CONTRIBUTED PAPER

Conservation Biology

Effects of deforestation on multitaxa community similarity in the Brazilian Atlantic Forest

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Article impact statement: Brazilian legislation is insufficient to prevent biotic homogenization of vertebrate and invertebrate communities in Atlantic Forest.

Abstract

Habitat loss can lead to biotic homogenization (decrease in β diversity) or differentiation (increase in β diversity) of biological communities. However, it is unclear which of these ecological processes predominates in human-modified landscapes. We used data on vertebrates, invertebrates, and plants to quantify β diversity based on species occurrence and abundance among communities in 1367 landscapes with varying amounts of habitat (<30%, 30−60%, or >60% of forest cover) throughout the Brazilian Atlantic Forest. Decreases in habitat amount below 30% led to increased compositional similarity of vertebrate and invertebrate communities, which may indicate a process of biotic homogenization throughout the Brazilian Atlantic Forest. No pattern was detected in plant communities. We found that habitat loss was associated with a deterministic increase in faunal community similarity, which is consistent with a selected subset of species being capable of thriving in human-modified landscapes. The lack of pattern found in plants was consistent with known variation between taxa in community responses to habitat amount. Brazilian legislation requiring the preservation of 20% of Atlantic Forest native

vegetation may be insufficient to prevent the biotic homogenization of faunal communities. Our results highlight the importance of preserving large amounts of habitat, providing source areas for the recolonization of deforested landscapes, and avoiding large-scale impacts of homogenization of the Brazilian Atlantic Forest.

INTRODUCTION

Habitat loss, the primary threat to global biodiversity (Barlow et al., 2018; Hansen et al., 2013), not only leads to a decline in species diversity (Fahrig, 2003; Watling et al., 2020), but also can cause changes in community composition, giving rise to opposing processes of biotic homogenization or differentiation. Biotic homogenization refers to the increase of compositional similarity among communities over time (i.e., decrease in β diversity) (McKinney & Lockwood, 1999; Olden & Rooney, 2006). Conversely, an increase in β diversity is associated with biotic differentiation (Baeten et al., 2012; Laurance et al., 2007). The homogenization of biological communities can lead to undesirable consequences, given that an increase in compositional similarity is frequently associated with a reduction in functional and phylogenetic diversity (Liang et al., 2019; Rivera et al., 2023), which in turn can reduce ecosystem resilience to future disturbances (Olden et al., 2004) and ecosystem services (Clavel et al., 2011; Marcacci et al., 2021). Therefore, maintaining compositional similarity is frequently a goal in conservation planning (Socolar et al., 2016).

Changes in β diversity are determined by deterministic and stochastic processes (Chase et al., 2011; Vellend, 2010) that are not mutually exclusive and can influence community composition simultaneously (Ning et al., 2019). As habitat loss progresses, a decrease in β diversity may occur due to the deterministic extinction of habitat specialists and the proliferation of habitat generalists (Newbold et al., 2018; Tabarelli et al., 2012), which can lead to a biotic homogenization among communities (Carrara et al., 2015; Karp et al., 2012, 2018; Kormann et al., 2018; Vázquez-Reyes et al., 2017). An increase in β diversity often emerges as a consequence of stochastic processes, such as increasing dispersal limitation due to the isolation of habitat patches and ecological drift (Hubbell, 2001; Zhou et al., 2014).

Such a pattern may also arise when habitat loss increases environmental heterogeneity (Arroyo-Rodríguez et al., 2013; Chase et al., 2011), for example, through the creation of edges (Laurance et al., 2007; Sfair et al., 2016). This heterogeneity can lead to the emergence of new environments occupied by habitat generalists (Filgueiras et al., 2021). Investigating the importance of deterministic and stochastic processes governing landscape-wide β diversity provides useful information for conservation theory and practice in human-modified landscapes (Vellend, 2010).

Although habitat patches may differ in quality and connectivity in human-modified landscapes (Lindenmayer & Fischer, 2013), dispersal abilities, such as movement capacity, dispersal mode, and life-history traits, associated with functional connectivity can also influence community composition (Newbold et al., 2013; Öckinger et al., 2010). In general, β diversity is expected to be lower among local communities of species with high dispersal abilities (e.g., bats and large-bodied mammals) than among less vagile species (e.g., trees, dung beetles, and other less mobile invertebrates). Differences in dispersal abilities may be particularly relevant in defining β diversity patterns in landscapes with low structural connectivity (i.e., those with low amounts of habitat, isolated fragments, and an inhospitable matrix) (Villard & Metzger, 2014). Several studies have investigated patterns of biotic homogenization and differentiation across human-modified landscapes worldwide (Li et al., 2020; Olden et al., 2018), but most focused on a single taxon (e.g., Arroyo-Rodríguez et al., 2013; Karp et al., 2012; Kormann et al., 2018) or a geographically restricted region (Baeten et al., 2012; Vázquez-Reyes et al., 2017). Thereby, the current understanding of how different taxa are influenced by different processes is still limited.

