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Biodiversity responses to restoration across the Brazilian Atlantic Forest

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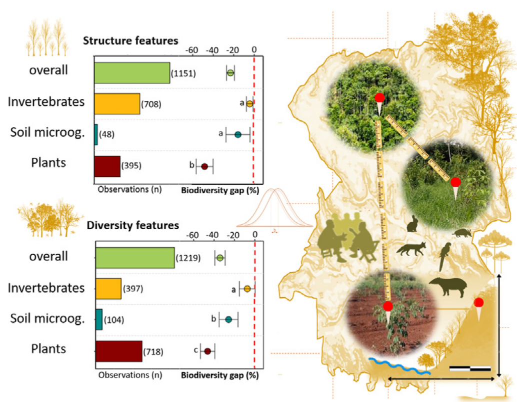
HIGHLIGHTS

- Diversity features showed a smaller recovery gap in the BAF.
- The recovery gap for structure features shortened after 20 years of restoration.
- Recovery depended more on the taxonomic group than the biodiversity feature.
- The recovery gap was higher for vascular plants than the other taxonomic groups.

GRAPHICAL ABSTRACT



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ABSTRACT

The UN Decade on Ecosystem Restoration is focussing attention and resources on restoration globally. Nowhere is this more crucial than in tropical forests that harbor immense biodiversity, but have also undergone widespread deforestation over the past few decades. We performed a meta-analysis to investigate how biodiversity features respond to forest restoration across the Brazilian Atlantic Forest (BAF), one of the most threatened biodiversity hotspots in the world. We assembled biodiversity in different metrics of structure and diversity features of three taxonomic groups (vascular plants, soil microorganisms, and invertebrates), generating a dataset with 2370 observations from 76 primary studies. We quantified the incomplete recovery of biodiversity (i.e., the rate of recovery to a pre-disturbance state) occurring during the restoration process, which we called the 'recovery gap'. Our results revealed that forests undergoing restoration in the BAF show a recovery gap of 34% for structure features and 22% for diversity features in comparison to reference reforests, considering all taxonomic groups investigated. For vascular plants, soil microorganisms, and

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Abundance
Forest structure
Diversity indexes

invertebrates the recovery gap ranged between 46 and 47%, 16–26%, and 4–7%, respectively. Overall, the recovery gap was influenced by the interaction of restoration actions (i.e., the past land use, restoration age and restoration approach – active and passive restoration), however, structure features responded more sensitively to the time elapsed since restoration started, while the recovery gap for diversity features depended more on the past land-use. Our study can help guide the prioritization of the aforenamed taxonomic groups in restoration, the regulation of potential biodiversity offsetting policies in the BAF, and understanding how coupled biodiversity features respond to the interaction of environmental conditions and restoration actions in a high fragmented tropical landscape.

Contents

1. Introduction

Biodiversity recovery (i.e., the rate of recovery to a pre-disturbance state) is a primary outcome for most forest restoration interventions (e.g., passive and active interventions), especially because biodiversity is a surrogate for many benefits of restoring ecosystems (Crouzeilles et al., 2019b; Stephens et al., 2015; Rozendaal et al., 2019). However, predicting the rate at which forests recover biodiversity through restoration is still challenging because there are several influencing factors involved, such as past land use, ecosystem resilience, the landscape context, and the restoration approach (Meli et al., 2017; Rodrigues et al., 2011). Eventually, forests can recover quickly when the source of degradation or the current land use (e.g., agriculture, logging) ceases and natural succession can proceed (Letcher and Chazdon, 2009). Conversely, areas with an intensive past of deforestation and land degradation can result in slow or arrested recovery of different taxonomic groups (Huang et al., 2019; Lamb et al., 2005; Reid et al., 2018). Previous research documented that rates of biodiversity recovery also depend on the type of variables being measured (Crouzeilles et al., 2016; Curran et al., 2014).

Despite the known importance of restoration for the recovery of biodiversity in tropical forests, its impacts across entire regions are scarcely investigated (Shimamoto et al., 2018). Since the characteristics of biodiversity are multidimensional (Lyashevska and Farnsworth, 2012), it is notoriously difficult to assess their responses to restoration by using a single metric approach such as diversity indices (Marcilio-Silva et al., 2018; Mooers, 2007). 'Biodiversity' is a broad term used to catch any of the multiple levels of biological complexity (Feest et al., 2010; Ferrier, 2002). To simplify the goal of measuring biodiversity, ecologists generally use metrics that allow accessing its features based on habitat condition, which is calculated and weighted across several habitat features (Davies and Cadotte, 2011; Marshall et al., 2020). Thus, to assess restoration effectiveness on biodiversity recovery it is necessary to integrate different biodiversity metrics and different organisms (Huang et al., 2019; Rodrigues et al., 2011), since simplistic metrics may fail to conserve ecological values they seek to protect (Marshall et al., 2020).

Previous meta-analyses already quantified the impacts of forest restoration on biodiversity and ecosystem services in agroecosystems (Barral et al., 2015) and agroforestry systems (Santos et al., 2019), some drivers of restoration success (Crouzeilles et al., 2016), and the effectiveness of restoration methods (Crouzeilles et al., 2017; Meli et al., 2017). However, we know little about how biodiversity features, such as d' change across highly fragmented tropical forest landscapes. However, we know little about how broad biodiversity features, such as structure and diversity features, change across highly fragmented tropical forest landscapes. Integrating different biodiversity metrics into these two features (i.e., structure and diversity features) may, therefore, be a useful approach to fill this knowledge gap (Schowalter, 2006; Huang et al., 2019). Here, we evoke 'biodiversity features' as a comprehensive term that seeks to integrate different biodiversity metrics that share a common nature.

