Landscape composition is more important than landscape configuration for phyllostomid bat assemblages in a fragmented biodiversity hotspot

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ARTICLE INFO

ABSTRACT

Human-modified landscapes are composed of different types of land covers in differing proportions (landscape composition), and each with differing spatial physiognomy (landscape configuration). Unfortunately, the information on the relative impact of these two components of landscape structure on biological assemblages is scarce, but urgently needed to improve conservation strategies. We assessed the relative influence of the composition (landscape forest cover and matrix composition) and configuration (degree of forest fragmentation and forest edge density) of 100-ha and 500-ha landscapes on the abundance, diversity, and evenness of phyllostomid bat assemblages in the Lacandona rainforest, Mexico. We assessed the complete bat assemblage and frugivorous bats separately, and we grouped frugivores into understory foragers and canopy foragers. Landscape forest cover was the main predictor of the complete bat assemblage, positively affecting species diversity, particularly the number of rare species. Thus, community evenness decreased in landscapes with higher forest cover. Although weaker, species diversity was positively related to fragmentation and negatively associated with edge density. Landscape composition also was relatively more important than configuration for frugivores. The number of common and dominant frugivorous species and the abundance of understory frugivores increased in landscapes with lower forest cover and dominated by secondary forests in the matrix. The abundance of canopy frugivores showed the opposite response. Thus, to preserve bat assemblages and their important functional roles, conservation initiatives should prioritize a reduction in deforestation and the increase of secondary forests in the matrix. Maintaining all remaining forest patches is needed to favor landscape complementation and supplementation dynamics.

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1. Introduction

Tropical forests are being rapidly and extensively lost worldwide, leading to the expansion of human-modified tropical landscapes (Melo et al., 2013). These landscapes can differ in the types and percentages of land cover patches (landscape composition), each showing different spatial arrangements (landscape configuration) (Dunning et al., 1992). Although both composition and configuration variables are known to affect the persistence of species in fragmented landscapes (Fahrig et al., 2011), some species respond more strongly to spatial composition variables, such as forest loss (Fahrig, 2003; Ávila-Cabadilla et al., 2012; Sánchez-de-Jesús et al., 2015), and others seem to be affected by both spatial composition and configuration variables (e.g. forest loss and fragmentation; Bolivar-Cimé et al., 2013; Carrara et al., 2015). Thus, additional studies on the topic are required to identify the landscape spatial attributes that contribute in maintaining species diversity in fragmented landscapes.

Among landscape composition variables, forest loss is considered the main threat to biodiversity (Fahrig, 2003, 2013), particularly impacting many forest-dependent species (e.g. bats: Ávila-Cabadilla et al., 2012; Ávila-Gómez et al., 2015; terrestrial mammals: Garmendia et al., 2013; birds: Carrara et al., 2015; dung beetles: Sánchez-de-Jesús et al., 2015). Forest loss not only reduces resource availability for forest-dependent species (e.g. Bolivar-Cimé et al., 2013), but it also leads to increasing inter-patch isolation distances (Fahrig, 2003, 2013), thus limiting the interchange of species and individuals between forest patches (Hanski, 1999). Furthermore, forest loss results in smaller forest patches (Fahrig, 2003) with higher edge effects (Ewers and Didham, 2006), within which the persistence of populations and communities may be limited (e.g. Hanski, 1999). All these threats may be, however, attenuated when the contrast between the forest and the adjacent matrix is relatively low (Harper et al., 2005; Santos-Filho et al., 2012), such as when the matrix is dominated by secondary forests and arboreal crops (Mesquita et al., 1999). Secondary forests can support resources and refuge for many forest-dependent species (e.g. Arroyo-Rodríguez et al., 2015). Thus, the composition of the matrix can be of key relevance for species persistence in fragmented landscapes (Ewers and Didham, 2006; Franklin and Lindenmayer, 2009).

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Regarding landscape configuration variables, the degree of forest fragmentation (here referred to as the number of forest patches in the landscape) and forest edge density have variable effects on biodiversity, including negative, positive, and neutral effects (reviewed by Fahrig, 2003; Ewers and Didham, 2006). For instance, forest fragmentation results in smaller forest patches and higher forest edge (Fahrig, 2003), and these two attributes of configuration can negatively affect biodiversity in human-modified tropical landscapes (e.g. Ewers and Didham, 2006). Forest edge density is also determined by the shape of the remaining forest patches in the landscape (Laurance and Yensen, 1991). Thus, edge effects will be higher in landscapes with higher forest edge density (Harper et al., 2005; Ewers and Didham, 2006). Yet, forest fragmentation and edge density can also have positive effects on many species, particularly on those that are able to persist in small patches, undertake long-distance dispersal movements, and make use of resources present in forest edges and the surrounding matrix (Fahrig, 2003; Ewers and Didham, 2006; Ethier and Fahrig, 2011). In fact, patches with more complex shapes may be colonized more frequently than patches with compact shapes (Ewers and Didham, 2006), and the proliferation of highly productive pioneer plant species in forest edges may contribute to an increase in resource availability for fruit-eating animals in landscapes with a higher degree of fragmentation and a higher edge density (Ethier and Fahrig, 2011). Forest fragmentation can also increase the number of subpopulations across the landscape, thus enhancing metapopulation dynamics and persistence (Fahrig, 2003). Unfortunately, because most fragmentation studies have been focused on assessing the impact of patch size and isolation (Fahrig, 2003), our knowledge on the relative impact of landscape composition and configuration variables is very limited. Such knowledge is urgently needed to improve management and conservation strategies (Fahrig et al., 2011).

