Bat phylogenetic responses to regenerating Amazonian forests

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Abstract

1. Throughout the tropics, regenerating secondary forests occupy vast areas previously cleared for agriculture and cattle ranching. However, despite the importance of regenerating forests in mitigating the pervasive negative consequences of forest loss and fragmentation on forest-associated biodiversity, longitudinal studies on species' phylogenetic responses to matrix regeneration are rare.

2. We surveyed bats in continuous primary forest, primary forest fragments and in the regenerating secondary forest matrix of a whole-ecosystem Amazonian fragmentation experiment, ~15 and ~30 years after forest clearance, to investigate how changes in matrix quality through forest recovery affect phylogenetic α- and β-diversity.

3. We found that temporal changes in phylogenetic α-richness were more marked in the secondary forest matrix than in forest fragments and continuous forest, evidencing a significant increase in total evolutionary history over time. However, when the effects of species richness were accounted for, the phylogenetic structure of each assemblage was reduced close to zero, evincing a random pattern of lineages in all habitat types. Temporal differences in phylogenetic β-diversity were driven mainly by $\beta_{\text{replacement}}$ in secondary forest and continuous forest ~30 years after forest clearance. Both habitats also clustered together in terms of β_{richness}, indicating similar levels of evolutionary heritage. Consequently, regenerating secondary forest showed a reduction in the extinction probability of lineages over time.

4. *Synthesis and applications.* Approximately 30 years of secondary forest regeneration were sufficient for phylogenetic richness to recover to levels similar to those observed in continuous forest. Promoting forest succession on degraded land through a combination of natural and active restoration, while ensuring the long-term protection of secondary forests regardless of their age is of key importance for conserving tropical bat diversity and their associated ecosystem services. Such restoration measures would stimulate the recolonization of

fragments and matrix habitats by evolutionarily distinct bat species, safeguarding phylogenetically diverse assemblages and ecological functions. Our study suggests that forest restoration in tropical degraded areas should be encouraged and secondary forests be protected by law, especially in countryside ecosystems with high primary forest cover, and in the surroundings of protected areas.

Keywords: Amazonia, Chiroptera, evolutionary history, habitat fragmentation, phylogenetic diversity, second growth, temporal dynamics, tropical forest restoration

1. Introduction

The future of humanity critically depends on the preservation of biodiversity, and our capacity to understand and limit the long-term negative impacts of fragmented and human-dominated landscapes will dictate the fate of many tropical species (Haddad et al., 2015). Recent evidence suggests that restoring 15% of degraded land in priority areas would avoid over 60% of predicted extinctions (Strassburg et al., 2020), highlighting the enormous potential for ambitious restoration targets to address global biodiversity decline. Habitat restoration is particularly relevant in tropical deforested and fragmented landscapes where restoring land through secondary forest regrowth can provide suitable habitat for numerous species (Chazdon et al., 2014; Bastin et al., 2019). In fragmented forest landscapes, secondary forest regeneration can buffer the pervasive consequences of edge effects and expand the effective area of fragments, reducing fragment-matrix contrast and accelerating the recovery of multiple biodiversity dimensions (Farneda et al. 2018a; Rozendaal et al., 2019). To assess the effects of human-induced habitat modification on biological communities, phylogenetic diversity metrics are better suited than simple taxon counting, as they are more closely linked to ecosystem functioning and provide a comparable evolutionary measure of biodiversity persistence through space and time (Srivastava, Cadotte, MacDonald, Marushia, & Mirotchnick, 2012).

Several recent studies have addressed the taxonomic and functional dimensions of wildlife responses to the temporal dynamics of fragmented tropical landscapes (e.g., Sayer, Bullock, & Martin, 2017; Farneda et al., 2018a; Rocha et al., 2018; Acevedo-Charry & Aide, 2019; Rutt, Jirinec, Cohn-Haft, Laurance, & Stouffer, 2019; Sierra, Toledo, Nascimento, Pereira, & Zartman, 2019; Wolf, Stouffer, Bierregaard Jr., Luther, & Lovejoy, 2020; Stouffer et al., 2021). By contrast, few have taken a phylogenetic diversity perspective (Edwards, Massam, Haugaasen, & Gilroy, 2017; Hughes, Edwards, Sayer, & Martin, 2020), indicating that regenerating secondary forests conserve high levels of species evolutionary heritage. Moreover, the effects of ecosystem recovery on the phylogenetic dimension of biodiversity have been overlooked in forest restoration programmes (Winter, Devictor, & Schweiger, 2013; Barber et al., 2017). Bats are a promising group for studying responses to fragmentation because they have high species richness and key ecological roles in tropical ecosystems, acting as important seed dispersers, pollinators, prey and predators (Kunz, Torrez, Bauer, Lobova, & Fleming, 2011). Furthermore, they are a group for which information on the temporal dynamics of fragmentation effects remain nil from an evolutionary perspective (Meyer, Struebig, & Willig, 2016).

Between 1996 and 2002, Sampaio (2000) and Bobrowiec and Gribel (2010) documented considerable spatial turnover of bats in the aftermath of forest loss and fragmentation, ~15 years after initial forest clearance in the early 1980s at the Biological Dynamics of Forest Fragments Project (BDFFP), Central Amazon. Our previous research showed that, ~30 years after the experimental clearing, old-growth specialist species have greatly benefited from the increased permeability of the matrix associated with secondary forest regeneration (Rocha et al., 2018). This taxonomic recovery was accompanied by a significant increase in functional diversity in the regenerating secondary forest matrix (Farneda et al., 2018a; 2018b). However, even these ~30 years of matrix regeneration were insufficient for taxonomic and functional diversity of bats at the BDFFP to effectively recover to levels observed in continuous primary forest (Farneda et al., 2018a; Rocha et al., 2018).