Structure features refer to general arrangements in a community (e.g., what organisms are present in a given environment, their relative abundances, and how they are related to each other) (Adey and Loveland, 2007). Structure features may also refer to the forest structure – the organization of individuals in space, their composition and the structural complexity of vegetation in the three-dimension (e.g., canopy cover, mean height and basal area) (Chirici et al., 2012; Chirici et al., 2011). The extent to which forests provide habitats for other species is strictly related to the diversity of their structure and complexity (Bartha et al., 2006; Michel and Winter, 2009). Therefore, forest structure can be both correlated with diversity in flora and fauna (Winter et al., 2005; Winter and Möller, 2008; McRoberts, 2009; Chirici et al., 2012). Diversity features represent two main biodiversity components, which are richness and evenness. Richness is the number of species in the community, whereas evenness is a measure of relative abundances (Schowalter, 2006). These two components can be represented by different diversity indices, describing ecological metrics that assess multiple species (Crouzeilles et al., 2019a; Marshall et al., 2020).

Because of its high level of endemism (Mittermeier et al., 2011; Gomes-da-Silva and Forzza, 2021), generalized land-use change (Mittermeier et al., 2004; Marcilio-Silva et al., 2018) and national pledges (Crouzeilles et al., 2019b), restoration efforts have been intense in the Brazilian Atlantic Forest (BAF). This tropical forest comprises one of the most threatened biodiversity hotspots in the world (Joly et al., 2014; Rezende et al., 2018). It encompasses five main types of forest: Dense Ombrophilous, Open Ombrophilous, Mixed Ombrophilous, Semideciduous Seasonal and Deciduous Seasonal (Marcilio-Silva et al., 2018; Oliveira-Filho and Fontes, 2000). Its long history of environmental impacts mirrors the fate experienced by other tropical forests worldwide. After about five centuries of human occupation, most landscapes are composed of small forest patches surrounded by open-habitat matrices (Joly et al., 2014). Several restoration projects with different objectives (e.g., to connect remaining fragments) have been implemented over the years in the BAF (Rodrigues et al., 2009), and many tested the efficacy of different restoration methods, techniques, and biodiversity responses of different taxonomic groups (Ferretti and de Britez, 2006; Guerra et al., 2020; Kauano et al., 2013).

Here we used meta-analysis to quantify the incomplete recovery of biodiversity occurring during the restoration process in the BAF, which we call the 'recovery gap'. This is a useful indicator of the magnitude of forest degradation, considering that even if biodiversity fully recovers, there is likely to be a long period until this happens, which would be important information to restoration practitioners and other decision-makers to plan their actions. Biodiversity metrics collected from field studies were reclassified into structure and diversity features to build a suitable baseline to answer the following questions: i) What is the current recovery gap (structure and diversity feature gaps) of forests undergoing restoration in the BAF compared with reference forests? ii) How do different taxonomic groups respond to the recovery of structure and diversity features? iii) How do restoration actions and environmental conditions influence the recovery gap?

2. Methods

2.1. Literature searching and data gathering

We performed a systematic search (Romanelli et al., 2021) of the peer-reviewed literature from the Web of Science (core collection: SCI-E, SSCI, and ESCI), Scopus, CAB Direct, and SciELO. We also used Google Scholar (GS) as a search engine. We searched these bibliographic sources with no restriction on publication year, using the following search string: '(restor* or recreat* or rehabilitat* or reforest* or afforest* or recover* or regenerat* or remediat* or revege*) AND (forest*) AND (Brazil* or Brasil*) AND (biodiversity or diversity)'. The full search history is available (Supplementary material S1). Only primary research that comprised the following eligibility criteria were included: i) population: Brazilian Atlantic Forest ecosystems, based on Joly et al. (2014); ii) interventions: active forest restoration planting (i.e., plantation of tree species) – under favorable conditions (e.g., mining areas were excluded); and passive restoration (i.e., forest regrowth following land abandonment or the cessation of disturbance pressure); both occurring in temperature zones ranging from 16 °C to 26 °C and altitude zones from 0 to 1000 m; iii) comparators: restoration outcomes were compared with reference forests (i.e., less undisturbed forest ecosystem in the area) within the same assessment, which could be secondary forests in the advanced stage of succession (e.g, >50 years), or ideally, primary forests (forests that have not been significantly disturbed). Based on the assumption that forests with distinct disturbances histories tend to differ in their attributes (Hobbs and Norton, 1996; Choi, 2004), and that, considering a spectrum of natural ecosystems as a reference has been recommended (Suganuma and Durigan, 2015), we included this two categories of reference forests in our analysis; iv) outcomes: we assumed biodiversity as a comprehensive variable; following Huang et al. (2019), we integrated the most monitored organisms in terrestrial ecosystems (i.e., vascular plants, soil microorganisms, and invertebrates) into the analysis. Typically extracted diversity features for all taxonomic groups were diversity indexes (e.g., Shannon, Simpson, Richness, Evenness, etc.). Structure features were mostly represented by abundance and density of individuals (for all taxonomic groups), and also by forest structure metrics (e.g., basal area, mean high, canopy cover, etc.) for vascular plants only (see Supplementary material S3). We detailed methods for all review stages (Supplementary material S1), particularly the screening process (Supplementary material S2), data extraction (Supplementary material S3), data analysis (Supplementary material S4), data synthesis (Supplementary material S5), and data reporting conduct (Supplementary material S6).

The geographical locations of field studies were extracted and mapped by ArcGIS 10.2. We standardized the mean annual temperature information of each study site from the nearest climate station provided by the INMET database (https://portal.inmet.gov.br/).

