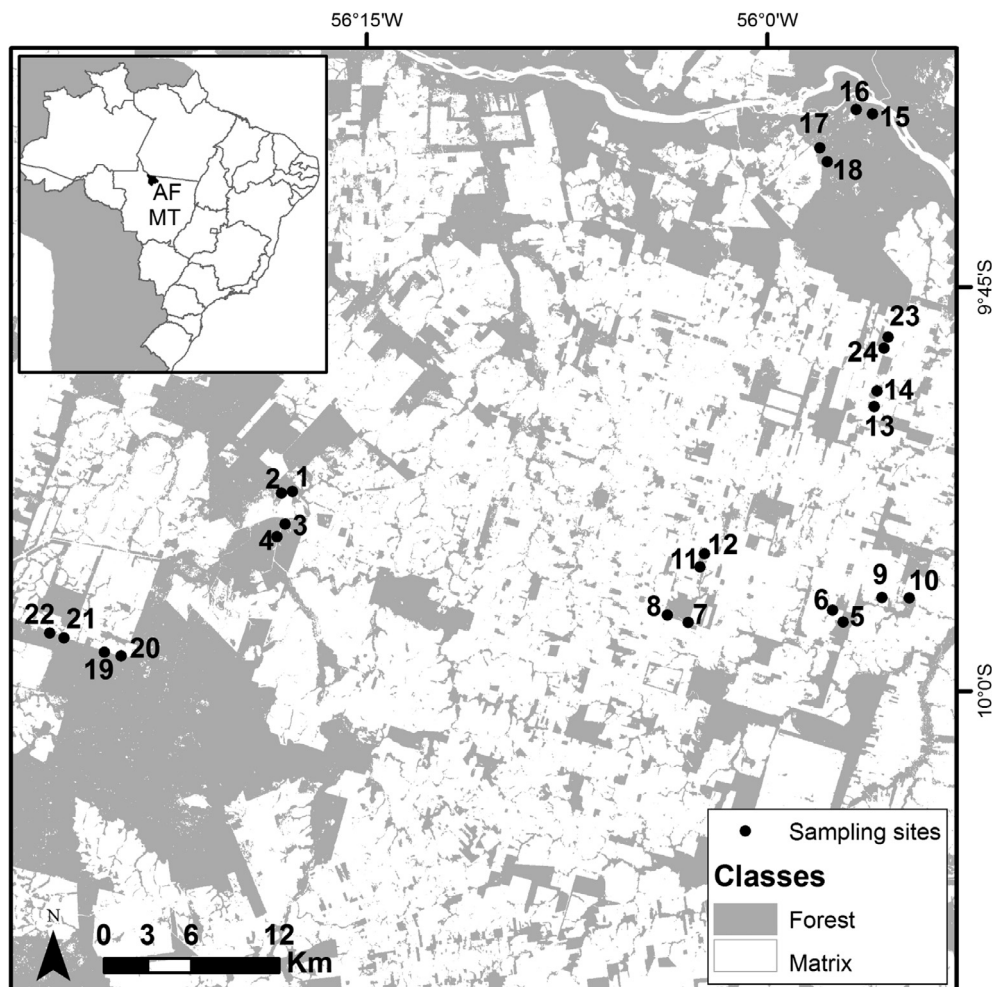


Fig. 1. Classified image of study area indicating the location of the 24 sampling sites (dots). Image in the upper-left corner shows location of the study area in black within Brazil (Municipality of Alta Floresta [AF], State of Mato Grosso).

was calculated for all phyllostomids, and separately for each of two broad foraging guilds, herbivores and animalivores.

Phylogenetic biodiversity reflects evolutionary differences among species based on the time since divergence from a common ancestor (Faith, 1992), thereby reflecting ecological and phenotypic differences that are phylogenetically conserved among species (Cavender-Bares et al., 2009). We assessed phylogenetic biodiversity based on lengths of branches of a bat supertree at the species level (Jones et al., 2005). This tree is one of the most accurate and complete phylogenies for bats. Of the 43 species of phyllostomids from study area, only four were not present in this tree. Missing species were replaced by the nearest congener present in the supertree: *Micronycteris megalotis* for *M. microtis*, *Artibeus aztecus* for *A. gnomus*, *Tonatia bidens* for *T. saurophila*, and *Platyrrhinus helleri* for *P. incarum*. The effects of such replacements are small because the lengths of the branches of congeners are similar. Phylogenetic biodiversity was estimated by Rao's quadratic entropy (Botta-Dukát, 2005), weighted by the abundance of each species.