A challenge to understanding the processes of biotic homogenization and differentiation is the many indices available

to quantify compositional similarity (Anderson et al., 2011). Indices of β diversity based on null models are particularly useful in the context of habitat loss because they control for differences in species richness (α diversity) among sampling sites. Without controlling for differences in α diversity, β diversity estimates between sites with low α diversity relative to the regional species pool (γ diversity)—a pattern commonly found in species-rich ecosystems—are likely to result in estimates of low similarity due to chance alone, leading to erroneous conclusions (Chase et al., 2011). Moreover, β diversity metrics based on null models allow measuring the relative contribution of both deterministic and stochastic processes (Chase et al., 2011; Ning et al., 2019). Although communities structured mainly through stochastic processes are expected to have β diversity patterns similar to a random species distribution (i.e., null model), communities governed by deterministic processes differ from those expected by chance (Chase et al., 2011). Finally, changes in β diversity can be underestimated if only species occurrence is considered, given that the impact of habitat loss is expected to primarily cause population reduction preceding species extinction (Cassey et al., 2008). For example, increased distance between habitat patches caused by habitat loss may prevent migration of individuals among patches (Jamoneau et al., 2012; Püttker et al., 2011), thereby limiting the increase in abundance or the rescue effect by immigration. However, likely due to the imprecision of common sampling methods in estimating the number of individuals of certain taxa (Montgomery et al., 2021), the use of abundance data to estimate β diversity in studies investigating biotic homogenization or differentiation is limited (Olden et al., 2018).

We used a multitaxa database on community composition in 1367 landscapes throughout the Brazilian Atlantic Forest biodiversity hotspot to investigate whether habitat loss leads to an increase or decrease in community-level β diversity. The Brazilian Atlantic Forest represents a natural laboratory for evaluating the consequences of habitat loss on β diversity patterns given its high level of biodiversity (Laurance, 2009; Ribeiro et al., 2011) and its marked gradient of habitat amount across landscapes, ranging from large continuous forest areas to landscapes comprised exclusively of small and isolated forest fragments (80% of which are <50 ha and on average 1440 m distance from other fragments [Ribeiro et al., 2009]).

Although general patterns of β diversity have been intensively investigated in the Brazilian Atlantic Forest, most studies focused on among-landscape comparisons. However, valid inferences about biotic homogenization and differentiation processes can only be generated by analyzing β diversity among landscapes in a given class of forest amount, followed by subsequent comparisons between the classes (Olden & Rooney, 2006). Furthermore, in studies relying on β diversity indices, authors often did not control for differences in α diversity (e.g., Carrara et al., 2015; Filgueiras et al., 2019; Souza et al., 2019; Vázquez-Reyes et al., 2017) or evaluate β diversity patterns exclusively for a particular group of taxa (e.g., Barreto et al., 2023; Filgueiras et al., 2016). We investigated the relationship between within-landscape β diversity, based on occurrence and abundance data with null models across 3 classes of landscape-wide habitat amounts (forest cover >60%, 30−60%, and <30%

of landscape area), and 3 major taxonomic groups (vertebrates, invertebrates, and plants). Because empirical studies in the Brazilian Atlantic Forest have shown the proliferation of habitat generalists and a decrease in disturbance-intolerant or forest-dependent species in highly deforested landscapes (Banks-Leite et al., 2014; Estavillo et al., 2013; Morante-Filho et al., 2015; Pardini et al., 2010), we hypothesize habitat loss has a deterministic influence on community composition that leads to an increase in similarity among local communities and, therefore, indicating biotic homogenization. Further, we expected changes in β diversity to vary among taxa, especially in communities in highly deforested landscapes, where differences in dispersal abilities among taxa are relevant in defining β diversity patterns (Leite et al., 2022).

METHODS

Data compilation

We obtained data on community composition of multiple taxa in forest fragments across the Brazilian Atlantic Forest from the Synthesis in Atlantic Forest Ecology and Sustainability Group (Püttker et al., 2020). This group is a network of researchers aiming to compile empirical datasets for the investigation of biodiversity patterns in Brazilian Atlantic Forest fragments. We included in our analyses only datasets for which sampling was conducted in forest fragments, targeted the same taxonomic group, and was conducted during the same period with standardized methods, and, therefore, provided comparable samples among sites in the same dataset. Abundance data had to be available to allow for the estimation of β diversity based on both occurrence and abundance so that we could recognize responses that are undetectable when relying on occurrence data only (Cassey et al., 2008; Püttker et al., 2015). The focus of the data had to be aboveground terrestrial communities, given that the composition of soil fauna communities is highly influenced by environmental variables at much smaller spatial scales than those we considered (Rantalainen et al., 2008). Finally, datasets had to contain at least 3 sampling sites in at least 2 of the 3 classes of habitat amount of <30%, 30−60%, and >60% in the landscape (thereby guaranteeing at least 3 estimates of β diversity in 2 classes of habitat amount per dataset).