2.2. Data analysis

We used a standardized procedure to collect biodiversity metrics from primary studies developed in the BAF, and then quantified the recovery gap for overall and three taxonomic groups by a meta-analysis. To ensure suitable baselines for comparisons, we reclassified biodiversity metrics into structure and diversity features and separated observations into restoration vs. reference. From the former, we assessed the current level of biodiversity occurring during the restoration process, and the latter allowed us to determine the recovery gap between restoration and reference forests.

We converted all collected biodiversity metrics to effect sizes by using meta-analysis, and the normalized effects (i.e., comparisons between restoration vs. reference state) allowed us to analyze all data together, despite the overwhelming heterogeneity of biodiversity metrics extracted from published studies (Balvanera et al., 2006; Huang et al., 2019). As a general concept, biodiversity can be understood as the sum of all biotic variations (Feest et al., 2010). So we could use the normalized effects of the three taxonomic groups (vascular plants, soil microorganisms, and invertebrates) to calculate the overall biodiversity features, despite the heterogeneity of organisms within and between species. The natural logarithm of the response ratio (*lnRR*) (Gurevitch and Hedges, 1999; Hedges et al., 1999) was chosen as the effect of forest restoration on biodiversity and calculated by Eq. (1).

$$lnRR = ln \frac{Xe}{Xc} \tag{1}$$

where, *Xe* and *Xc* are the means of a biodiversity metric in the experimental group (restoration) and control group (reference state), respectively.

We calculated the unweighted and weighted mean of the natural logarithm of the response ratio by using the "Metafor" package in R software (Viechtbauer, 2010; R Core Team, 2021). We converted the *lnRR* into the change percentage (*A*) to estimate the recovery gap by Eq. (2), and the recovery gap was considered significant if the confidence interval (*CI*) of the change percentage at the 95% level did not overlap with zero (Koricheva et al., 2013).

$$A = \left(e^{lnRR} - 1\right) \times 100\% \tag{2}$$

Case removal (i.e., exclusion of studies) reduces the sample size and may introduce bias into the analysis (Raghunathan, 2004). To avoid complete case removal due to the absence of information on the standard deviation or standard error – a common issue in ecological data sets (Ellington et al., 2015), we performed a comparative analysis of unweighted and weighted meta-analysis to account for potential pseudoreplication bias and deal with weighting. Weighted meta-analysis is considered a more reliable approach when dealing with ecological data synthesis (Hedges et al., 1999; Romanelli et al., 2020) because information relying on the mean variances are included and studies with more replication or sampling effort (e.g., the number of plots and the plot size, respectively) can be counted more heavily (Huang et al., 2019). Thus, we performed a sensitivity analysis by using a reduced dataset including only complete data for each field study (weighted meta-analysis) and comparing results between the reduced and the whole dataset. The comparison between these two approaches (unweighted meta-analysis – full dataset; and weighted meta-analysis – reduced dataset) showed the same general trends for recovery gaps. Thus, results regarding the whole dataset were presented in the main text due to the larger number of observations included (Supplementary material S5). Some studies provided biodiversity outcomes using more than one metric, and these multiple observations might not be independent (Huang et al., 2019).

We checked for potential outliers by generating a funnel plot (Koricheva et al., 2013), and used the conditional residuals along with corresponding sampling variance in publication bias tests (Nakagawa and Santos, 2012), which showed no publication bias in our meta-analysis from subjective and quantitative perspectives (Supplementary material S5).

To identify potential sources of the heterogeneity in biodiversity responses, we used one-way analysis of variance (ANOVA) in R software to identify whether biodiversity change percentages differed among the levels of different subgroups (Supplementary material S5): (1) biodiversity features: structure and diversity; (2) taxonomic groups: vascular plants, soil microorganisms, and invertebrates; (3) restoration approaches: active restoration and passive restoration; (4) restoration age groups (years): 0–10, 10–20 and > 20; (5) past land use/cover types: degraded forestland, grasslands or croplands; (6) altitude groups (meters): 0–500 and 500–1000; and (7) temperature groups (°C): 16–19, 19–22 and 22–26. For additional information about variables grouping, see supplementary material S1 (data synthesis section). When testing whether normality and homogeneity of variance were passed and significance was observed at $p < 0.05$, Shapiro-Wilk and Tukey tests were used to compare the recovery gaps for multiple treatments. The multi-way ANOVA was used to test whether the interactions among restoration actions (past land use/cover types, restoration approaches, and restoration age groups) and environmental conditions (altitude and temperature) were significant for the recovery gap.

3. Results

Our searches resulted in a list of 3133 peer-reviewed studies after duplicates removal. According to the inclusion criteria, we selected 194 studies for full-text analysis (Supplementary material S2). The final database included 2370 observations (i.e., comparisons of biodiversity metrics between restoration vs. reference) from 76 studies. Field studies that involved more than one restoration action or taxonomic group were treated as multiple observations. Reclassified as biodiversity features, biodiversity metrics from different taxonomic groups resulted in 1219 observations of structure and 1151 of diversity (Supplementary material S3). Information on passive restoration comprised most of the data, for both features, as well as for the other subgroups of variables. Data of vascular plants and invertebrates occurred in similar proportions in the dataset and represented about 94% of the observations. Soil microorganisms encompassed the remainder of the data (6%).

3.1. Impacts of forest restoration on recovery gap

The restoration forests showed an overall recovery gap of 34% for structure features and 22% for diversity (Fig. 1). For structure features, the gap was higher for vascular plants (46%), than for soil microorganisms (26%), and invertebrates (7%) (Fig. 1a). Biodiversity responded similarly for diversity features, with vascular plants showing the higher gap (47%), followed by soil microorganisms (16%), and invertebrates (4%; Fig. 1b). The recovery gap depended more on the taxonomic group than the biodiversity feature, with the gap being, in general, higher for vascular plants than for invertebrates and soil microorganisms.