Eight non-phyllostomid species (*Eptesicus chiriquinus*, *Myotis nigricans*, *Myotis riparius*, *Pteronotus parnellii*, *Cormura brevirostris*, *Saccopteryx canescens*, *Saccopteryx leptura*, *Thyroptera tricolor*) were recorded; these species were not used in analyses because they are not as effectively sampled via mist nets at ground level (Kalko et al., 1996; Kalko and Schnitzler, 1998).

2.4. Guild-Level characteristics

We estimated biodiversity and abundance of bat guilds based on the same suite of metrics used to characterize community-level attributes. Assessments were conducted separately for each of the two species-rich, broadly-defined foraging guilds: herbivores (frugivores and nectarivores) and animalivores (insectivores, carnivores, and sanguinivores).

2.5. Population-Level characteristics

We estimated abundances of species as the cumulative number of unique individuals captured each season at a site. A priori, we restricted analyses to species for which at least 24 individuals (i.e., mean capture per site of at least one individual). Consequently, infrequently captured species were not analyzed at the population level.

2.6. Vegetation structure

The structure of forest vegetation for each site was estimated from four plots (36 m²/6 × 6 m) along a 120 m transect (32 m spacing between plots) based on point-quarter methodologies (i.e., each plot was divided into four quadrants). Spatially, this transect corresponded to the array of 12 10-m nets used to capture bats at a site. Five metrics of vegetation structure were estimated for each site. Basal area was estimated based on the diameter at breast height (DBH) of the focal tree (nearest tree whose diameter exceeded 10 cm) in each quadrant. One focal tree (i.e., the tree closest to the center of the plot) was selected and measured in each quadrant, thus mean basal area and mean tree height was estimated using 16 trees per site. Tree density (td) was calculated from the relationship between sample area and mean distance between focal trees: $td = 10,000/\text{mean}(\text{distance}^2)$, which estimates how trees are "packed" at each site. Understory clutter (from the ground to 3 m) was estimated using a 3-m pole, graduated into 10 cm units. The pole was placed perpendicular to the transect on each side, with the number of units that could be seen representing the absence of vegetative cover. Thus, based on eight transect

points at each site, the percentage of vegetative clutter was calculated by:

$$\text{Clutter} = \left[1 - \left(\frac{nv}{30} \right) \right] \times 100,$$

where *nv* is the number of visible units on the graduated pole. Canopy openness was estimated as the mean proportion of open areas from 16 photos per site, two digital photographs taken with a wide-angle lens at the center of each plot. Each pair of photos was taken at the edges of the plot center line, 6 m apart from each other.

2.7. Statistical analyses

We used generalized linear mixed-effects models and linear mixed-effects models (Crawley, 2007; see Chapter 19, Mixed-Effects Models; *glmer* and *lmer*, R Development Core Team, 2013) to quantify relationships of each metric of biodiversity (i.e., population-, guild-, and community-level characteristics) with metrics of forest structure. Mixed-effects models were used to remove the random effect of the blocks (paired sites at the 3 km and 7 km spatial scales) on metrics of biodiversity (Crawley, 2007). These random factors also helped correct for possible overdispersion in the data (Harrison, 2014). For each metric of biodiversity, we evaluated simple univariate relationships with respect to canopy height, canopy openness, tree density, tree basal area, and understory clutter, as well as multivariate relationships with respect to all five structural characteristics in a single model (Table 1). Analyses found no evidence of multicollinearity for these five vegetative structure variables.

We conducted omnibus statistical analyses to (1) identify which aspects of bat biodiversity were related to the suite of habit characteristics (global model), and (2) determine the identity of the habitat characteristics that likely contributed to overall significance. More specifically, we executed multivariate regressions (global model) to identify response variables (i.e., abundance, diversity metric) that were significantly related to vegetation characteristics. If the global model was significant, we subsequently executed univariate analyses to identify vegetation characteristics that likely contributed to the significance of the respective multivariate models.