Here, we employ a range of α- and β-diversity metrics, as well as measures of evolutionary distinctiveness to elucidate how secondary forest regeneration affects the evolutionary dimension of bat diversity in the BDFFP landscape, focusing again on the changes that occurred in the period spanning ~15 and ~30 years after forest clearance. Our general hypothesis was that the successional advance of the regenerating secondary vegetation would promote the recovery of phylogenetic diversity of bat assemblages in primary forest fragments and secondary forest matrix sites through the recolonization by different species lineages. We predicted that secondary forest would regain the most evolutionary heritage due to bats from diverse lineages responding positively to the greater diversity of available niches associated with matrix regeneration. In this case, it is expected that phylogenetic diversity in regenerating matrix sites increases proportionately to increasing species richness. Consequently, matrix regeneration should buffer the negative impacts of edge effects resulting from the abrupt transition between two adjacent ecosystems, and increase connectivity between fragments (Laurance et al., 2017), increasing also the phylogenetic diversity in fragment interiors. Therefore, we predicted that over time (1) phylogenetic α-diversity would increase in fragments and matrix sites and, (2) differences in phylogenetic β-diversity would be determined mainly by markedly distinct lineages in fragments and matrix sites. Likewise, we anticipated that (3) the extinction probability of evolutionarily unique lineages would decrease in fragments and matrix sites.

2. Material and methods

2.1 Study area

The BDFFP spans ~1000 km^2 and is located ~80 km north of Manaus (2°25'S, 59°50'W), Central Amazon, Brazil (Fig. S1). The area is characterized by a mosaic of unflooded (*terra firme*) rainforest, primary forest fragments (1, 10 and 100 ha), and regenerating secondary forest. Rainfall can exceed 300 mm/month between November and May and drop below 100 mm/month between June to October, during the dry season (Ferreira et al., 2017). The terrain is relatively flat (80-160 m elevation), and is intersected by small streams. Primary forest canopy height is ca. 23 m, with occasional emergent trees reaching 55 m (Gascon & Bierregaard, 2001). Eleven fragments were experimentally isolated from continuous forest in the early 1980s. Originally located within 3,000-5,000 ha cattle ranches, fragments became gradually embedded in a regenerating secondary forest matrix following the cessation of livestock activities (Laurance et al., 2017). Fragment isolation is maintained by clearance of a 100 m-wide strip of regenerating vegetation every ca. 10 years around each fragment (Rocha et al., 2017b). The matrix is composed of secondary forests dominated mainly by *Cecropia* spp. (areas that were cleared without fire) and *Vismia* spp. (areas that were cleared and burned) (Mesquita, Ickes, Ganade, & Williamson, 2001). Prior to this study, the most recent re-isolation occurred between 1999 and 2001 (Rocha et al., 2017b).

2.2 Bat sampling

Approximately 15 years after fragment creation, extensive bat surveys were carried out at the BDFFP, targeting six continuous forest sites and six forest fragments (three of 1 ha and three of 10 ha; sampling period: 1996-1999, Sampaio 2000), as well as seven sites in the regenerating secondary forest matrix (sampling period: 2001-2002, Bobrowiec and Gribel 2010). Between 2011 and 2013, i.e., ~30 years after initial forest clearance, we employed identical methods to resurvey the same 19 sites (Fig. S1). For simplicity, we refer to these two periods as early and late regeneration hereafter.

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: early regeneration = 18-24 nets, late regeneration = 14 nets; 7-12 sampling nights per site), and erected 100 m from one of the borders of each fragment in the regenerating secondary forest matrix (early = 8 nets, late = 7 nets; 3-7 sampling nights per site). Nets were exposed for six hours after dusk. Same-site visits were spaced 3-4 weeks apart during both dry and rainy seasons to avoid bias in capture rates as a result of net shyness (Marques et al., 2013). Total sampling effort was 28,959 mist-net hours (mnh, 1 mnh equals one 12-m net open for 1 h). Early regeneration: continuous forest = 8,757 mnh, forest fragments = 9,429 mnh, secondary forest = 860 mnh. Late: continuous forest = 4,009 mnh, forest fragments = 3,963 mnh; secondary forest = 1,941 mnh. Only phyllostomids and the mormoopid *Pteronotus* spp. were included in subsequent analyses given the choice of sampling method (Kalko, Handley, & Handley, 1996). Same-site recaptures were excluded. Fragment interiors of both sizes were analyzed jointly because they did not differ significantly in species richness (Rocha et al., 2017a). Further, we did not distinguish between *Cecropia*- and *Vismia*-dominated regrowth given the small number of sites for each, and because the abundances of the most common bat species did not differ significantly between these habitats (Bobrowiec & Gribel, 2010). A total of 6,109 bats of 46 species were used in the analysis.

2.3 Phylogeny

We used the species-level phylogeny of bats proposed by Rojas, Warsi and Dávalos (2016), as it covers all the species that occur at the BDFFP and avoids a known mislabeling error for *Phyllostomus discolor* present in other published phylogenies (Dávalos, Cirranello, Geisler, &

Simmons, 2012). The bat tree was pruned to obtain the local phylogeny (R package ‘picante’, Kembel et al., 2010), and the phylogenetic pairwise distance matrix was obtained from the local phylogeny (function ‘cophenetic.phylo’, R package ‘ape’, Paradis, Claude, & Strimmer, 2004). Taxonomic nomenclature follows Garbino et al. (2020).