In total, our database included 43 datasets with considerable variation regarding number of sampling sites, species richness, and spatial extent (Appendix S1). Although most data were collected with standardized sampling effort among sampling sites, 14 datasets were based on unbalanced samplings (∼32% of the database). To control for disproportional differences in sampling effort, we excluded all sites with a sampling effort outside 2 SDs from these datasets, which led to a total of 1367 sampling sites across all datasets included. No restrictions were established regarding habitat preference (e.g., forest specialists or habitat generalists) or taxon, resulting in a wide spectrum of taxa: 24 vertebrate datasets (amphibians, birds, lizards, reptiles, small, medium, and large mammals), 7 invertebrate datasets (ants, bees, beetles, butterflies, and termites), and 12 plant datasets (trees, bryophytes, and epiphytes).

All species were identified by the authors of the individual datasets. Specimens that could not be identified to species level were assigned to a unique morphospecies (mostly for plants and invertebrates).

Landscape-scale habitat amount

Although biotic homogenization and differentiation are defined as changes in β diversity over time (McKinney & Lockwood, 1999; Rolls et al., 2023), detailed data on communities across time ranges are rare, especially when considering taxa with extended lifespans like plants. Therefore, ecological studies in general, and investigations of biotic homogenization and differentiation in particular (Kramer et al., 2023), commonly adopt a space-for-time approach, substituting the lack of repeated observations over time with a single observation across multiple locations along a gradient of habitat loss (Pickett, 1989). Although the space-for-time approach has been criticized (Damgaard, 2019), recent comparisons of both approaches in the context of the effects of habitat loss led to remarkably similar results (Attinello et al., 2024). While acknowledging its limitations, we argue that changes in community similarity over space likely allow for inference on biotic homogenization and differentiation. Thus, we assumed that a decrease in β diversity showing that habitat loss caused an increase in community similarity can indicate biotic homogenization of biological communities. Conversely, an increase in β diversity can indicate the occurrence of biotic differentiation.

We defined each sampling site as a local landscape following a patch-landscape approach (Arroyo-Rodríguez & Fahrig, 2014; Fahrig, 2013), where the area surrounding the point coordinates represented the corresponding spatial extents (landscape sizes). Based on 30-m spatial resolution land cover maps (Project MapBiomas, 2023), we classified all native forest classes (i.e., deciduous and semideciduous forest) as habitat in each local landscape and all other classes (i.e., pasture, urban areas, and water) as nonhabitat (matrix). We then calculated total forest cover at local landscapes with landscapemetrics R package 1.5.4 (Hesselbarth et al., 2019), which was then classified into 1 of 3 classes of habitat amount: <30%, 30−60%, and >60% (Figure 1). We defined these classes based on evidence of nonlinear effects of habitat loss on biodiversity (thresholds) through the entire gradient of habitat amount (0−100%). When habitat amount is above ∼60%, large amounts of resources and landscape percolation (Stauffer & Aharony, 1992; With & Crist, 1995) reduce the impact of habitat loss on species richness (Pardini et al., 2010; Püttker et al., 2020). When the amount of habitat ranges from approximately 30% to 60%, landscape configuration varies widely (Villard & Metzger, 2014), resulting in local species richness strongly dependent on local conditions. Finally, when habitat amount is below ∼30%, distances among habitat patches increase exponentially, thereby reducing structural connectivity and potentially leading to regional extinction of habitat specialists (Boesing et al., 2018). To evaluate the scale of effect (i.e., spatial extent at which landscape attributes have the strongest impact on species−landscape relationships [Jackson & Fahrig, 2015]), we tested 5 distinct landscape sizes surrounding the point coordinates (radii of 0.5, 1, 2, 4, and 8 km). All estimates were based on maps corresponding to the median year of data collection of each dataset, thereby ensuring that information from maps and community data refer to the same period.

Estimation of β diversity

Standard β diversity indices of community composition, such as Jaccard and Sørensen indices, are influenced by α diversity patterns and thus may result in biased estimates (Chase et al., 2011). Because α diversity is affected by habitat loss (Fahrig, 2003; Watling et al., 2020), we used the modified Raup−Crick β diversity indices (Raup & Crick, 1979). Raup−Crick β diversity indices control for differences in α diversity among sampling sites through the use of random permutations of observed communities as a null model for estimating β diversity based on occurrence (hereafter $\beta_{RC\text{-}occur}$) (Chase et al., 2011) or abundance data (hereafter $\beta_{RC\text{-}abund}$) (Stegen et al., 2013). Although $\beta_{RC\text{-}occur}$ indicates the similarity regarding species presence and absence between sites, $\beta_{RC\text{-}abund}$ is used to evaluate community similarity based on numbers of individuals of each species among sites. Additionally, the use of the null model allows for discerning the relative influence of deterministic and stochastic processes on observed β diversity changes. Both $\beta_{RC\text{-}occur}$ and $\beta_{RC\text{-}abund}$ indices range from −1 to +1 and indicate whether community composition at 2 sites is more similar (close to −1) or more dissimilar (close to +1) from the null model (close to 0). Values of Raup−Crick β diversity closer to $|1|$ indicate a strong contribution of deterministic processes, whereas values approaching 0 indicate community composition more similar to community assemblies governed mainly by stochastic processes. The threshold of $|\beta_{RC}| = 0.95$ reflects a significant difference between observed values and the null model expectation. Hence, values $|\beta_{RC}| > 0.95$ indicate that communities are governed primarily by deterministic processes (Chase et al., 2011; Stegen et al., 2013).