Each metric of forest structure was standardized (*scale*, Z-Score) prior to analysis to ensure that all were scaled equivalently. We used function *prcomp* in R to conduct a principal components analysis (PCA) on forest structure variables to visualize variation among sites. Response variables evinced different error term distributions, and thus different distribution families were used in *glmer* and *lmer* analysis (*lme4* package, Bates et al., 2015; R Development Core Team, 2013). For example, count data had a Poisson distribution (all abundances, richness, and rarity); dominance and phylogenetic diversity had a Gamma distribution (link identity); and taxonomic diversity had a Gaussian distribution. Significance was evaluated by comparing each univariate model to a null model via an Analysis of Variance (*anova*, ANOVA), whereas the coefficient of determination (R^2) was computed via ordinary least squares regression, performed by function *r.squaredGLMM* (Nakagawa and Schielzeth's, 2013). Finally, lack of fit for each significant model was explored via visual inspection of trends in residuals (errors associated with homogeneity of variance, independence, and normality).

3. Results

In total, 1683 phyllostomid bats representing 43 species were collected at the 24 sites in study area (Supplemental Tables S1, S3). Site richness ranged from 8 to 21 species (mean ± SD;

Table 1

Multivariate and univariate relationships of metrics of biodiversity with five forest structural characteristics. Y is the dependent variable. Independent variables are “Height” (mean tree height), “Canopy” (canopy openness), “Density” (tree density), “Basal Area” (mean tree basal area), and “Understory” (understory clutter).

Models
<i>Multivariate model/Global model</i>
Y ~ Height + Canopy + Density + Basal Area + Understory
<i>Univariate models/Simple models</i>
Y ~ Density
Y ~ Height
Y ~ Basal area
Y ~ Understory
Y ~ Canopy

15 ± 4), and site abundance ranged from 22 to 154 individuals (mean ± SD; 71 ± 35, [Supplemental Table S1](#)).

Sites differed greatly in forest structure ([Fig. 2](#), [Supplemental Table S2](#)), providing insight into their history of disturbance. Older and less disturbed forests are characterized by taller and larger trees ([Steininger, 2000](#); [Peña-Claros, 2003](#)), thus tree height and tree basal area indicate the age of forests. Higher values of understory clutter and canopy openness indicate forests with more recent anthropogenic modification. PCA extracted three PCs, accounting for 75% of the total variation in the vegetation data. More specifically, PC1, PC2, and PC3 accounted for 30%, 23%, and 22% of the total variation, respectively. In general, sites represented continua with respect to two independent axes: from high basal area with closed canopies (lower right quadrant, [Fig. 2](#)) to low basal area with open canopies (upper left quadrant), and from tall trees with high understory clutter (upper right quadrant) to

shorter trees with less understory clutter (lower left quadrant). Fragments with tall trees and understory clutter represent areas of recent or active tree extraction, whereas areas with shorter trees and little understory clutter represent forests in which the secondary forest is old enough to effectively shade out understory vegetation (<3 m from the ground). Importantly, these forests are subjected to continual anthropogenic activities, with disturbances occurring at different frequencies, intensities, extents and temporal intervals.

3.1. Community level

At the community level, total abundance, species dominance, species diversity, and phylogenetic diversity ([Supplemental Table S3](#)) were related to forest structure, whereas species richness and species rarity were not ([Table 2](#)). Canopy openness was the only forest characteristic that exhibited a consistent negative effect on biodiversity. Taxonomic and phylogenetic biodiversity increased with average basal area of the trees, and decreased with average canopy openness. Moreover, phylogenetic biodiversity increased with tree height. Total abundance increased with basal area, but decreased with canopy openness. Dominance increased with tree height and basal area and decreased with canopy openness.