2.4 Data Analysis

2.4.1 Local phylogenetic diversity

The total amount of phylogenetic richness of each assemblage was quantified using Faith’s index (PD; Faith, 1992). Differences in capture effort between early and late regeneration were accounted for using individual-based rarefaction (1000 runs, R package ‘BAT’, Cardoso et al., 2015), rarefying to the lowest abundance observed across all habitat categories, i.e., 602 individuals in continuous forest during the late regeneration period. Similarly, the phylogenetic structure of each assemblage was quantified using “mean pairwise distance” (MPD; Webb, Ackerly, McPeek, & Donoghue, 2002). MPD is more strongly influenced by the basal branches of a phylogeny, and as our local phylogeny consisted of closely related species with quite a balanced topology, MPD could underestimate phylogenetic clustering in the terminal branches (Vamosi, Heard, Vamosi, & Webb, 2009). We therefore also calculated the “mean nearest taxon distance” (MNTD; Webb et al., 2002) as it is more sensitive than MPD to detecting clustering in the terminal structure of the phylogenetic tree (Tucker et al., 2017). While high values of MPD indicate more species with above-average branch lengths, for MNTD they indicate that some species have branches much longer than average (Vamosi et al., 2009). Significance was inferred by examining the overlap of 95% confidence levels. To remove any effect of species richness on these metrics, we additionally applied a ‘richness’ null model using the standardized effect size (SES; R package ‘picante’, Kembel et al., 2010). To calculate SES, species richness for each site was fixed, and species across tips of the phylogeny were randomized 1000 times. Significant positive SES values indicate over-dispersed phylogenetic structure, whereas significant negative values indicate phylogenetic clustering (Webb et al., 2002). Significant temporal changes in community structure were inferred by examining if the values for SES_{PD}, SES_{MPD}, and SES_{MNTD} lie above or below the 95% and 5% quantiles of the null distribution. Further, we used the R function “poncho” to better understand how community phylogenetic information is structured along the environmental gradient based on species’ presence/absence data (Dambros, 2020). This analysis, which is typically used to visualize species turnover along gradients or nested patterns of community structure, summarizes the sites and species information into the first ordination axis of a principal coordinates analysis (PCoA).

2.4.2 Landscape *β*-diversity

To elucidate the temporal difference in shared total branch lengths between assemblages based on the evolutionary lineages, we partitioned the total phylogenetic *β*-diversity ($P\beta_{total}$) into its replacement ($P\beta_{replacement}$) and richness ($P\beta_{richness}$) components (R package ‘BAT’, Cardoso et al., 2015). While higher values of $P\beta_{replacement}$ suggest stochasticity in colonization-extinction rates, for $P\beta_{richness}$ they suggest deterministic processes shaping assemblages (Cardoso et al., 2014). To further investigate between-period changes in phylogenetic *β*-diversity, we also calculated the “inter-community mean pairwise distance” (COMDIST; R package ‘picante’, Kembel et al., 2010). Functional *β*-diversity components were calculated using rarefaction (1000 runs, Jaccard dissimilarity index, R package ‘BAT’, Cardoso et al., 2015), rarefying to the lowest number of captures across habitat categories (602 individuals in continuous forest, late regeneration). $P\beta_{total}$, $P\beta_{replacement}$, $P\beta_{richness}$, and COMDIST were visualized through “unweighted pair group method with arithmetic mean” (UPGMA; function ‘hclust’, R Core Team, 2020). While UPGMA will cluster assemblages with similar amount of phylogenetic richness in Pβ_{richness}, for P$\beta_{\text{replacement}}$ it will cluster assemblages with similar lineages, and for COMDIST it will cluster closely related assemblages.

2.4.3 Temporal change in evolutionary distinctiveness

Estimated extinction probabilities for each phylogenetic branch were calculated across all habitat categories for both early and late regeneration, using the metric "expected evolutionary distinctiveness" (eED; function 'eED', R package 'mallorn', Davis, 2020). eED is the projected amount of unique evolutionary history that can be attributed to each tip of the phylogenetic tree (Redding, Mazel, & Mooers, 2014; Davis, Faurby, & Svenning, 2018). Species with no close relatives and branches deep in the tree have higher evolutionary distinctiveness values, while the opposite is true for closely related species (Davis, 2020). The probability of each phylogenetic branch to be extinct was set based on relative species abundances (range from 0 to 1) to account for differences in sampling effort between habitats. For this, relative abundances of the eight most abundant species were rounded down to 1 so as to not overemphasize their weight in the analysis (see Table S1).

3. Results

3.1 Local phylogenetic diversity

Temporal changes in phylogenetic richness were most marked in secondary forest compared to forest fragments and continuous forest. Secondary forest maturation was accompanied by a significant increase in rarefied PD (Fig. 1; Fig. S2). While early-successional sites (~15 years) had lowest species richness and PD, these sites had an elevated representation of different species and lineages after ~30 years of regeneration (Fig. 2). When the effect of species richness was accounted for (SES_{PD}, SES_{MPD}, SES_{MNTD}), phylogenetic structure across all habitats was random (SES close to zero; Fig. 1), i.e., there was no evidence of the preservation of distinct lineages or particular clades.