Using NST R package 3.1.3 (Ning et al., 2019), we estimated $\beta_{RC\text{-}occur}$ and $\beta_{RC\text{-}abund}$ among all pairs of local landscapes in each dataset. To generate null models, we defined all species (or individuals) in the respective dataset as the regional species pool (or regional pool of individuals), from which 10,000 simulated communities were drawn assuming random spatial distribution across local landscapes. Because we were interested in maintaining the relationship between habitat amount and species richness in null models, we fixed species frequencies and defined species richness in local landscapes as proportional to the richness in the original data (SIM4 algorithm [Gotelli, 2000]). Because the number of local landscapes per class of habitat amount (<30%, 30−60%, and >60%) varied in most datasets, sampling effort was unbalanced between classes. These differences in numbers of local landscapes among classes may lead to a biased regional species pool because classes with a higher number of local landscapes (therefore, representing a higher number in the regional pool) would lead to overrepresentation of species occurring in those classes due to chance alone (Vellend et al., 2007). We, therefore, corrected
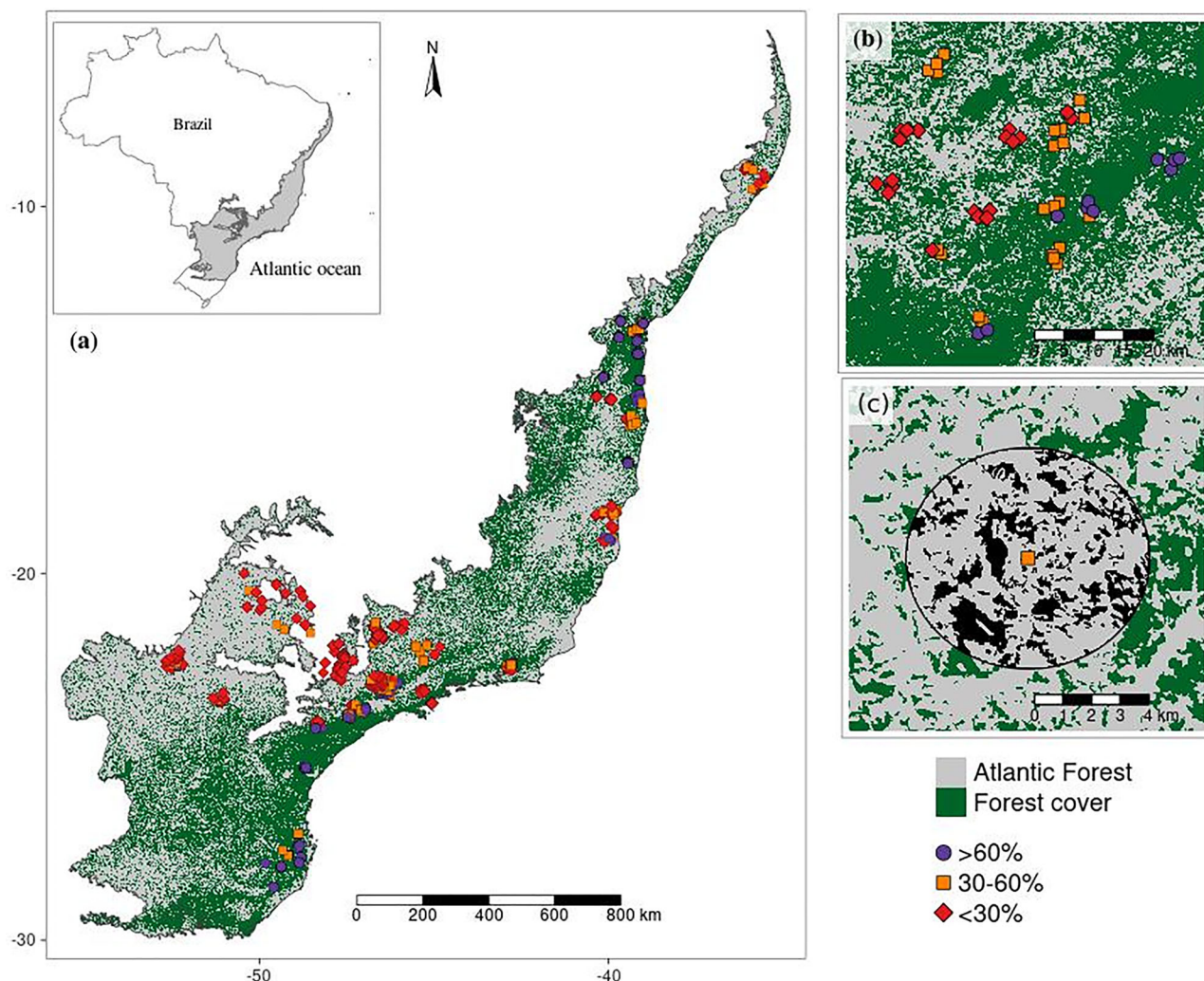
FIGURE 1 (a) Spatial range of the Brazilian Atlantic Forest (gray in inset) and distribution of sampling sites across the study region (shaded area, original extent of the Brazilian Atlantic Forest; green, forest cover in 2019 [obtained from Project MapBiomas 7.0]; red diamond, <30% habitat amount; orange square, 30−60% habitat amount; purple circle, >60% habitat amount), (b) example of sampling site distribution from a single dataset (Boesing et al., 2018), and (c) local landscape (circular area, 4-km radius from coordinates of a sampling site) with forest remnants included in the calculation of habitat amount (black).