3.2. Guild-Level

Herbivores and animalivores were more abundant in forests with larger trees (higher basal areas) and more closed canopies (lower canopy openness), and each had greater phylogenetic biodi-

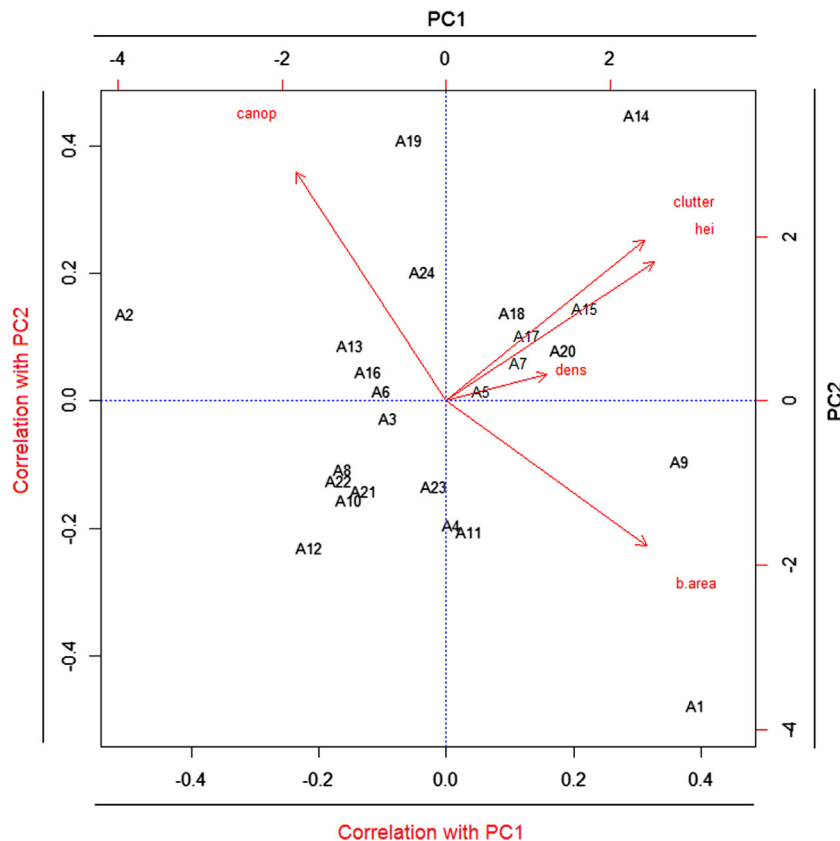


Fig. 2. Principal Components Analysis of forest structure at 24 sites in southern Amazonia, Brazil. Site numbers correspond to those in [Fig. 1](#) and [Supplemental Table S2](#). Correlations of the metrics of forest structure (i.e., “b.area”, mean tree basal area; “canop”, canopy openness; “clutter”, understory clutter; “dens”, tree density, and “hei”, mean tree height) with PC1 and PC2 (bottom and left axes, respectively). PC1 and PC2 scores for each site are indicated by top and right axis labels, respectively.

Table 2
Models representing relationships (R^2 and p -values) between phyllostomid biodiversity and forest structural characteristics. R^2 values were adjusted for the number of independent variables in significant models (bold text). Negative association are indicated parenthetically. NA (not applicable) indicates univariate models that were not tested because the global model was not significant. Independent variables are “Height” (mean tree height), “Canopy” (canopy openness), “Density” (tree density), “Basal Area” (mean tree basal area), and “Understory” (understory clutter). Types of models are: glmer/P, generalized mixed model with Poisson error term; lmm, linear mixed model with Gaussian error term; and glmer/G, generalized mixed model with Gamma error term with link identity.

Models Model type	Richness glmer/P	Abundance glmer/P	Dominance glmer/G	Rarity glmer/P	Taxonomic Diversity lmm	Phylogenetic Diversity glmer/G
Global model	0.12 (0.9)	0.13 (0.001)	0.73 (0.002)	0.4 (0.9)	0.78 (0.003)	0.91 (0.001)
Y ~ Density	NA	0.10 (0.903)	0.26 (0.77)	NA	0.27 (0.41)	0.54 (0.42)
Y ~ Height	NA	0.16 (0.56)	0.54 (0.01)	NA	0.49 (0.04)	0.68 (0.02)
Y ~ Basal Area	NA	0.21 (0.0004)	0.42 (0.03)	NA	0.40 (0.19)	0.57 (0.01)
Y ~ Understory	NA	0.17 (0.60)	0.22 (0.41)	NA	0.15 (0.40)	0.52 (0.5)
Y ~ Canopy	NA	0.20(-) (0.0001)	0.35(-) (0.049)	NA	0.38(-) (0.04)	0.51(-) (0.01)

