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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.

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 landcape 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 silvicolum*) 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., carolliines), 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