species frequencies in the regional pool for each dataset following Vellend et al. (2007). For $\beta_{RC\text{-}occur}$, we first calculated the proportion of local landscapes occupied by each species per class of habitat amount and then defined the mean proportion of occupied fragments among the 3 classes of habitat amount as species frequencies in the regional pool used to generate the null models. For $\beta_{RC\text{-}abund}$, we applied an analogous procedure, but we used individuals (instead of species) to define a regional pool. Thus, we weighted individuals in the regional pool based on the mean number of individuals per local landscape among classes of habitat amount.

Data analyses

To test for differences in mean $\beta_{RC\text{-}occur}$ and $\beta_{RC\text{-}abund}$ among the 3 classes of habitat amount, only estimates from the same class in a dataset were considered (comparisons between local landscapes from distinct habitat amount classes were discarded) as response variables in linear mixed models (LMMs) with Gaussian distribution (goodness-of-fit graphs in Appendix S2). We included classes of habitat amount as a fixed factor and the identity of each dataset as a random intercept. Because the spatial extent at which the effect of habitat amount best predicts $\beta_{RC\text{-}occur}$ and $\beta_{RC\text{-}abund}$ (i.e., scale of effect) (Jackson & Fahrig, 2015) was unknown, a priori we built LMMs considering the 5 landscape sizes (i.e., 0.5, 1, 2, 4, and 8 km). The definition of the best scale of effect was based on the highest conditional R^2 values (R^2_C), where the variance explained included fixed and random variables (Nakagawa & Schielzeth, 2013) among the 5 LMMs with different landscape sizes. To test whether differences in the results depended on the taxonomic group investigated, we repeated the analyses for each of the 3 subsets of the data corresponding to 3 distinct taxonomic groups (vertebrate, invertebrate, and plant). Discrimination of subsets at lower taxonomic levels

was not possible due to low sample sizes in habitat amount classes.

Geographic distances among sampling sites varied considerably across datasets among landscape sizes and taxonomic groups (Appendices S3–S6). Therefore, we included the geographic distance between the same pair of local landscapes considered in β diversity estimates as an additional fixed factor in all models.

We applied Tukey post hoc tests to test for pairwise differences in mean $\beta_{RC\text{-}occur}$ and $\beta_{RC\text{-}abund}$ between habitat amount classes. Because at least 3 local landscapes had to represent at least 2 classes of habitat amount per dataset (see "Data Compilation"), the number of datasets and mean number of sampling sites per class of habitat amount varied among LMMs among the 5 landscape sizes (Appendix S7). Considering overall biodiversity (i.e., vertebrates, invertebrates, and plants combined), the best scale of effect was 4 km for both occurrence and abundance models (Appendix S7). However, it varied depending on the taxonomic groups and β diversity index (Appendix S8).

Because different forest physiognomies are present throughout the Brazilian Atlantic Forest (e.g., semideciduous seasonal forest and dense ombrophylous forest), variation in β diversity could be influenced by differences in forest physiognomies among sampling sites in datasets and among datasets. We tested for the possible effect of forest physiognomy in the models, but because the results did not change qualitatively (Appendix S9) and our analyses, therefore, proved to be robust regarding this factor, we present only the results based on the original models. We conducted all statistical analyses in R 4.2.1 (R Core Team, 2022). We used the packages lme4 1.1-27.1 (Bates et al., 2015), the distm' function (method = haversine) in geosphere 1.5-14 (Hijmans, 2021), and the emmeans 1.7.5 (Lenth, 2021).