versity in forests with high basal areas and taller trees (Table 3). Nonetheless, responses to forest structure differed between guilds: (1) herbivore dominance responded positively to the height of the trees, whereas animalivore dominance increased with basal area and decreased with canopy openness; (2) taxonomic diversity of animalivores was positively affected by understory clutter and basal area of trees, whereas taxonomic diversity of herbivores was not affected by any characteristic of forest structure; (3) phylogenetic biodiversity of herbivores decreased with canopy openness, whereas phylogenetic biodiversity of animalivores was not affected by this forest characteristic.

3.3. Population level

Abundances of eight of the 14 most common bat species (i.e., *Carollia perspicillata*, *Rhinophylla pumilio*, *Artibeus planirostris*, *A. obscurus*, *A. lituratus*, *Lonchophylla thomasi*, *Glossophaga soricina* and *Uroderma bilobatum*) were related significantly to one or more metric of forest structure (Table 4). Generally, responses were species-specific.

Abundances of *C. perspicillata* were lower in forests with higher trees, whereas those of *R. pumilio* were higher in habitats with containing trees with greater basal area. Some canopy frugivores were associated with closed canopy forests (e.g., *A. planirostris*, *A. lituratus*), whereas others were associated with less understory clutter

(e.g., *A. obscurus*). The nectarivore, *L. thomasi*, had greater abundances in forests with lower tree density, whereas abundances of *G. soricina* were lower in forests with greater tree height, tree basal area and density of trees. The two common species of animalivore, *Phyllostomus elongatus* and *Lophostoma silvicolium*, were not affected by forest structure.

4. Discussion

Bat abundance and diversity often are affected by the structure of forest vegetation (Bradbury et al., 2005; Jung and Kalko, 2011; Marciente et al., 2015). Abundance-based descriptors of community structure typically are more variable than those based on incidence and could better resolve underlying environmental gradients of community organization (Stevens and Gavilanez, 2015). In Alta Floresta, bat taxonomic and phylogenetic biodiversity were greater in forests with larger trees and closed canopies. Tree height and basal area reflected the age of forests (e.g., Steininger, 2000; Peña-Claros, 2003), and older forests have greater vertical complexity and more varied niche opportunities for bats, enhancing in greater taxonomic and phylogenetic biodiversity. The negative influence of the canopy openness on phylogenetic biodiversity (Tables 2 and 3) likely reflects the fact that many closely related species are highly abundant in forests with open canopies (e.g., *Carollia* spp., *Rhinophylla* spp.). Bat composition is

Table 3
Models representing relationships (adjusted R^2 and p -values) between bat biodiversity for two broadly defined foraging guilds, herbivores (H) and animalivores (A), and forest structural characteristics. Significant p -values (<0.05) are in bold. NA (not applicable) indicates univariate models that were not tested because the global model was not significant. Independent variables are “Height” (mean tree height), “Canopy” (canopy openness), “Density” (tree density), “Basal Area” (mean tree basal area), and “Understory” (understory clutter). Negative associations are indicated parenthetically. Types of models are: glmer/P, generalized mixed model with Poisson error term; lmm, linear mixed model with Gaussian error term; and glmer/G, generalized mixed model with Gamma error term with link identity.