3.2. Effects of restoration actions on recovery gap

In the comparison of structural features of restoration vs. reference, the recovery gap was similar among past land-use types and restoration approaches, but not restoration age (Fig. 2a). When analyzing the past land-use types, we found a recovery gap for structure features of 35% for the restoration of degraded grassland, 33% for forestland, and 32% for croplands. Conversely, in the comparison of diversity features, the gap varied notably, being 14% for restored grasslands, but higher and similar for croplands (28%) and forestlands (34%; Fig. 2b).

Considering the different restoration approaches (i.e., active and passive restoration), the recovery gap was rather similar between active and passive restoration for both structure (41 and 31% respectively) and diversity features (21 and 22% respectively).

The recovery gap decreased with the increasing restoration age for structure (Fig. 2a), but not for diversity features (Fig. 2b). Compared with the reference state, the gap for structure features was 44% for restoration with the age < 10 years, 37% for 10–20 years, and 17% for >20 years, even though only the last age showed a different decrease in the gap. For diversity features, the recovery gap was similar between age groups (24%, 21%, and 23%, for <10 years, 10–20 years, >20 years, respectively). Observations for restoration age were relatively evenly distributed among all age groups (<10 years accounting for 28% of observations, 10–20 years about 35%, and > 20 years around 37%) (Fig. 2). However, in the last age group (i.e., >20 years), a great variation in the time since restoration started was seen for both restoration approaches, with active

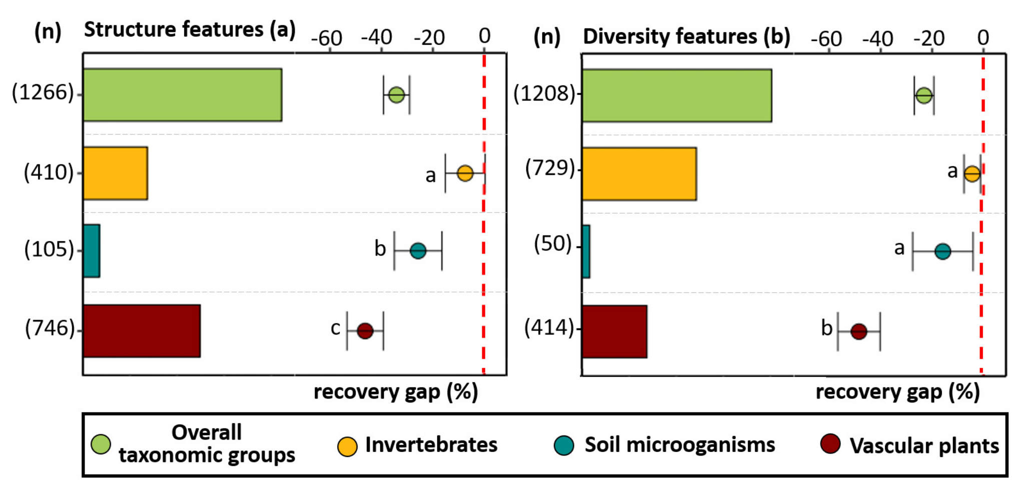

Fig. 1. Mean effects of biodiversity recovery for overall structure (a) and diversity features (b), and for three taxonomic groups in restoration forests. The number of observations (n) is illustrated by the bar charts and values in parentheses. Horizontal whiskers extending from the means denote bias-corrected 95% confidence intervals (CI's). If CI does not overlap with zero (red dotted line), the recovery effects are considered to be significant (restoration vs. reference). Values (%) close to zero (red dotted line) represent a shorter recovery gap; therefore, levels of biodiversity close to the reference forests. The different letters indicate a significant difference at $p < 0.05$ according to the Tukey test (comparing the three taxonomic groups).

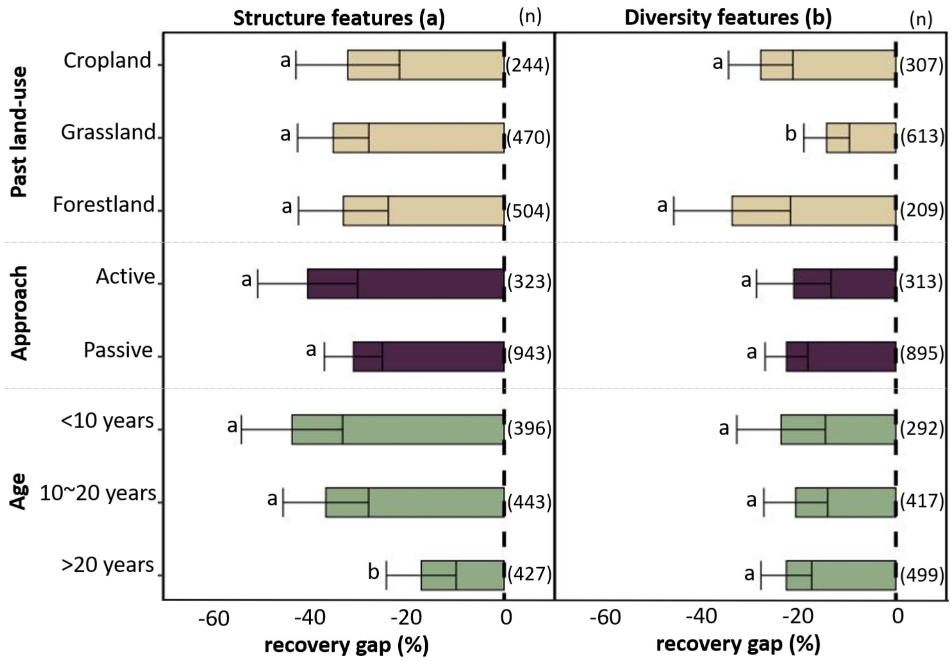

Fig. 2. Effects of restoration actions (past land use/cover types, restoration approaches, and restoration age groups) on recovery gaps percentages in the comparison restoration vs. reference. Bars represent recovery gap percentages and the number of observations is shown in parentheses. Whiskers extending from the bars denote bias-corrected 95% confidence intervals (CIs). The effect is considered to be significant when the 95% CI does not overlap with zero (black dotted line). The different letters above the bars indicate a significant difference at $p < 0.05$.

