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The Road to Functional Recovery: Temporal Effects of Matrix Regeneration on Amazonian Bats

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Abstract

Across the tropics, vast deforested areas are undergoing forest regeneration due to land abandonment. Although secondary forest is an expanding type of landscape matrix that has been shown to buffer some of the negative consequences of forest loss and fragmentation on taxonomic diversity, little is known in this regard about the functional dimension of biodiversity. We took advantage of an ecosystem-wide fragmentation experiment to investigate longer term changes in functional diversity of a mega-diverse Amazonian bat assemblage associated with regrowth development in the matrix. We found that matrix regeneration affected several facets of bat functional diversity in secondary forest over time, increasing functional α diversity, species- and community-level functional uniqueness, altering functional trait composition, and resulting in functional β-diversity changes via trait gains. However, approximately 30 years of matrix regeneration were insufficient for functional diversity to recover to the same levels as in continuous forest. Our results suggest that a combination of natural, human-assisted, and active restoration is likely to be the most successful strategy for restoring functional biodiversity of bats in human-modified tropical landscapes, a finding that most likely also applies to many other taxa.

Keywords

Chiroptera, habitat fragmentation, habitat restoration, functional diversity, second growth

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Many fragmentation studies are hampered by the fact that they typically only provide a brief snapshot in time as most research is carried out in the form of short-term projects. In contrast to the evaluation of species responses to the spatial aspects of fragmentation (variation in habitat composition and configuration), which has received considerable attention in the conservation literature (Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013), the temporal dynamics of the effects of matrix regeneration on animal assemblages remain little explored (but see e.g., Lindenmayer et al., 2015; Rocha et al., 2018; Stouffer, Johnson, Bierregaard, & Lovejoy, 2011). However, the incorporation of a temporal perspective in the study of fragmentation impacts on wildlife species is crucial for a comprehensive understanding of the

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biodiversity changes associated with fragment-matrix dynamics and for implementing effective conservation measures.

Although woody vegetation change in Latin America and the Caribbean between 2001 and 2010 was dominated by deforestation (approximately 541,835 km^2), roughly two thirds of the land subsequently underwent forest regeneration (Aide et al., 2013). Secondary forests represent an expanding, low-contrast type of landscape matrix and act as important reservoirs of tropical biodiversity and an important source of ecosystem functions and services in fragmented landscapes (Chazdon, 2014). In countryside ecosystems, the matrix often includes agricultural land and secondary vegetation, offering resources which many patch-dependent species might use (Mendenhall, Kappel, & Ehrlich, 2013).

At the Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon, the world's largest and longest-running experimental study of habitat fragmentation (Laurance et al., 2018), an inventory of the bat fauna was first conducted by Sampaio (2000) approximately 15 years after fragment creation in the early 1980s. She sampled bats in forest fragments and control plots in continuous forest, while a few years later, Bobrowiec and Gribel (2010) documented bat assemblages associated with the then early-stage secondary forest matrix. Recent resampling of the same sites approximately 30 years after the initial forest clearance offered unique insights into how changes in matrix quality and composition alter response patterns of bats in this fragmented landscape across both the taxonomic (Rocha et al., 2018) and functional biodiversity dimension (Farneda et al., 2018).

Since the cessation of livestock activities at the BDFFP, the pastures have gradually turned into secondary regrowth, which has markedly lessened the effects of fragmentation on primary forest specialist bats (Rocha et al., 2018). Similar results have been found for understory birds (Stouffer et al., 2011) and dung beetles (Quintero & Roslin, 2005) at the BDFFP. Using a recent methodological framework for quantifying various facets of bat functional diversity (Ricotta et al., 2016), we found that temporal changes in functional diversity were stronger in the secondary forest matrix than in primary forest fragments and continuous primary forest. The addition over time of species that perform different ecological functions increased functional α diversity, species- and community-level functional uniqueness, altered functional trait composition, and resulted in functional β-diversity changes via trait gains that were most prominent in secondary forest (Farneda et al., 2018). Fragmentation-sensitive species, such as some animalivorous bats, benefited from