Models Model type Feeding Guild	Richness		Abundance		Dominance		Rarity		Taxonomic diversity		Phylogenetic diversity	
	glmer/P		glmer/P		glmer/G		glmer/P		lmm		glmer/G	
	H	A	H	A	H	A	H	A	H	A	H	A
Global model	0.05 (0.97)	0.20 (0.32)	0.11 (0.01)	0.5 (0.0008)	0.68 (0.009)	0.3 (0.06)	0.28 (0.9)	0.37 (0.14)	0.64 (0.09)	0.47 (0.002)	0.84 (0.0005)	0.4 (0.04)
Y ~ Density	NA	NA	0.10 (0.89)	0.004 (0.67)	0.38 (0.81)	NA	NA	NA	NA	0.004 (0.75)	0.54 (0.32)	0.0001 (0.95)
Y ~ Height	NA	NA	0.16 (0.13)	0.04 (0.19)	0.53 (0.04)	NA	NA	NA	NA	0.13 (0.06)	0.71 (0.03)	0.15 (0.03)
Y ~ Basal Area	NA	NA	0.43 (0.01)	0.14 (0.003)	0.46 (0.08)	NA	NA	NA	NA	0.34 (0.001)	0.63 (0.03)	0.21 (0.01)
Y ~ Understory	NA	NA	0.18 (0.63)	0.03 (0.2)	0.34 (0.52)	NA	NA	NA	NA	0.013 (0.56)	0.52 (0.87)	0.045 (0.31)
Y ~ Canopy	NA	NA	0.41 (-) (0.005)	0.28 (-) (0.005)	0.41 (0.08)	NA	NA	NA	NA	0.13 (0.06)	0.59(-) (0.04)	0.04 (0.31)

Table 4

Significant results (adjusted R^2 and p-values in parenthesis) of GLMM models (Poisson distribution) for relationships between abundances of each common bat species and metrics of forest structure. Significant p-values (<0.05) are in bold. NA (not applicable) indicates univariate models that were not tested because the global model was not significant. Independent variables are "Height" (mean tree height), "Canopy" (canopy openness), "Density" (tree density), "Basal Area" (mean tree basal area), and "Understory" (understory clutter). Negative associations are indicated parenthetically.

Dominant guilds	Herbivores										Animalivores			
	Understory frugivores				Canopy frugivores						Nectarivores		Insectivores	
Fine classification	Cp	Cb	Rp	Rf	Ap	Ao	Al	Dc	Pi	Ub	Lt	Gs	Pe	Ls
Models/ Species	Cp	Cb	Rp	Rf	Ap	Ao	Al	Dc	Pi	Ub	Lt	Gs	Pe	Ls
Global model	0.43 (0.0002)	0.08 (0.67)	0.79 (0.049)	0.69 (0.1)	0.22 (9e-05)	0.77 (0.004)	0.53 (0.0009)	0.31 (0.47)	0.31 (0.2)	0.78 (0.045)	0.65 (0.22)	0.56 (0.01)	0.34 (0.54)	0.41 (0.15)
Y ~ Density	0.34 (0.38)	NA	0.70 (0.72)	NA	0.001 (0.38)	0.48 (0.16)	0.16 (0.042)	NA	NA	0.56 (0.63)	NA	0.12 (0.03)	NA	NA
Y ~ Height	0.48(-) (0.01)	NA	0.70 (0.50)	NA	0.008 (0.91)	0.49 (0.17)	NS	NA	NA	0.58 (0.46)	NA	0.44(-) (0.003)	NA	NA
Y ~ Basal Area	0.37 (0.92)	NA	0.76 (0.01)	NA	0.05 (0.01)	0.53 (0.08)	0.07 (0.03)	NA	NA	0.67 (0.19)	NA	0.39(-) (0.01)	NA	NA
Y ~ Understory	0.33 (0.09)	NA	0.68 (0.40)	NA	0.044 (0.052)	0.57(-) (0.002)	NS	NA	NA	0.68 (0.07)	NA	0.18 (0.07)	NA	NA
Y ~ Canopy	0.30 (0.77)	NA	0.76 (0.06)	NA	0.14(-) (0.001)	0.45 (0.79)	0.18(-) (0.002)	NA	NA	0.66 (0.10)	NA	0.21 (0.13)	NA	NA

Carollia perspicillata (Cp), *Rhinophylla pumilio* (Rp), *Artibeus planirostris* (Ap), *Carollia brevicauda* (Cb), *Artibeus obscurus* (Ao), *Artibeus lituratus* (Al), *Phyllostomus elongatus* (Pe), *Lophostoma silvicolum* (Ls), *Dermanura cinerea* (Dc), *Lonchophylla thomasi* (Lt), *Glossophaga soricina* (Gs), *Plathirrhynchus incarum* (Pi), *Uroderma bilobatum* (Ub), *Rhinophylla fischeriae* (Rf).

strongly influenced by structural characteristics of the forest, as bat species differ in abilities to avoid physical obstruction while flying (Neuweiler, 1989; Schnitzler and Kalko, 2001), and because forest structure can affect the availability and abundance of particular resources on which bats forage.