RESULTS

Overall biodiversity

The model based on $\beta_{RC\text{-}occur}$ fitted the data well (R^2_C = 0.34) (Appendix S7) and showed that $\beta_{RC\text{-}occur}$ was higher for 30−60% habitat amounts than for <30% habitat amounts, whereas estimates did not differ between 30−60% and >60% classes (F = 7.85, p < 0.01) (Figure 2a). Mean estimates of $\beta_{RC\text{-}occur}$ were negative (Appendix S10), indicating that, although not significantly different from the null-model expectation (i.e., none of the $\beta_{RC\text{-}occur}$ values were < −0.95), communities were generally more similar than expected by chance, regardless of the class of habitat amount (Figure 2a). The model based on $\beta_{RC\text{-}abund}$ fitted the data better than the one based on $\beta_{RC\text{-}occur}$ (R^2_C = 0.42) (Appendix S7) and showed that estimates were higher for >60% habitat amount than for 30−60% and higher for 30−60% habitat than <30% habitat (F = 8.55, p < 0.01) (Figure 2b). However, contrary to $\beta_{RC\text{-}occur}$, mean estimates of $\beta_{RC\text{-}abund}$ were positive (Appendix S10), indicating that, although like $\beta_{RC\text{-}occur}$ not being significantly different from null-model expectation (i.e., none of the $\beta_{RC\text{-}abund}$ values were > 0.95), species abundance in commu-

nities was less similar than expected by chance, regardless of habitat class (Figure 2b). Variation in the spatial scale we considered and increasing the minimum number of sampling sites in habitat amount classes had little effect on the results because almost all LMMs resulted in very similar estimates of $\beta_{RC\text{-}occur}$ and $\beta_{RC\text{-}abund}$ and statistical significance (Appendices S7 & S11).

Taxonomic groups

We found distinct community composition responses to changes in habitat amount at local landscapes among taxonomic groups. For vertebrates, $\beta_{RC\text{-}occur}$ and $\beta_{RC\text{-}abund}$ were higher for >60% than for <30% habitat amount classes (respectively, R^2_C = 0.42, F = 4.24, p <0.05 [Figure 3a]; R^2_C = 0.47, F = 14.5, p <0.001 [Figure 3b]) (Appendices S8 & S12), similar to our findings for overall biodiversity. For invertebrates, whereas mean $\beta_{RC\text{-}occur}$ differed between communities containing >60% habitat amounts compared with those with 30−60% and <30% habitat amounts (R^2_C = 0.49, F = 23.62, p < 0.01) (Figure 3c), mean $\beta_{RC\text{-}abund}$ showed no differences among classes of habitat amount (R^2_C = 0.31, F = 2.56, p = 0.25) (Figure 3d, Appendices S8 & S13). Finally, for plants, we found no difference between classes of habitat amount for either $\beta_{RC\text{-}occur}$ or $\beta_{RC\text{-}abund}$ (i.e., although analysis of variance was significant, the post hoc test did not reveal differences between means) (respectively, R^2_C = 0.21, F = 7.84, p < 0.05 [Figure 3e]; R^2_C = 0.60, F = 1.81, p = 0.27 [Figure 3f]) (Appendices S8 & S14). The notably large 95% CIs in $\beta_{RC\text{-}abund}$ for plants indicated high variation in shared species abundance similarity between local landscapes, especially in landscapes with <30% habitat amount.

DISCUSSION

Our multitaxa evaluation of β diversity variation across the Brazilian Atlantic Forest revealed an increase in similarity of vertebrate and invertebrate communities with habitat loss. A general pattern emerged for both the occurrence and abundance data when considering overall biodiversity, indicating that habitat loss can induce community-level biotic homogenization. Because there was no such an effect for plants, we understand that the response mechanisms to habitat loss vary depending on the taxonomic group. Further, our results support the idea of habitat loss acting as an ecological filter on species occurrence, which can cause deterministic community change (i.e., $\beta_{RC\text{-}occur}$ approaching −1) and increase the influence of stochastic processes on species' abundance (i.e., $\beta_{RC\text{-}abund}$ approaching 0). Considering the wide taxonomic and spatial extent of data, our results provided robust evidence of habitat loss effects on community composition in human-modified landscapes in the Brazilian Atlantic Forest.

We found consistent responses of overall biodiversity to habitat amount at the landscape scale. Based on species occurrence, communities in landscapes below 30% forest cover were more similar than those above this threshold, indicating that
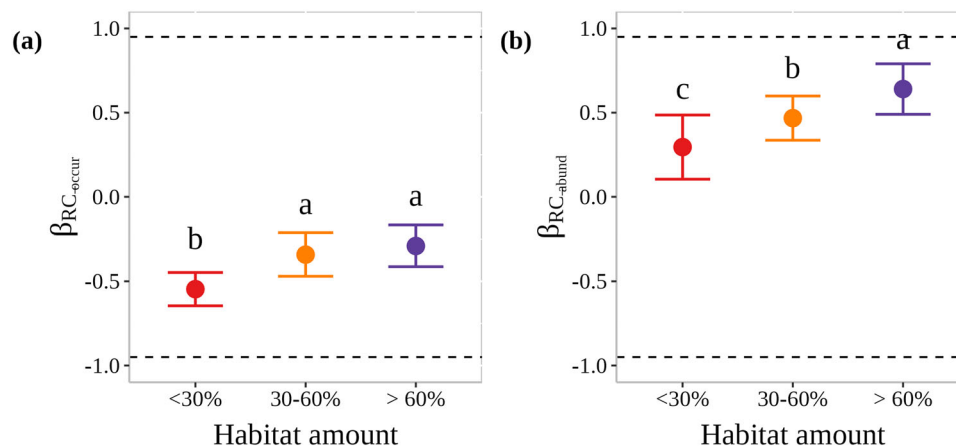
FIGURE 2 Mean (circles) within landscape Raup−Crick β diversity estimates and 95% CIs (bars) based on the (a) occurrence ($\beta_{RC\text{-}occur}$) and (b) abundance ($\beta_{RC\text{-}abund}$) data on vertebrates, invertebrates, and plants across habitat amount classes (red, <30% habitat amount; orange, 30−60% habitat amount; purple, >60% habitat amount; dashed lines, thresholds of $|\beta_{RC}| = 0.95$ reflecting significant differences between observed values and values expected by a random distribution [null model]; differing letters, statistically significant differences in observed values among habitat amount classes).

