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Functional recovery of Amazonian bat assemblages following secondary forest succession

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ABSTRACT

Regenerating forests occupy large areas in the tropics, mostly as a result of deforestation for livestock and agriculture, followed by land abandonment. Despite the importance of regenerating secondary forests for tropical biodiversity conservation, studies of temporal effects of matrix regeneration on species responses in fragmented landscapes are scarce. Here, we used an Amazonian whole-ecosystem fragmentation experiment to investigate how changes in matrix quality over time through secondary forest regeneration affect bat assemblages from a functional perspective. We found that forest regeneration in the matrix positively affected functional α diversity, as well as species- and community-level functional uniqueness, reflecting an increase of species that perform different ecological functions in secondary forest over time. According to functional trait composition, animalivorous species showed the clearest signs of recovery associated with matrix regeneration. Consequently, between-period differences in functional β-diversity were highest in secondary forest compared to fragments and continuous forest, determined mainly by trait gains. However, ~30 years of secondary forest regeneration were not sufficient for the functional recovery of bat assemblages to levels observed in continuous forest. Restoring degraded habitats while protecting primary forest will be an important strategy for safeguarding high functional diversity of bats and their vital contributions to ecosystem functioning in fragmented tropical landscapes.

1. Introduction

Despite increased forest loss and fragmentation over the last decades (Haddad et al., 2015), vast abandoned areas in the tropics are undergoing regeneration due to secondary forest succession. As a result, secondary forests are now often the predominant forest type in many tropical fragmented landscapes (Chazdon et al., 2009; Arroyo-Rodriguez et al., 2017). In the Brazilian Amazon, approximately 21% of ~720,000 km^2 of deforested land is under forest regrowth (Almeida et al., 2016). A secondary forest matrix in fragmented landscapes may function as a buffer to the pervasive negative consequences of edge effects, expanding the effective area of fragments, facilitating the movement of species between forest patches and providing suitable habitat for numerous species, including many primary forest-interior specialists (e.g. Antongiovanni and Metzger, 2005; Kupfer et al., 2006; Lindenmayer et al., 2008; Franklin and Lindenmayer, 2009; Stouffer et al., 2011; Driscoll et al., 2013). On the other hand, in systems with more pronounced patch-matrix contrast, environmental conditions can act as a strong filter allowing only a narrow spectrum of species and functional traits to persist (e.g. Meyer et al., 2008; Newbold et al., 2013; Lindenmayer et al., 2015; Wordley et al., 2017). Promoting secondary forest regeneration and protection may effectively reduce fragment-matrix contrast and maintain overall functional trait diversity of animal assemblages, and hence ecosystem functioning (Kupfer et al., 2006; Farneda et al., 2015; Sayer et al., 2017). Thus, the consequences of fragmentation for biodiversity can be better understood when the vegetation dynamics in the matrix are considered in experimental design.

Functional diversity summarizes the variation in trait values of an

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organism that potentially affects its performance, fitness and ecological function within a community (Violle et al., 2007). Incorporating a temporal functional dimension into the study of fragmentation effects can advance our understanding of ecosystem functioning and help devise more effective conservation plans (Cadotte et al., 2011; Mouillot et al., 2013). However, the only study exploring temporal changes in functional diversity of animal assemblages comes from birds in a fragmented temperate landscape in Australia, reporting a decline over time in bird functional diversity in the interiors of woodland patches embedded in a matrix dominated by exotic pine plantations (Lindenmayer et al., 2015). For tropical ecosystems, the present study is the first to quantify the temporal dynamics of fragmentation effects from a functional perspective and to evaluate how functional trait responses are mediated by matrix regeneration over time. Bats are a promising group for studying responses to landscape fragmentation because they display a high diversity of ecological roles in tropical communities, acting as important seed dispersers, key pollinators, prey and predators (Kunz et al., 2011). Moreover, they are a group for which the effects of landscape change on the functional dimension of biodiversity remain little explored (Cisneros et al., 2015; Meyer et al., 2016; Wordley et al., 2017).

Surveys conducted between 1996 and 2002 by Sampaio (2000) and Bobrowiec and Gribel (2010) documented rapid spatial turnover of phyllostomid bat species at the Biological Dynamics of Forest Fragments Project (BDFFP) in the Central Brazilian Amazon. This turnover was mainly explained by the disappearance of primary forest-interior species following deforestation, and an increase of opportunistic shrub-frugivores in the secondary forest matrix that are able to exploit the forest regrowth that surrounded forest fragments. Using this extensive data set as a baseline, unique for this region of the Amazon, here we evaluate how matrix regeneration over time affects bat assemblages from a functional perspective in continuous primary forest, primary forest fragments, and secondary forest matrix ~15 years after the studies by Sampaio (2000) and Bobrowiec and Gribel (2010). Control sites in continuous forest sampled in both periods allow us to unveil whether an observed temporal change in functional diversity of bat assemblages in fragments was in fact a result of matrix regeneration or whether it is due to natural temporal variability of bat populations.