3.2 Landscape *β*-diversity

Between-period differences in $P\beta_{total}$ suggest that late-stage regenerating forest harbored more lineages than the phylogenetically impoverished early-stage regenerating forest (Fig. 3). During late regeneration, secondary forest showed higher values in terms of $P\beta_{total}$ and $P\beta_{replacement}$ compared to forest fragments, and clustered together with continuous forest regarding $P\beta_{richness}$ (Fig. 3), suggesting similar amounts of phylogenetic richness among them. Dendrograms based on the evolutionary history shared between assemblages ($P\beta_{total}$, $P\beta_{replacement}$, $P\beta_{richness;}$ Fig. 3) were relatively similar to lineages within assemblages, as the same habitats did not cluster together across time periods (COMDIST; Fig. S3).

3.3 Temporal change in evolutionary distinctiveness

Between-period changes in projected bat extinctions were more conspicuous in regenerating secondary forest than in forest fragments and continuous forest, indicating recovery of evolutionary history with secondary forest maturation (Fig. 4, Fig. S4). Extinction probability decreased for over half of the species with secondary forest regeneration. While 24 species showed a high probability of extinction during early regeneration, this number was reduced to 11 species during late regeneration (Fig. 4). While lineages at high (= 1) extinction risk in early regeneration were composed mainly of gleaning animalivorous bats (11 species), during late regeneration they were mainly represented by nectarivores (four species) (Fig. 4). For continuous forest and forest fragments during both regeneration stages, approximately one quarter of all species had high (= 1) species' extinction probability, which followed a similar pattern between the same habitats across time periods (Fig. S4).

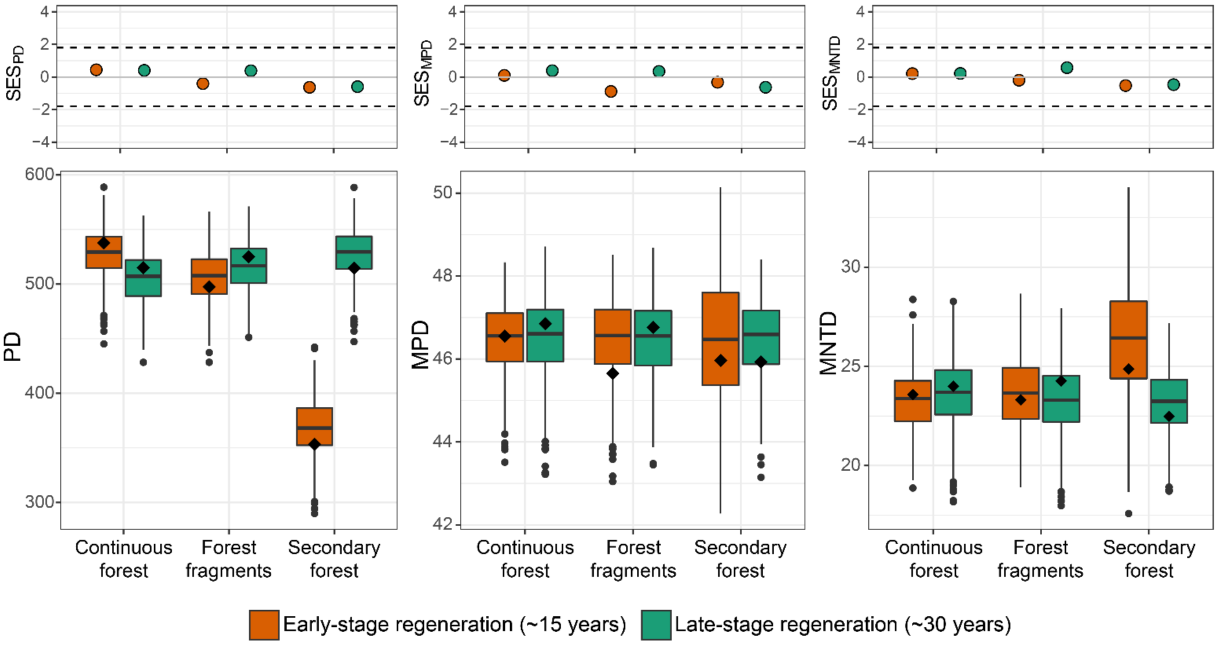

Fig. 1. Standardized effect size (SES; dots) along with 5% and 95% quantiles (dashed lines) of the simulated null communities of Faith's phylogenetic diversity (PD), mean pairwise distance (MPD), and mean nearest taxon distance (MNTD) (box and whisker plots). For SES, high quantiles (> 95%) indicate a significantly phylogenetically over-dispersed assemblage, whereas low quantiles (< 5%) indicate a significantly phylogenetically clustered assemblage. In the boxplots, mean values of observed PD, MPD, and MNTD overlaid on the simulated null communities are indicated by a black diamond. Black circles represent outliers. Significance was inferred by examining the overlap of 95% confidence levels. Bat species were sampled in continuous primary forest, primary forest fragments, and regenerating secondary forest during two time periods: ~15 years (orange) and ~30 years (green) after forest clearance at the BDFFP, Central Amazon.