restoration ranging from 21 to 45 years, and passive restoration varying from 21 to 130 years.

The multi-way ANOVA showed that the recovery gap in both features depends on the interaction among the past land use/cover type, the restoration approach (i.e., active and passive restoration), and age (Table 1). In the comparison of structure features, the interaction between past land use/cover type and restoration approach influenced biodiversity changes, but the effect of age was only significant with the interaction of the three factors (i.e., past land use/cover type, restoration approach and age). Diversity features were influenced by the interaction of past land use/cover type and restoration approach, and also by the past land use/cover type and age (Table 1). The interaction among the three factors (i.e., past land use/cover type, restoration approach and age) seemed to be stronger in influencing diversity features than structure features.

3.3. Effects of environmental conditions on recovery gap

In general, both biodiversity features (structure and diversity) responded similarly to environmental conditions (Fig. 3). In terms of altitude, compared with the reference state, the recovery gap appeared to be inversely related to altitude. We found a higher recovery gap at 0–500 m for both structure and diversity features (37% in the two cases) than at 500–1000 m (28 and 10% for structure and diversity features, respectively)

Table 1
Interaction effects of recovery gap among restoration actions using multi-way ANOVA. Recovery gaps between restoration and reference forests, considering structure and diversity features; PLU, past land use/cover type; APP, restoration approach; AGE, restoration age; ns, non-significant ($p > 0.05$); *, significant at $p < 0.05$; **, significant at $p < 0.01$; ***, significant at $p < 0.001$; *Df*: degree of freedom.

Interaction effects	Df	F value	Sig. (p-value)	Df	F value	Sig. (p-value)
	Recovery gap of structure			Recovery gap of diversity		
PLU × APP	2	5.284	0.00519**	2	4.754	0.00879**
PLU × AGE	4	1.858	0.11556 ns	4	6.618	0.00289 **
APP × AGE	2	0.616	0.54044 ns	2	0.080	0.92288 ns
PLU × APP × AGE	4	2.735	0.02772*	4	7.914	0.00000***

(Fig. 3a, b). However, biodiversity responses at the two altitudes were different only for diversity features (Fig. 3b).

Temperature also appeared to influence the recovery gap. We found a higher recovery gap in the lowest and the highest temperature groups (i.e., 16–19 °C and 22–26 °C), while in the median temperature group (i.e., 19–22 °C) the recovery gap was lower for both structure and diversity features (Fig. 3). The recovery gap was 38%, 22% and 48% for structure (Fig. 3a), and 24%, 9% and 49% for diversity features (Fig. 3b), at 16–19 °C, 19–22 °C and 22–26 °C, respectively. The gap resulted similarly among 16–19 °C and 19–22 °C for both features (Fig. 3a), but different between 19–22 °C and 22–26 °C, for both features, and the recovery gap was higher at 22–26 °C. The interaction between altitude and temperature significantly influenced biodiversity responses for both features (Supplementary material S5).

4. Discussion

4.1. Impacts of forest restoration on recovery gap

Restoration is an effective way to increase biodiversity and ecosystem function (Crouzeilles et al., 2016; Curran et al., 2014; Huang et al., 2019), so we asked what factors appeared to influence biodiversity recovery in the BAF over intermediate timescales. Although our results were expressed as recovery gaps (that is, the potential incomplete recovery of biodiversity occurring during the restoration process), we can clearly understand the results as an increment of biodiversity seeing a shorter gap as a better (or even ideal) condition, since values next to zero represent levels of biodiversity close to the reference forests.

Compared with reference sites, forests undergoing restoration in the BAF showed a recovery gap of 34% for structure and 22% for diversity features (Fig. 1); results were consistent with a previous global meta-analysis (Moreno-Mateos et al., 2017), which documented a higher recovery gap for abundance (structure feature) than for diversity (45% and 35%, respectively), also integrating different biodiversity metrics, restoration approaches and organisms across different forest ecosystems. Conversely, Huang et al. (2019) conducted a meta-analysis in China and found a very small gap for diversity features between restoration and reference forests