Response variables insensitive to the distribution of species abundances (i.e., species richness and rarity) did not respond to any aspect of forest structure; this was unexpected as ground-vegetation clutter has been shown to decrease species and guild richness elsewhere in lowland Amazonia (Marciente et al., 2015). Perhaps responses differed because *terra firme* forest in the southern edge of the Amazon is generally shorter and more degraded than its counterpart in northern Amazonia (Nogueira et al., 2008). In contrast, total bat abundance and abundance-weighted diversity metrics (both taxonomic and phylogenetic) were higher in habitats with mature undisturbed forest. These responses likely are caused by greater forest structural complexity, which provides a greater abundance and diversity of roosting habitats (Barclay and Kurta, 2007) as well as dietary resources for bats (Haddad et al., 2009).

Taxonomic biodiversity of herbivores based on dominance was higher in areas with greater tree height (n.b., after transformation to Hill number, high values mean low dominance for the Berger-Parker metric), which may be due to the larger number of productive niches that can support abundant populations. Taxonomic biodiversity of animalivores based on dominance and Shannon diversity were greater at sites containing trees with greater basal area that provide an abundance and diversity of roosts and microhabitats (large trunks, loose bark, holes and crevices, and termite nests) for gleaning animalivores.

Species-specific population-level responses to vegetation structure probably are linked to diet and foraging strategy. Canopy and understory frugivores differ in diet (Cosson et al., 1999; Fleming, 1986; Rex et al., 2011), resulting in differences in habitat use. Canopy frugivores (e.g., *A. planirostris*, *A. lituratus*) were more abundant in forests with closed canopies, the forest stratum in which they forage. Abundance of another canopy species (e.g., *A. obscurus*) was closely associated with less cluttered understory, which likely represents a similar response, as forests with closed canopies generally have less dense understory vegetation. Moreover, *A. obscurus* exhibits considerable niche overlap with other large species of *Artibeus* (Gardner, 2007).

Understory frugivores consume fruit from shrubs and small trees. Unsurprisingly, the abundance of *C. perspicillata* evinced a

negative relationship with mean tree height, preferring younger forests that probably have greater understory clutter and greater abundance and diversity of the fruits on which they forage. In contrast, the other common carolline, *R. pumilio*, was more abundant in forests with large trees, indicating that as an understory consumer, *R. pumilio* may prefer more mature forests with closed canopies. However, documented responses of *R. pumilio* to habitat loss and degradation are highly variable. In the central Amazon, *R. pumilio* was abundant in early secondary forest, but avoided open areas of abandoned pastures (Bobrowiec and Gribel, 2010). In contrast, in the Peruvian Amazon, *R. pumilio* was more abundant in areas cleared for small scale subsistence farming than in secondary or primary forests (Willig et al., 2007). It is unclear what may cause this variation in responses by *R. pumilio*; likely candidates include the spatial scale of disturbance, the types of land use in disturbed areas, or changes in resource availability that affect the strength of competitive interactions with closely related and functionally similar species.

Abundances of animalivore species (*P. elongatus* and *L. silvicola*) did not exhibit any consistent response to variation the forest structure. This may be due to their great maneuverability, which enables them to effectively forage or disperse through many kinds of forest environment (e.g., dense, open, altered, or preserved; Norberg and Rayner, 1987; Denzinger and Schnitzler, 2013). Alternatively, the degraded nature of forest patches and surrounding landscapes may result in low abundances of gleaning animalivores regardless of the vegetation structure of the forest fragment. Indeed, gleaning animalivores are highly sensitive to forest degradation, as they are absent from or occur at low abundance in secondary regrowth forests (Fenton et al., 1992; Brosset et al., 1996; Medellín et al., 2000; Faria et al., 2006; Castro-Luna et al., 2007a, b; Willig et al., 2007; Pardini et al., 2009; Bobrowiec and Gribel, 2010; de la Peña-Cuéllar et al., 2012).