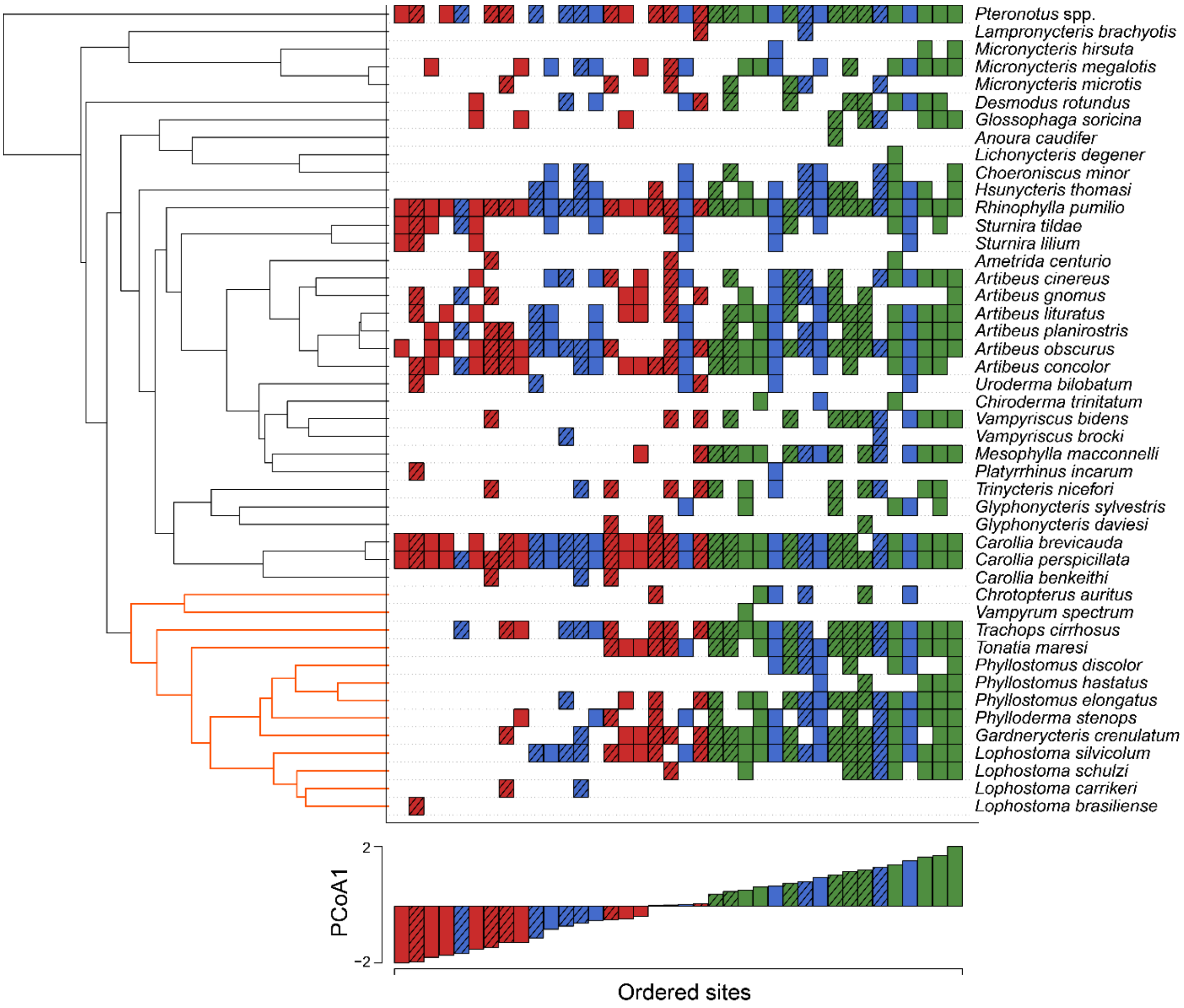

Fig. 2. Bat phylogenetic relationships at the BDFFP and their occurrence in continuous primary forest (green), primary forest fragments (blue), and regenerating secondary forest (red). Time after forest clearance is represented by ~15 years (□) and ~30 years (▨). Sites were ordered according to their species composition using the first axis of a principal coordinates analysis (PCoA) based on species' presence/absence data. Species were ordered by their average position in the PCoA ordination axis, constrained by their position in the phylogeny. The orange branches in the phylogenetic tree indicate the most representative clade in continuous primary forest.