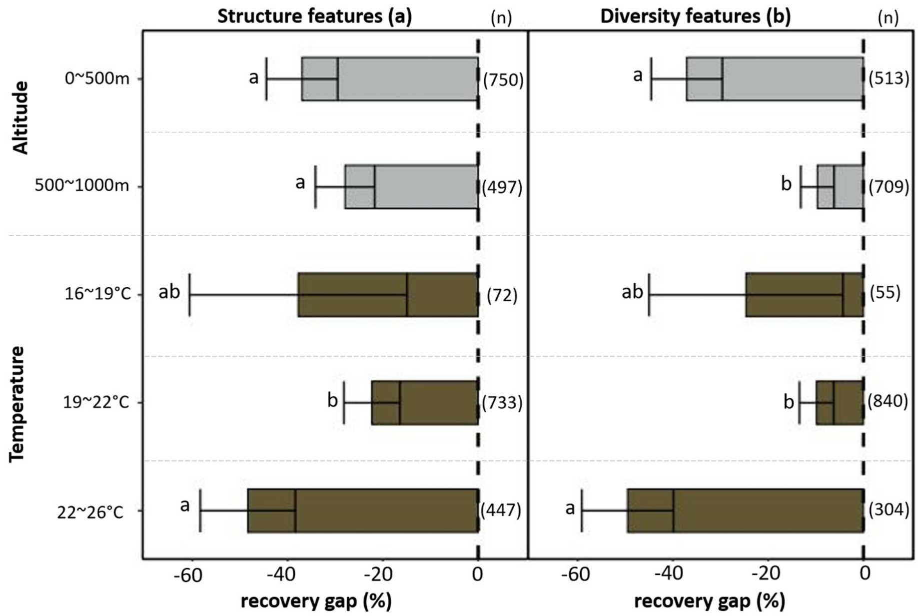

Fig. 3. Effects of environmental conditions (temperature and altitude) on biodiversity recovery to forest restoration. Observation numbers are shown in parentheses. Whiskers extending from the bars denote bias-corrected 95% confidence intervals (CIs). The effect is considered to be significant when the 95% CI does not overlap with zero (black dotted line). The different letters above the bars indicate a significant difference at $p < 0.05$.

(~3%), considerably lower than our results for the BAF, while the gap for structure features in their study was higher (~16%) but still lower than results found here, which may be associated with environmental quality and the intensity of previous disturbances (Rozendaal et al., 2019). The recovery gaps differed for the two biodiversity features (diversity and structure) that we investigated, reinforcing the need to consider different measures to assess restoration success.

Our results indicated a shorter recovery gap for diversity features in relation to structure features, but the latter responded more sensitively to the time elapsed since restoration started (Fig. 1a). Nonetheless, it is important to emphasize that we assumed diversity and structure features to be broad biodiversity measures. Therefore, some specific and important aspects of the diversity may not be effectively revealed, for example, the species composition (i.e., species identity and relative abundance). According to existing literature (e.g., Rozendaal et al., 2019; Abbas et al., 2019), species composition does not recover rapidly. Conversely, diversity and richness metrics, which were common in our dataset, may be able to recover to a certain degree whether the species pool is not heavily damaged, but they represent just partly the diversity features. Furthermore, it has been shown in several studies (Viapiana et al., 2019; Pedraza et al., 2021; Siminski et al., 2021) that at an early stage of restoration, often fast-growing pioneer species are responsible for species richness and vegetation structure, but climax species are not or only very slowly recovering. Previous studies have also pointed out that the recovery of structure features are likely to take orders of magnitude longer than species diversity (Dunn, 2004; Helmer et al., 2008), particularly in tropical forests (Meli et al., 2017). The recovery of structure features may be affected by several factors during the restoration process, for example, grass invasion, which can impede plant establishment, and alter numerous vegetation descriptors such as biomass, density, and abundance (Weidlich et al., 2020). As plants are key species in ecosystems, improving microhabitats for other species (Kreyling et al., 2010), structural features for other taxonomic groups (e.g., abundance) may also be affected.

Our results also revealed that the recovery of biodiversity features differed among the three taxonomic groups. Although most forest restoration projects in the BAF have been focusing on vegetation recovery and succession in the last decades (Rodrigues et al., 2009), recovery levels of soil microorganisms and invertebrates were significantly higher than that of vascular plants (Fig. 1). Huang et al. (2019) found this same tendency across restoration sites in China. Soil microorganisms and invertebrates have been described as very sensitive taxonomic groups to habitat changes and environmental quality (Lawes et al., 2017; Stephens et al., 2016), and they also have short generation times and disperse well, which may explain why they showed a shorter recovery gap in the restoration process.

Overall, diversity features showed similar recovery gaps across all restoration age groups (Fig. 1b). Conversely, gaps for structure features decreased as the age increased (Fig. 1a). Thus, biodiversity recovery levels in the BAF would be mainly reflected in early ages (i.e., <20 years) in enhancing the diversity features rather than the structure features. Nevertheless, it is crucial to reinforce that we refer to the structure features in a broad sense as well, comprising a myriad of community patterns and arrangements (Chirici et al., 2011, 2012). Therefore, results may not be sensible enough to strictly reflect characteristics of the three-dimension arrangements (for plants), such as the dynamics of the canopy cover.

Because there were differences in the recovery gaps of the three different taxonomic groups, a higher taxonomic and functional data resolution would improve and advance our understanding in future research on how organisms can differ in biodiversity recovery within a class (Meli et al., 2014). We recommend incorporating both structural and diversity components during the planning, implementation, and assessment phases of forest restoration programs in the BAF for sustainable and adaptive management. Nonetheless, it is worthy to highlight that only focusing on these features could be insufficient for the recovery of ecological functions since diversity and structure themselves would not fully reflect ecosystem functioning (Meli et al., 2017, 2014; Moreno-Mateos et al., 2017). Therefore, they are not the main driver of restoration success (Crouzeilles et al., 2016); although biodiversity features might often be a prerequisite to achieving functional ecosystem recovery (Moreno-Mateos et al., 2017; Ren et al., 2017).

Further studies are still needed to clarify whether and how biodiversity enhancement indicates that the composition of flora and fauna has been recovered in relation to reference forests. Under such circumstances, forest ecosystem recovery should be emphasized. Only increasing the quantity of low-functional restoration forests may be inadequate alternatives to advance sustainable restoration projects in the tropics (Moreno-Mateos et al., 2017), mainly, during the UN Decade on Ecosystem Restoration.