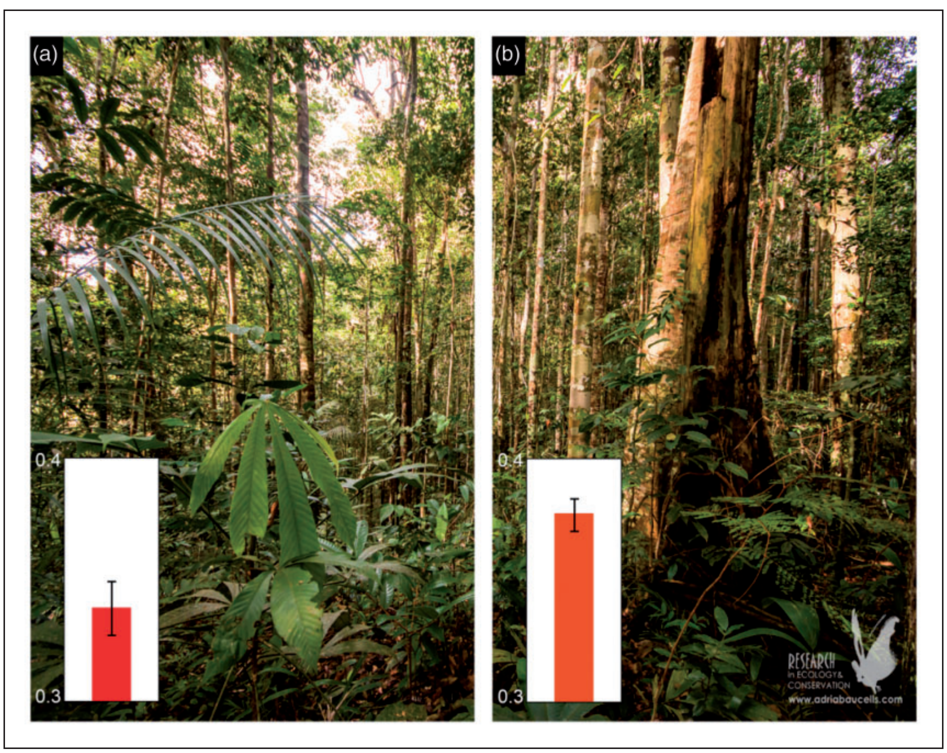

Figure 1. Differences in forest physiognomy and structure between (a) late-stage secondary forest (approximately 30 years of regeneration) and (b) continuous primary forest at the Biological Dynamics of Forest Fragments Project, Brazil. Values in each bar plot represent mean ± 95% confidence intervals of functional α diversity (Rao's index *Q*).

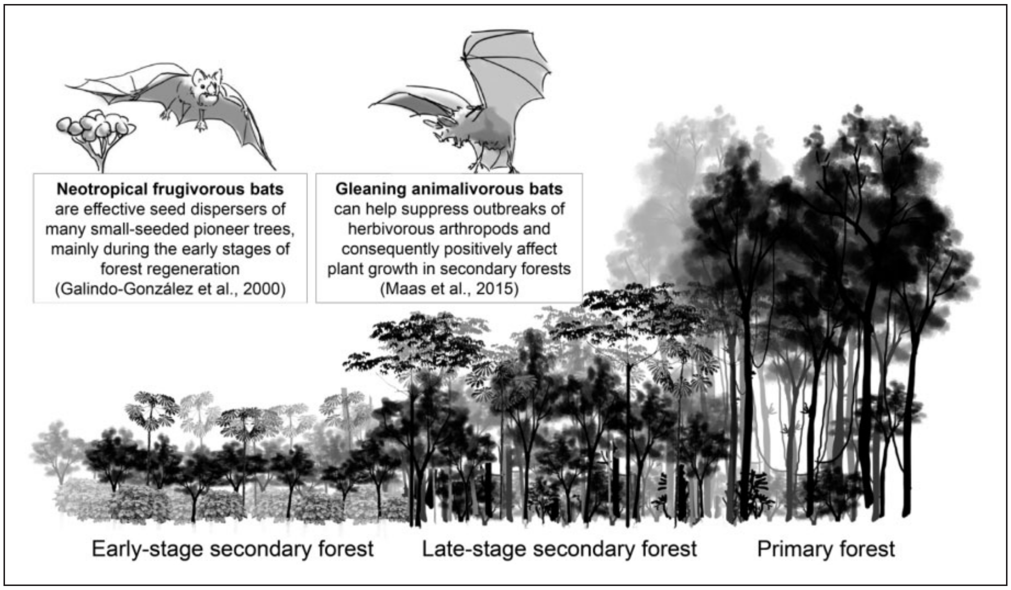

Figure 2. Ways by which Neotropical frugivorous and gleaning animalivorous bats contribute to natural secondary forest regeneration.

matrix regeneration. However, even though approximately 30 years of secondary forest regeneration have alleviated the negative impacts of fragmentation, importantly we also found this time to still be insufficient for bat functional diversity to effectively recover to levels similar to those observed in continuous forest (Figure 1).

But how long does it take for bat assemblages in secondary forest to attain levels of functional diversity as in continuous forest? We anticipated that complete functional recovery of local bat assemblages will only occur when the secondary forest reaches the biomass levels and plant species composition of mature continuous forest, a process that in the Amazon can take on the order of 100 years (Fearnside, 1996). In this sense, our findings suggest that the sole reliance on restoring fully functional bat assemblages via natural regeneration is unlikely to be the most effective strategy. Rather, the most promising approach for accelerating forest succession in fragmented landscapes seems to be to employ management strategies that foster natural regeneration (i.e., the spontaneous recovery of native plant species that colonize and establish following disturbance) while also investing in active restoration (i.e., requiring planting or direct seeding). Although a recent pantropical meta-analysis (Crouzeilles et al., 2017) found that natural regeneration trumps active restoration in achieving forest restoration success for a number of taxonomic groups, we concur with the authors' conclusion that mixing both restoration approaches seems key to increasing species richness, and we contend the same applies to the recovery of functional diversity.

In fragmented tropical landscapes, matrix regeneration and remaining forest patches guide the movements of frugivorous and insectivorous bats, affecting the spatial patterns of seed dispersal and suppression of herbivorous insects (Figure 2). As Neotropical frugivorous bats use olfaction to detect mature fruits, essential oils from ripe chiropterochorous fruits have been suggested as a possible way to attract bats to degraded areas and increase seed rain (Bianconi, Suckow, Cruz-Neto, & Mikich, 2010). Although more studies on the efficacy of artificial bat roosts as catalysts of succession are needed, this is another example of human-assisted regeneration that can accelerate forest recovery in degraded areas (Kelm, Wiesner, & von Helversen, 2008; Reid, Holste, & Zahawi, 2013). Conservation strategies in tropical disturbed landscapes should, in addition to ensuring the preservation of large areas of primary forest, promote the regeneration and long-term protection of secondary forests regardless of their age.

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Declaration of Conflicting Interests

The author(s) declare no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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