habitat loss led to deterministic changes in community composition. This result contrasts with the assumption that habitat loss induces species extinctions through stochastic processes (Hubbell, 2001; Zhou et al., 2014). Instead, our results support the idea of ecological filtering (Leibold et al., 2004; Püttker et al., 2015), with only a particular subset of species from the original regional pool persisting in highly deforested landscapes. Our results are consistent with multiple studies that show the proliferation of habitat generalists in disturbed areas (Filgueiras et al., 2021; Newbold et al., 2018) and with studies reporting biotic homogenization as a consequence of habitat loss in the Brazilian Atlantic Forest for mammals (Püttker et al., 2015), trees (Lôbo et al., 2011; Thier & Wesenberg, 2016), birds (Banks-Leite et al., 2014; Morante-Filho et al., 2016), and other taxonomic groups elsewhere in the tropics (Carrara et al., 2015; Kormann et al., 2018; Vellend et al., 2007).

Consistent with observed patterns based on species occurrence, habitat loss increased the similarity in relative species abundances. However, abundance values that declined progressively toward zero as habitat was lost indicated a more random distribution of individuals in highly deforested landscapes compared with those in landscapes with > 30% forest cover. Generally, higher values of $\beta_{RC\text{-}abund}$ compared with $\beta_{RC\text{-}occur}$ are expected, considering the low probability of the same species occurring at every site with similar abundance. In addition, species abundance is expected to vary due to local factors, such as the presence of competitors and predators and resource availability. These findings may be associated with changes in landscape configuration. As habitat loss increases, the size of habitat patches decreases, the amount of matrix area increases (Fahrig, 2003) (in our case, nonforested areas), and the number of fragments increases nonlinearly, particularly around 20−30% of habitat amount (Villard & Metzger, 2014). These alterations in the landscape structure often result in lower abundances and higher local extinction rates for species restricted to core areas. In addition, such alterations create

new conditions that can benefit habitat generalists capable of exploiting resources in matrix areas (Ewers & Didham, 2006), likely contributing to an overall increase in the randomization of abundance across the habitat loss. Thus, the combination of the results based on $\beta_{RC\text{-}occur}$ and $\beta_{RC\text{-}abund}$ indicate that habitat loss not only increases the similarity in species occurrence, but also abundance.