Our general hypothesis was that functional recovery of bat assemblages would occur in fragments and matrix sites with secondary forest succession through the addition of different species' functional traits. We anticipated that this increase in functional trait diversity in secondary forest would in part come about by frugivorous bats responding positively to the higher abundance of fruits of successional plant species, whereas gleaning animalivorous bats would increase as the successional stage of secondary forest progresses due to increased availability of roosts and food, such as arthropods and small vertebrates. We predicted that, between periods, (1) functional and taxonomic α diversity and community-level functional uniqueness (sensu Ricotta et al., 2016) would increase in fragments and matrix sites, (2) species-level functional uniqueness would increase in fragments and matrix sites, (3) functional trait composition in fragments and matrix sites would shift to mirror more closely that of continuous forest, and (4) differences in functional β-diversity in fragments and matrix sites are determined mainly by the replacement of functional traits and only to a limited extent by the gain of traits.

2. Material and methods

2.1. Study area

Fieldwork was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located ~80 km north of Manaus (2°25′S, 59°50′W), Central Amazon, Brazil (Fig. 1). The area is characterized by a mosaic of unflooded (*terra firme*) Amazonian rainforest, primary forest fragments (1, 10 and 100 ha), and secondary forest (~8325 ha). Annual rainfall varies from 1900 to 3500 mm, with a dry season between June and October (Laurance et al., 2017). The topography is relatively flat (80–160 m elevation), intersected by small streams. The primary forest canopy is ca. 23 m tall, with occasional emergent trees reaching 55 m (Gascon and Bierregaard Jr., 2001). In the early 1980s, 11 fragments were isolated from continuous forest by distances of 80–650 m. Following abandonment of the cattle ranches, secondary regrowth developed around the fragments, which were periodically re-isolated by clearance of a 100 m-wide strip of vegetation around them (Rocha et al., 2017a). This 100 m distance from the fragment edge represents the interface between younger and older secondary forest, which together make up the inter-fragment matrix in our study landscape. The matrix is composed of secondary forest dominated mainly by *Cecropia* spp. (areas that were cleared without fire) and *Vismia* spp. (areas that were cleared and burned) (Mesquita et al., 2001). The most recent re-isolation prior to this study occurred between 1999 and 2001 (Rocha et al., 2017a).

2.2. Bat sampling

The impacts of fragmentation on the bat fauna at the BDFFP were first assessed by Sampaio (2000) who sampled six continuous forest sites and six forest fragments (three of 1 ha and three of 10 ha) between January 1996 and June 1999. In addition, between October 2001 and November 2002, Bobrowiec and Gribel (2010) sampled bats at seven sites in the secondary forest matrix. That is, both studies were conducted ~15 years after fragment creation in the early 1980s (Fig. 1). Using identical methods as those employed by Sampaio (2000), Sampaio et al. (2003) and Bobrowiec and Gribel (2010), we resurveyed the same 19 sites between August 2011 and June 2013, i.e. ~30 years after initial forest clearance.

In both periods, bats were sampled with ground-level mist nets (12 × 2.5 m) placed along trails in the interior of continuous forest and fragments (for each habitat: period 1 = 18 to 24 nets, period 2 = 14 nets), and erected 100 m from one of the borders of each fragment in the matrix (period 1 = 8 nets, period 2 = 7 nets). The nets were opened from dusk until 6 h later, and checked at intervals of ~25 min. Bias in capture rates due to net-shyness (Marques et al., 2013) was avoided by spacing visits to the same site by three to four weeks, and sampling was interrupted during heavy rains. Total sampling effort during both periods was 28,959 mist-net hours (mnh), whereby 1 mnh equals one 12-m net open for 1 h (continuous forest: period 1 = 8757 mnh, period 2 = 4009 mnh; forest fragments: period 1 = 9429 mnh, period 2 = 3963 mnh; secondary forest: period 1 = 860 mnh, period 2 = 1941 mnh).

We restricted our analyses to phyllostomids and the mormoopid *Pteronotus parnellii*, which can be sampled adequately with mist nets (Kalko et al., 1996). Same-site recaptures were excluded. Canopy net data obtained in the interiors of the continuous forest sites and fragments in both periods were used merely for assigning species to a particular forest stratum ('vertical stratification' trait, see below), and were not included in the analyses. We analyzed 1 and 10 ha fragment interiors jointly because they did not differ significantly in species richness (see Rocha et al., 2017b). We also considered secondary forest as a single habitat due to small sample size for *Cecropia*- (three sites) and *Vismia*-dominated regrowth (four), and because none of the most common bat species differed significantly in abundance between these habitats (see Bobrowiec and Gribel, 2010). A total of 6109 bats of 46 species were used in the analysis. Bat sampling was conducted under ICMBio permit (26877-2) and followed the ethical guidelines approved by the Animal Care and Use Committee of the American Society of Mammalogists (Sikes, 2016).

2.3. Species functional traits

We used five functional traits that reflect diet and foraging