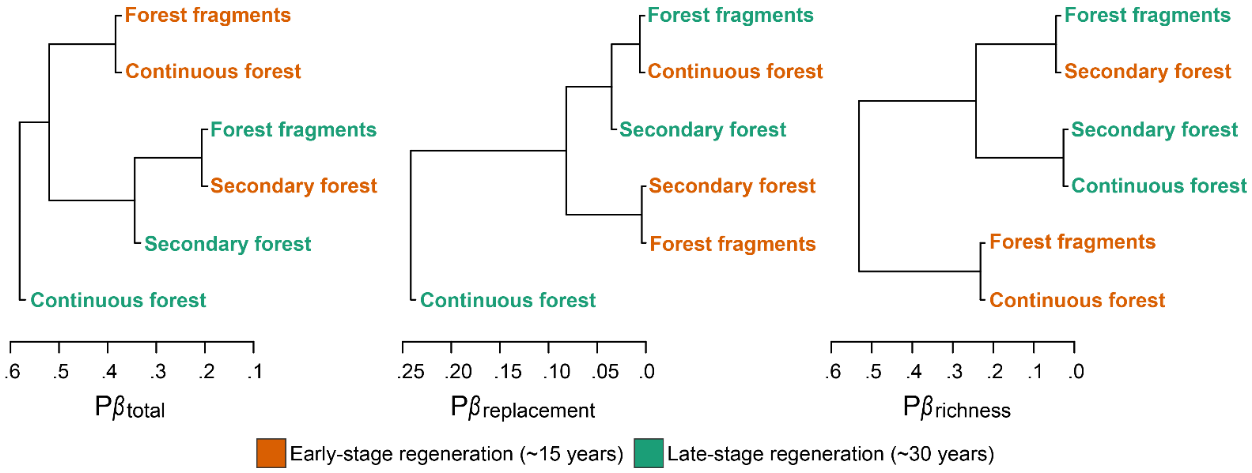

Fig. 3. Unweighted pair group method with arithmetic mean (UPGMA) indicating the degree of dissimilarity between habitats and clustering of bat total phylogenetic β-diversity (Pβ_{total}) partitioned into its replacement (P$\beta_{\mathrm{replacement}}$) and richness (P$\beta_{\mathrm{richness}}$) components. Bat species were sampled in continuous primary forest, primary forest fragments, and regenerating secondary forest ~15 years (orange) and ~30 years (green) after forest clearance at the BDFFP, Brazilian Amazon.

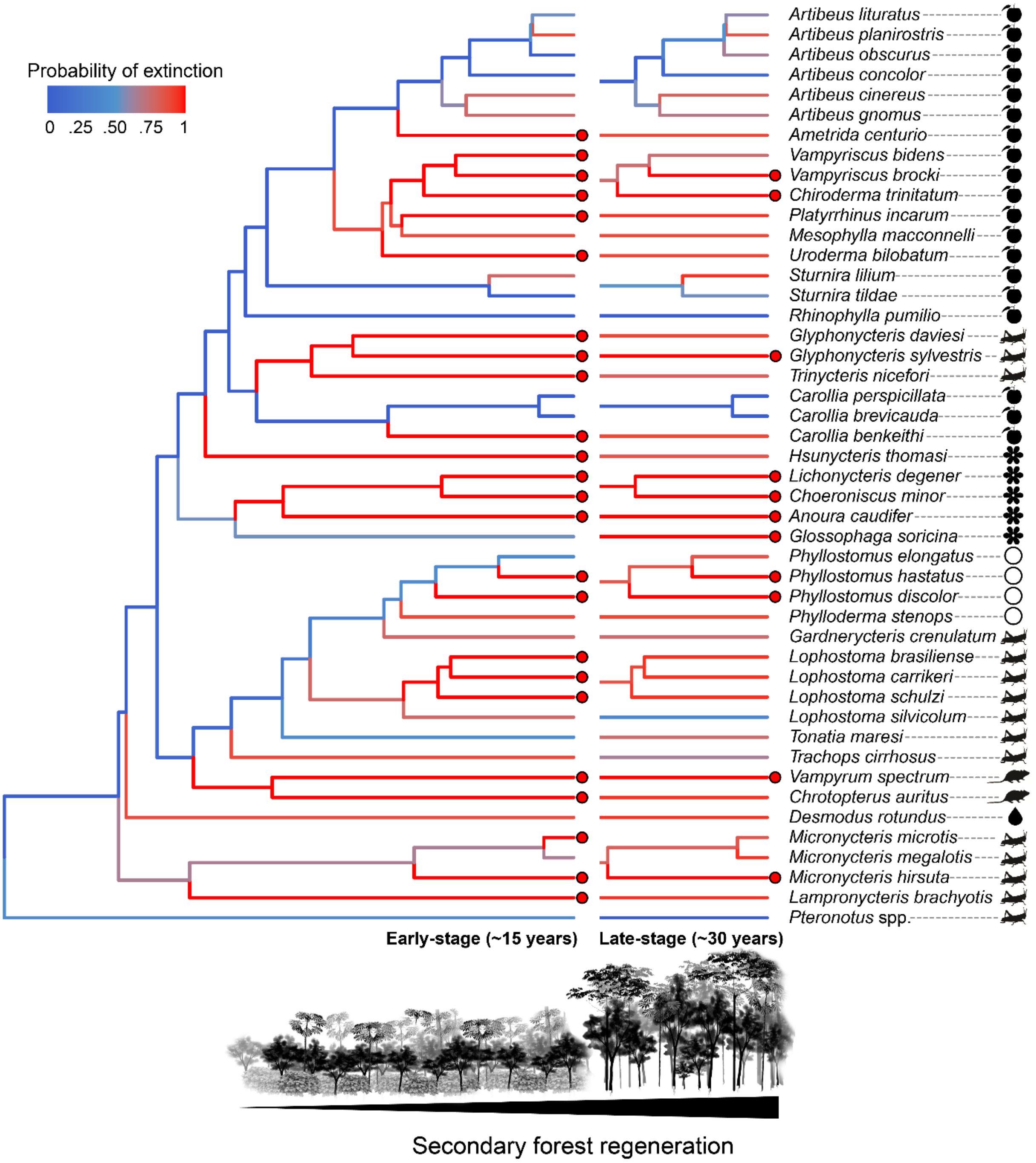

Fig. 4. Projected bat extinctions ~15 and ~30 years after forest clearance at the BDFFP, Central Amazon. Branches of the phylogeny and species are coloured according to their respective probability of being extinct. Species with extinction probability equal to 1 are also highlighted by a red circle at the terminal branches. The main diet of each species is represented by symbols: 🍎 (frugivorous), 🦗 (insectivorous), ✱ (nectarivorous), ○ (omnivorous), 🐀 (carnivorous), 💧 (hematophagous).