4.2. Effects of restoration actions on recovery gap

We found that the time elapsed since restoration started is correlated with the recovery of structure features (Fig. 2a), but results became significantly lower only after 20 years of restoration. However, compared with the reference forests, the recovery gap in restoration forests remained relatively high (~17%). For diversity features, the gap ranged from 21 to 24% across all ages in restoration sites (Fig. 2b).

Congruently with our findings, previous work has reported that diversity features (e.g., species richness) tend to converge to old-growth reference values within a century, species similarity (e.g., Sørensen) takes about twice as long, and assemblage composition can take up to an order of magnitude longer (hundreds to thousands of years) (Curran et al., 2014). Similarity and species composition are generally the last diversity features recovering in tropical forests undergoing restoration for two main reasons (Dalmaso et al., 2020; Jakovac et al., 2021). First, at early ages plant communities in restoration sites are often limited to a few species. Second, it is difficult to recover the pool of species that exist in mature forests, where diversity is the result of coevolution, and inter- and intraspecific interactions among species over time (Dalmaso et al., 2020; Jakovac et al., 2021). This probably prevented us from detecting a strong influence of restoration age on the diversity recovery of taxonomic groups. Hence, time is required for restored systems to reach similar values of biodiversity to those found in reference systems. Previous research has confirmed that time is a key factor for explaining forest restoration success, for both diversity and structure features (Cole et al., 2014; Martin et al., 2013).

We found no differences in recovery gaps for all taxonomic groups considering the different restoration approaches (i.e., active and passive), for both structure and diversity features (Fig. 2). Similar to previous research (Barral et al., 2015; Curran et al., 2014), our comparison of active and passive approaches suggested that both restoration action types may lead to an increase in biodiversity recovery. This underscores the fact of seeing the two strategies not as mutually exclusive alternatives (Reid et al., 2018) but as complementary approaches that can be combined to maximize biodiversity recovery and conservation (Crouzeilles et al., 2019a; Rey Benayas and Bullock, 2012; Chazdon et al., 2021). For diversity recovery under active restoration, it is important to keep in mind that the identities and relative proportions of species involved at the beginning of the restoration process, as well as the complexity and quality of reference forests, will influence biodiversity responses and allow to predict a certain level of diversity in restoration forests (Crouzeilles et al., 2019a; Meli et al., 2014; Rozendaal et al., 2019).

Furthermore, active restoration initiatives are generally not exposed to the same environmental filters as passive restoration (Reid et al., 2018), and the process of passive restoration can be highly variable (Gilman et al., 2016; Holl and Zahawi, 2014). However, due to inherent uncertainty and risks of restoration failure (Curran et al., 2014), future offset actions in the BAF should consider exceeding the level of recovery gaps we found to be used in practical applications. Since passive restoration is generally less costly than active restoration, the former may be a feasible alternative to enhance biodiversity when budgets are limited, and landscape features are favorable (Kauano et al., 2013). Previous research indicated that it is often worthwhile to observe natural forest recovery for a certain time to assess if natural regeneration will achieve management objectives before deciding whether some form of active intervention is warranted (Holl and Aide, 2011).

Congruently with past studies (Crouzeilles et al., 2016; Huang et al., 2019; Meli et al., 2017), our results showed that forest restoration should be evaluated relative to the past land use. Previous disturbance types are key drivers influencing vegetation succession and restoration success (Brancalion et al., 2016; Crouzeilles et al., 2016). We found that restoration of degraded grasslands in the BAF resulted in the lower recovery gap for diversity features, but we found no difference of past land use influencing structure features. Past land use should be carefully evaluated for restoration initiatives in the BAF because this ecological domain has been subjected to diverse disturbances over the years, for example, sugar cane in the northeast and coffee plantations in the southeast, to timber extraction activities in the south (Carlucci et al., 2021; Lins-e-Silva et al., 2021). Along with other factors such as soil characteristics and water availability, the past land use, and the disturbance regime are important filters to the seedling establishment in restoration sites (Brudvig, 2011; Holl et al., 2000).

Finally, the interaction effects among past land use/cover type, restoration approach, and restoration age influenced both the recovery of structure and diversity features (Table 1). Results for diversity were mainly influenced by the past land use/cover type interacting with the other variables, which is confirmed by the negative effect in the interaction among restoration approach and age. For structures features, interactions of effects were strictly due to past land use/cover type and restoration approach. Biodiversity recovery depends on the degradation level of the environment, and also the remaining species pool. If a lot of species remain nearby, biodiversity recovery tends to be high, otherwise, there is hardly any recovery (Pardini et al., 2010). Considering the restoration approach, the more destroyed the ecosystem, the more planting or any other damage mitigation would be needed in active interventions (Morrison and Lindell, 2011). In the BAF, remnant forests patches are scattered in the landscape, which may act as propagule sources for recovery. Therefore, the recovery of both structure and diversity features in the BAF may be favored by the landscape, when compared with other damaged ecosystems around the world.

4.3. Effect of environmental conditions on recovery gap

Biodiversity is not evenly distributed across spatial scales (Perillo et al., 2021), and among the main factors explaining species diversity are latitudinal (Willig et al., 2003) and elevational gradients (Bueno et al., 2021; Janzen, 1967). The drives influencing broad-scale species pool diversity have challenged ecologists for centuries (Peters et al., 2016; Vetaas et al., 2019), and yet, the relationship between environmental conditions and biodiversity patterns is poorly understood or immature (Kidane et al., 2019; Rahbek, 2005).