We assessed the relative influence of landscape composition and configuration on phyllostomid bat assemblages in the fragmented Lacandona rainforest, Mexico. Neotropical phyllostomid bats are an appropriate model group to test this question, as they are a rich family, with more than 140 species (Wetterer et al., 2000), and are considered a good indicator of habitat modifications (Medellín et al., 2000; Castro-Luna et al., 2007). Yet, the available information on the impact of landscape structure on these vertebrates shows variable effects depending on the species, region and spatial scale of analyses. For example, positive (Gorresen and Willig, 2004; Ávila-Gómez et al., 2015) and negative (Klingbeil and Willig, 2009; Bolivar-Cimé et al., 2013; Ávila-Gómez et al., 2015) effects of landscape forest cover on the abundance and richness of tropical bat assemblages have been reported (reviewed by García-Morales et al., 2013). Ethier and Fahrig (2011) also found that the effects of forest loss differ among species, whereas forest fragmentation per se (i.e. independent of the amount of forest) has a consistent positive effect on all bat species in a temperate forest in Ontario, Canada. Bolivar-Cimé et al. (2013) also found that forest fragmentation and forest edge density are positively related to the abundance of frugivorous bats in a fragmented semi-deciduous tropical forest in the Yucatan Peninsula, Mexico. Yet, Ávila-Cabadilla et al. (2012) in a semi-deciduous tropical forest in Jalisco, Mexico, demonstrate that the abundance of frugivorous bats is positively and more strongly associated with the percentage of riparian forest in the landscape than to several configurational variables. Thus, we are still far from being able to draw general conclusions about the impact of landscape composition and configuration on bat assemblages, especially considering that these related aspects need to be analyzed in a way that allows their differing effects to be separated (Fahrig et al., 2011).

Here we aimed at determining the relative effects of landscape composition (i.e. percentage of old-growth forest cover in the landscape, and percentage of secondary forest in the matrix) and landscape configuration (i.e. degree of forest fragmentation and forest edge density) on the diversity, abundance and evenness of bat assemblages, considering both the complete phyllostomid assemblage and frugivorous bats

separately. Because species responses to landscape structure can be scale dependent (e.g. Klingbeil and Willig, 2009; Arroyo-Rodríguez et al., 2013; Ávila-Gómez et al., 2015), we measured the landscape metrics at two spatial scales, i.e. within 100-ha and 500-ha landscapes. Based on previous findings with bats (Klingbeil and Willig, 2009, 2010; Ávila-Cabadilla et al., 2012) and other organisms (Smith et al., 2011; Carrara et al., 2015; Sánchez-de-Jesús et al., 2015), we expected that forest loss would be relatively more important than its spatial configuration in shaping bat assemblages. In particular, landscape forest cover would be positively related to species diversity, but negatively related to community evenness, as rare species, such as many animalivorous bats, usually depend on large tracts of old-growth forest to forage (e.g. Gorresen and Willig, 2004). The abundance of large canopy frugivorous bats would also increase with forest cover (Giannini and Kalko, 2004; Muscarella and Fleming, 2007). Yet, because small understory frugivorous bats can use resources from the matrix, particularly in secondary forests and forest edges (de la Peña-Cuéllar et al., 2012; Hernández-Montero et al., 2015), we predicted that the abundance of small frugivorous bats will increase in landscapes with a higher percentage of secondary forests in the matrix, with a higher degree of fragmentation, and with a higher forest edge density (also see Ethier and Fahrig, 2011; Bolivar-Cimé et al., 2013).

2. Materials and methods

2.1. Study area

We conducted the study in the Lacandona rainforest, a region located in the southern part of Chiapas, Mexico (100–1500 m.a.s.l.; Appendix Fig. A1). This region is considered a priority area for biodiversity conservation as it preserves the largest Mexican tropical rainforest (13,000 km^2). This rainforest has been, however, strongly deforested during the last 40 years, principally for the expansion of cattle ranching and agricultural lands. This process has been particularly extensive in the Marqués de Comillas region (MCR), which is located in the southeastern border of the Montes Azules Biosphere Reserve (MABR; Fig. A1). Annual precipitation averages 2500–3500 mm, and average monthly temperatures vary between 24 and 26 °C. We studied two adjacent lowland areas (100–200 m.a.s.l.): the continuous forest of MABR and the fragmented forest of MCR (Fig. A1). Both areas show similar weather and soil conditions, and hence, we avoided potential confounding factors related to altitude, weather and soil.

2.2. Study landscapes and explanatory variables

We adopted a patch–landscape approach (sensu Mcgarigal and Cushman, 2002), i.e. response variables (bat diversity and abundance) were evaluated within old-growth forest patches (forest patches hereafter) and landscape variables were measured within a specified radius from the center of these patches. Specifically, we sampled 15 sites: 12 forest patches (3 to 92 ha) in MCR separated from each other by at least 2 km, and three reference areas (100-ha each) within the continuous forest of MABR, separated from each other by at least 4 km and located at least 1 km from the MABR edge (Fig. A1). Using recent (March 2011) SPOT 5 satellite images and the "region growing" algorithm in GIS SPRING (Câmara et al., 1996), we made a supervised classification considering six land cover types: old-growth forests, secondary forests, shrub crops (i.e. corn, chili and bean plantations), arboreal crops (i.e. palm and rubber plantations), cattle pastures, and human settlements (overall classification accuracy was 77%). We then characterized the composition and configuration of the landscapes surrounding each site (i.e. forest patches and reference areas) at two spatial scales: within a 100-ha buffer (564 m radius) and within a 500-ha buffer (1262 m radius) from the center of each sampling site (100 and 500-ha landscapes, hereafter) using GIS GRASS (GRASS, 2011). We selected these buffer sizes because they are each large enough to include the home range of