4.1. Management implications

The future of tropical biodiversity will critically depend on effective management of large expanses of regenerating secondary forests (Chazdon et al., 2009; Chazdon, 2014). As logging of primary forests continues, secondary forests will constitute an ever increasing proportion of forested habitat in tropical landscapes (Chazdon, 2014). Furthermore, improved ecological understanding of faunal responses to land-use change will be of little use to soci-

ety if it is not translated into effective management practices that ensure long-term conservation and maintenance of critical ecosystem services (Meyer et al., 2016).

Because of the ecosystem services they provide, the responses of bat populations, guilds, and communities to forest structure have important consequences to conservation, management, and policy. Our results demonstrate that all forests do not have the same value to bats, and that vertical complexity of the forest must be considered to ensure effective ecosystem management and persistence of vital ecosystem services (e.g., insect pest management, seed dispersal, pollination) in Amazonian forests.

In general, older forests with larger trees and closed canopies (Steininger, 2000; Peña-Claros, 2003) harbor more diverse and abundant bat faunas (e.g., Fenton et al., 1992; Kalko et al., 1996; Cosson et al., 1999; Faria et al., 2006; Castro-Luna et al., 2007a,b; Estrada and Coates-Estrada, 2002; Willig et al., 2007; Jung et al., 2012; Table 2). Consequently, these bat communities likely provide more ecosystem services and harbor more functional redundancy associated with each ecosystem service compared to communities in younger successional forests. Indeed, bat assemblages in well-managed forests that have suitable source pools may return to pre-disturbance levels of abundance and diversity (Clarke et al., 2005).

To preserve source populations of forest flora and fauna, as well as to protect key ecosystem services such as seed dispersal and pollination provided by insects, birds, and bats, managers should protect forests with large trees and intact canopies (Kunz et al., 2011). This is particularly important for animalivorous bats (e.g., *Lophosoma* spp., *Micronycteris* spp., *Trachops cirrhosus*), which are known for their susceptibility to forest degradation, and will require large tracts of mature forest to maintain viable populations in fragmented landscapes with extensive patches of human-dominated land uses. Maintenance of such mature, closed canopy forests may provide benefits to agricultural endeavors in the landscape via provision of biological pest control as mediated by animalivorous components of the bat fauna.

5. Conclusions

The study area occurs in a highly fragmented region that is dominated by pastures maintained for livestock. Nonetheless, extant fragments, many of which represent degraded forest due to timber extraction, harbor a great diversity of bats (51 species representing 5 families captured during the study). Because much of the matrix habitat does not provide resources (e.g., roosts, habitat safe from predators, food) for bats, areas of secondary forest surrounding forest fragments are important for maintaining local populations and for enhancing connectivity among fragments for many faunal groups. In addition, forest fragments in this region are not part of current conservation efforts, making them susceptible to future conversion to pasture or cultivation. Loss of these fragments will likely lead to local extinction of many species and the contraction of geographic ranges. Moreover, the extensive loss of habitat in Alta Floresta suggests that an extinction debt may already exist in these forests. Reduction in the amount of suitable habitat increases the risk of stochastic extinction for relatively isolated populations, and the isolation of habitat patches reduces the likelihood that rescue effects can sustain local populations (Kuussaari et al., 2009). Importantly, the vagility of bats may result in a particularly long time lag for extinction at the regional scale, especially for populations of forest specialists. Nonetheless, many of the metapopulations of forest-specialists may eventually suffer extinction if the current low levels of forest cover and connectivity persist or become further reduced in the region (Hanski and Ovskainen, 2002).

All forests do not provide the same value to different faunal groups. The relationships between bat biodiversity at multiple levels and the physical structure of the forest should inform management decisions about forest restoration. The preservation of older fragments with tall trees and closed canopy is crucial for the management of regional biotas as they serve as source populations for secondary and regenerating forests. Restoration of massive tracts of Amazonia to tall, closed canopy forest is unlikely in the foreseeable future. Consequently, management to support a mosaic of secondary forest types in the landscape in proximity to closed canopy forest patches can help to ensure the persistence of keystone pollinators, seed dispersers, and arthropod consumers. Moreover, the conservation of these species may reduce risks to the integrity of ecosystem processes.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.02.039>.

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