4. Discussion

Phylogenetic approaches have become a pivotal tool for studying evolutionary dynamics and implementing more effective conservation plans in diverse ecosystems worldwide (Frishkoff et al., 2014; Pellens & Grandcolas, 2016; Hughes et al., 2020). However, studies targeting the phylogenetic responses of species assemblages to the temporal dynamics of matrix regeneration in human-dominated landscapes are scarce. Our results show that the phylogenetic α-diversity of bat assemblages in regenerating forests increased over a ~15-year period, whereas limited change occurred in forest fragments and continuous forest. Although evidence of the preservation of distinct lineages or particular clades was limited according to SES values, increases in phylogenetic richness in the regenerating matrix were mostly associated with the gain of species, suggesting that evolutionary history is lost along with species during forest clearance. Phylogenetic β-diversity exhibited strong evidence that bat assemblages did not clearly cluster based on the same habitat category during both successional stages, probably due to higher temporal phylogenetic $\beta_{\text{replacement}}$ in secondary forest. Moreover, our findings with regard to extinction probabilities suggest that phylogenetic erosion was particularly mitigated by the regeneration of the secondary forest matrix. However, the significant phylogenetic recovery following secondary forest regeneration is likely only possible due to the close proximity of large expanses of continuous primary forest, which helps maintain the pool of bat evolutionary history within our study landscape.

A significant positive relationship between phylogenetic diversity and habitat quality in human-modified landscapes has been documented for multiple tropical vertebrate assemblages (e.g., Frishkoff et al., 2014; Edwards et al., 2017; Mestre et al., 2020; Palmeirim, Farneda, Vieira, & Peres, 2021), including Neotropical bats (e.g., Frank, Frishkoff, Mendenhall, Daily, & Hadly, 2017; Carvalho et al., 2021). In our study, the marked increase of phylogenetic richness in secondary forest echoes the taxonomic and functional recovery of bat assemblages at the BDFFP (Farneda et al., 2018a, 2018b; Rocha et al., 2018), emphasizing the crucial importance of late-stage secondary forests (> 30 years of regeneration) as repositories of species diversity, ecological functions, and evolutionary history. Our results reflect the current capacity of the BDFFP matrix to provide resources for numerous fragmentation-sensitive phyllostomid species and select traits and lineages favoured by their permeability (Farneda et al., 2015; Aninta, Rocha, López-Baucells, & Meyer 2019). However, contrary to our first prediction, the relatively low fragment–matrix contrast after ~30 years of vegetation succession resulted in non-significant changes in phylogenetic richness in forest fragments. Forest fragments at the BDFFP are relatively small (1 and 10 ha) and displayed a wider variation in bat phylogenetic responses compared to continuous forest.

Although we observed a significant increase in phylogenetic richness in regenerating secondary forest over time, this became non-significant when we removed the effects of species richness on phylogenetic metrics (SES_{PD}, SES_{MPD}, and SES_{MNTD}). This indicates that early secondary regrowth contains species that are relatively similar in terms of terminal branches to those in late regeneration when species are randomized within sites, and that clades could become extinct without guarantee that more basal evolutionary history would be preserved after forest clearance. Habitats characterized by closely related lineages (i.e., greater phylogenetic homogenization) can experience more clumped evolutionary relationships over time (Cadotte, Dinnage, & Tilman, 2012; Edwards, Gilroy, & Thomas, 2015). Due to phylogenetic homogenization this can lead to a disproportionately lower loss of phylogenetic richness than SES_{PD} (Edwards et al., 2017) because while phylogenetic richness tends to increase with more species even if they are clumped, SES_{PD} decreases.

Secondary forest showed higher values of $P\beta_{replacement}$ compared to forest fragments and clustered close to continuous primary forest regarding $P\beta_{richness}$ during late-stage regeneration. UPGMA clustering of COMDIST also revealed that the secondary forest habitats did not group together across time periods. This suggests that patterns of phylogenetic diversity in our study system are mainly structured by matrix regeneration. In this case, ~30 years of regeneration seem to have substantially reduced the effects of environmental filtering on phylogenetic richness and lineage composition, and the considerable phylogenetic turnover of some lineages in secondary forest and continuous forest suggests that colonization and extinction became more stochastic in these habitats (Cardoso et al. 2014; Aguirre, Montaño-Centellas, Gavilanez, & Stevens, 2016). Phylogenetic α- and β-diversity of phyllostomid bat assemblages across the interior-edge-matrix and forest size gradient at the BDFFP are also driven by the pervasive fragmentation effects associated with smaller fragments (1 ha) and edge effects (Aninta et al., 2019).

We also documented a reduction in extinction probability of lineages associated with the successional advance of the regenerating secondary forest matrix. This reduction was particularly noticeable for lineages of fragmentation-sensitive animalivorous bats (e.g., *Chrotopterus auritus*, *Glyphonycteris daviesi*, *Lampronycteris brachyotis*, *Lophostoma brasiliense*, *L. carrikeri*, *L. schulzi*, *Micronycteris microtis*, *Trinycteris nicefori*), thus increasing the structural and compositional phylogenetic similarity between the regenerating matrix and continuous forest habitats. Species functional traits and environmental variables jointly shape the patterns of bat occupancy and abundance in tropical fragmented landscapes (Cisneros, Fagan, & Willig, 2015; Farneda et al., 2015; Núñez et al., 2019), and most lineages of gleaning animalivorous bats are underrepresented in human-degraded habitats in comparison to those of phytophagous species (Frank et al., 2017; Aninta et al., 2019).