Our results confirmed the assumption that biodiversity varies with environmental conditions (Harris et al., 2006; Mantyka-pringle et al., 2012; Rozendaal et al., 2019), and that altitude is tightly related to temperature in this process (Huang et al., 2019; Tang et al., 2006), and influenced the recovery gap in restoration forests in the BAF. The recovery gap was higher for both structure and diversity features at the temperature group 22–26 °C (~49%) and significantly lower at the temperature group 19–22 °C (22% and 9% for structure and diversity, respectively). Among altitude groups (0–500 m and 500–1000 m), the recovery gap differed only for diversity features, being lower at the altitude group 500–1000 m (~10%) than in the altitude 0–500 m (~37%). Most observations occurred at temperature groups 19–22 °C (64%) and 22–26 °C (30%), which implied that the quantitative evidence of these two groups was more reliable, and had a great influence on our results. Observations between altitude groups were evenly distributed.

Our results suggest that the temperature ranging from 19 to 22 °C and altitudes ranging from 500 to 1000 m may favor both the recovery of diversity and structure features in the BAF. This is likely because the warm and humid under these environmental conditions may favor vegetation succession and increment, and create diversified habitats for fauna (Kullberg and Moilanen, 2014; Suding et al., 2015).

Higher temperatures and water availability have been associated with faster and more diverse patterns of forest recovery in the Neotropics (Rozendaal et al., 2019), and high plant species richness is expected in low latitudes (Wang et al., 2011). Past research documented that differently to plant species richness distribution, the recovery rates of woody plant species in tropical forests can be higher in low temperatures, and high precipitation may favor forest recovery at high elevations (Wang et al., 2011). Species richness tends to increase with water availability as a result of weaker environmental filtering (Huston, 1994). However, the relatively low recovery rates of diversity features in humid areas may also be related to the pool of species, since in drier forests the potential lower number of species present may allow for faster recovery rates (Rozendaal et al., 2019). As the BAF comprises different types of forest (Joly et al., 2014; Marcilio-Silva et al., 2018), the mechanisms on how temperature, altitude, and other environmental factors influence biodiversity recovery in this region need to be further investigated since evidence (Marcilio-Silva et al., 2018; Rozendaal et al., 2019) suggest that forest type is an important variable to be considered when analyzing biodiversity changes.

4.4. Limitations, uncertainties, and recommendations

By integrating data from a variety of sources and restoration locations, we increased our understanding of the mechanisms underlying general patterns and processes for biodiversity recovery in the BAF, helping to develop new avenues for future research. Since biodiversity is a complex topic that covers many aspects of biological variation (Huang et al., 2019; Mooers, 2007), there may be some intersections in our reclassification of biodiversity metrics into diversity and structure features (Supplementary material S3). Here, we echo recommendations from others (Huang et al., 2019), that future studies explore biodiversity features, restoration actions and environmental conditions in different ways (i.e., groups of variables) and reveal how they potentially may change following forest restoration. Also, even though we addressed potential pseudoreplication, we point out that some studies in our database presented a large number of observations (>100) compared to others (<10), and the reference forests age wasn't a controlled factor, therefore, these issues should be the object of detailed analysis in the continuation of this research.

Since a myriad of conditions affects the responses of biodiversity to restoration actions, we support Reid et al. (2018) claim that reliable comparisons among restoration approaches would be benefited by paired assessments at the same site. However, due to the intrinsic complexities of underground restoration projects, empirical research that follows this specific design (i.e., comparisons of strategies at the same site) is scarce. Thus, we could expect high variable restoration results. For example, comparisons of different restoration approaches in separate study areas of varying ages are affected by confounding factors (Meli et al., 2017). Furthermore, although key restoration practices and environmental conditions from each included study were represented, there may be a potential geographic bias in our pool of studies, since most observations occurred in the south and southeast region of Brazil (Fig. S1, Supplementary material S1). Despite many simplifications and assumptions in our analysis, we believe that the general trends in results are robust, and our conclusions appropriate. Lastly, we recommend that authors of primary research provide detailed information on study site characteristics, restoration history, and complete statistical data because it is important to control effects from these variables to increase the predictive power of future meta-analytic studies.

5. Conclusions

We reveal that diversity features reflected better biodiversity recovery in the BAF in the short term (<20 years of restoration), showing a recovery gap of 12% lower than structure features. As restoration did not result in similar values of biodiversity to those of reference forests, we argue that primary forests in the BAF are irreplaceable for the maintenance of biodiversity. We investigated fours groups of influence variables (i.e., biodiversity features – in the highest hierarchy, taxonomic groups, restoration actions, and environmental conditions) on the effectiveness of biodiversity recovery, among which vascular plants, soil microorganisms, and invertebrates represented all observations. The recovery gap depended more on the taxonomic group than the biodiversity feature, being the gap, in general, higher for vascular plants than for soil microorganisms and invertebrates. The latter group, in particular, was the unique taxonomic group that achieved levels of recovery close to reference forests. Our results support the assumption that restoration approaches (i.e., active and passive restoration) must be seen as complementary and synergistic strategies. Thus, restoration approaches in the BAF should be combined as required by the landscape context, and changes in the recovery gap understood as case-dependent. We found areas comprising the temperature group 19–22 °C and the altitude group 500–1000 m showing the lowest recovery gap for both features. Our study may be useful in guiding restoration practitioners in varied decision-making processes, showing the directions to the recovery of different biodiversity features, which can potentially contribute to biodiversity offsetting policies in the BAF, and help to understand how coupled biodiversity features respond to the interaction of environmental conditions and restoration actions in a fragmented tropical landscape.

CRediT authorship contribution statement

JPR, PM, AVR, RRR conceived the ideas and designed methodology; JPR, JPBS, IJ, LRS, DPT collected the data; JPR, PM, AVR analyzed the data. All the authors led to the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

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Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

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