In the Neotropics, the pre-adaptation of phytophagous bat species (mainly from the subfamilies Stenodermatinae and Carolliinae) to disturbed habitats is largely associated with their dietary specialization (Farneda et al., 2020). While the multiple evolutionary pathways of frugivorous species were constantly stimulated by the diversification of angiosperms in a more recent time period, the rate of diversification of animalivorous bats (most of which are mainly insectivores) was more constant throughout the course of their adaptative radiation (Rojas, Vale, Ferrero, & Navarro, 2011; Peixoto, Braga, & Mendes, 2018). However, it is important to note that matrix regeneration does not seem to reduce the extinction probability of lineages of nectarivorous species (e.g., *Anoura caudifer, Choeroniscus minor, Lichonycteris degener*, see Fig. 4 and Fig. S5). At the BDFFP, secondary forests are dominated mostly by *Cecropia* spp. and *Vismia* spp. trees, which probably did not co-evolve with nectarivorous bats (Tschapka & Dressler, 2002), and resources on which nectarivores rely can be more restricted to continuous forest. Less disturbed habitats, as continuous forest, also revealed high extinction risk for some bat lineages over time. At the BDFFP, reduced abundance in the absence of deforestation has been documented for some insectivorous bird species, which probably is associated with climate change (Stouffer et al., 2021).

Although the regeneration of the BDFFP matrix is still ongoing, ~30 years of secondary forest maturation were apparently sufficient for bat phylogenetic richness in previously deforested areas to recover to comparable levels to those of continuous primary forest. In tropical secondary forest, bird phylogenetic richness recovery to old-growth forest levels also occurred in ~30 years (Edwards et al., 2017). Our results add to a growing body of evidence (e.g., Edwards et al., 2017; Hughes et al., 2020) indicating that secondary forest in an advanced successional stage increases phylogenetic heterogeneity and mitigates some of the negative effects of fragmentation. Notably, we failed to identify species that seemed particularly sensitive to forest clearance but also sufficiently resilient to return after regeneration. Part of the evolutionary history is lost together with the species during forest clearance. Although some species can persist in surrounding habitats and recolonize regenerating areas, it is likely that more intensive disturbances will lead to long-term phylogenetic impacts and to the permanent loss of evolutionary history. Our analyses are restricted to the captures of phyllostomids (45 species) and the mormoopid *Pteronotus* spp. using mist-nets at understory level (i.e., ~41% of the 111 bat species that are likely to occur at the BDFFP; see Table S2), and the inclusion of canopy nets and aerial-hawking insectivorous bat species (e.g., Emballonuridae, Molossidae, and Vespertilionidae) through acoustic sampling in the analysis may result in different patterns than the ones reported here.

4.1 Implications for forest restoration and management

Long-term, whole-ecosystem manipulations offer unique opportunities to disentangle the complex responses of biodiversity to forest regeneration. Our findings reveal that tropical regenerating forests are dynamic repositories of phylogenetic diversity, and emphasize the need for long-term management and legal protection of regenerating secondary forests regardless of their age to maximize conservation benefits. Across the tropics, evolutionary gains from ecological restoration projects will be greatest in landscapes with high primary forest cover (Crouzeilles et al., 2020), and in the surroundings of protected areas due to their pivotal role in buffering the negative consequences of edge effects and expanding their effective area (Fonseca & Joner, 2007). Furthermore, our study highlights the importance of large expanses of old-growth in the Amazon (Laurance, 2005; Gibson et al., 2011) for mitigating the negative effects of deforestation and forest degradation on species lineages that are more vulnerable to extinction, and to sustain high phylogenetic diversity over the long term.

The secondary forests of the BDFFP are sheltered from many of the human-imposed pressures that plague contemporary regenerating landscapes (e.g., logging). Yet, the “rescue” potential of regenerating secondary forests is, as evidenced by this and other longitudinal studies from the BDFFP (e.g., Rutt et al., 2019) and elsewhere in the tropics (e.g., Xu et al., 2015), of prime relevance if restoration ecology is to fully realize its promise. Our findings reinforce that long-term natural forest regeneration is a valid avenue for the restoration of fragmented tropical landscapes (Gilroy et al., 2014; Crouzeilles et al., 2020). Effective public policies to promote a more forest-based economy through the sustainable use of forest products should be applied to protect secondary and primary forests from deforestation, and improve habitat quality and connectivity in fragmented tropical landscapes. Regenerating secondary forests are now an increasingly predominant type of forest cover across the tropics (Chazdon, 2014). Safeguarding this dynamic reservoir of biodiversity is likely to be one of the most successful strategies to reverse the ongoing erosion of evolutionary history and ecosystem services.

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Authors’ contributions

FZF and CFJM designed research; SGA, FZF and CSD performed the data analyses; FZF led the writing of the manuscript; FZF, RR, AL-B, JMP, PEDB and CFJM collected data at the

BDFFP during late-stage regeneration; EMS and PEDB collected data during early-stage regeneration. All authors contributed critically to the drafts, gave final approval for publication.

Conflict of interest

The authors have declared no conflicts of interest.

Data availability statement

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.dz08kprz9 (Farneda et al., 2021).

Supporting information

Additional supporting information may be found online in the Supporting Information section.

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