None of the estimates of β diversity was significantly different from values expected by chance alone (i.e., none of the estimates exceeded $|0.95|$). This result implies that neither species distribution nor the distribution of individuals was influenced exclusively by the landscape habitat amount. However, estimates were relatively distant from zero, showing that deterministic and stochastic processes acted in combination on both occurrence and abundance, regardless of habitat amount. In addition, the existence of significant relations among classes of habitat amount showed that the relative importance of deterministic and stochastic processes changed according to the index applied and the class of habitat amount. The influence of deterministic processes on species occurrence increased as forest loss increased, indicating that deforestation acted as an ecological filter that can only be overcome by a subset of species, instead of generating random extinctions. The importance of deterministic processes in the distribution of individuals decreased as habitat loss increased, that is, the distribution of individuals became more similar to the distribution expected by chance as deforestation intensified. The increase in similarity in numbers of individuals among forest fragments at highly deforested landscapes might be at least partly due to a decrease in dispersal limitation of species that are able to pass the ecological filter (i.e., abundances of habitat generalists that are able to use the matrix as supplementary habitat do not depend strongly on local conditions in fragments, and dispersal among fragments allow for synchronization of population dynamics across fragments) (Liebhold et al., 2004; Matter & Roland, 2010).
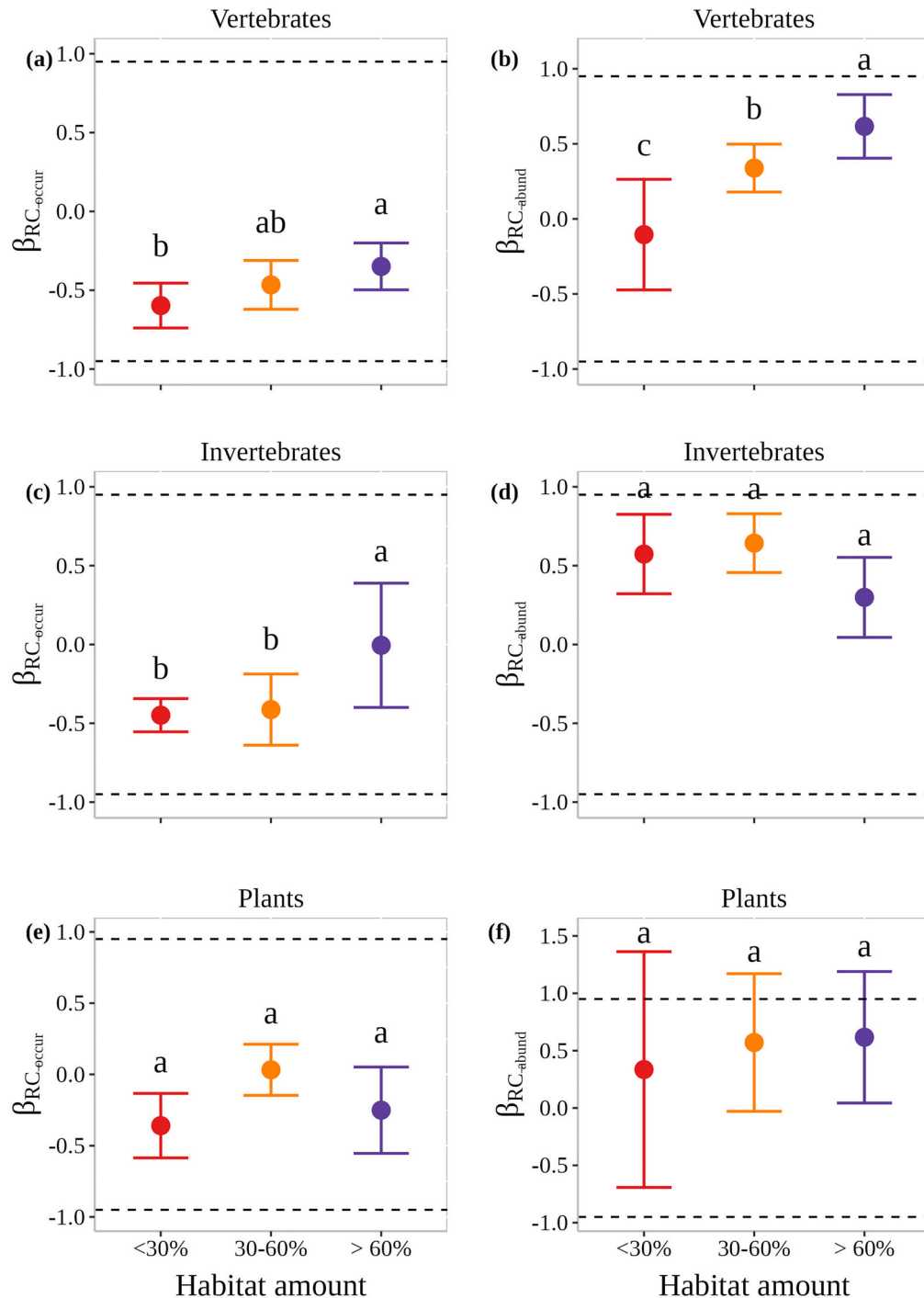
FIGURE 3 Mean (circles) within landscape Raup−Crick β diversity estimates and 95% CIs (bars) based on the occurrence ($\beta_{RC\text{-}occur}$) and abundance ($\beta_{RC\text{-}abund}$) data for (a, b) vertebrates, (c, d) invertebrates, and (e, f) plants across habitat amount classes (red, <30% habitat amount; orange, 30−60% habitat amount; purple, >60% habitat amount; dashed horizontal lines, thresholds of $|\beta_{RC}| = 0.95$ reflecting significant differences between observed values and values expected by a random distribution [null model]; differing letters, statistically significant differences in observed values among habitat amount classes).

Communities of animals mirrored the occurrence patterns of overall biodiversity. Vertebrates showed a gradual increase in similarity as habitat amount decreased, whereas invertebrates responded strongly only to initial deforestation (above >30% forest cover). A possible explanation for these distinct results might be associated with the dispersal abilities among groups.

Vertebrates, in general, are mobile organisms likely presenting higher dispersal abilities than invertebrates and are, therefore, more capable of moving between habitat patches, even in deforested landscapes (e.g., <30%) where habitat patches are more distant (Boesing et al., 2018; Leite et al., 2022). In contrast, for less mobile animals, such as amphibians and some forest

specialist invertebrates, low connectivity between habitat patches in moderately forested landscapes may substantially limit dispersal (Ryser et al., 2019). This filtering effect likely favors habitat generalists able to disperse among fragments even in moderately forested landscapes, contributing to an observed abrupt increase in community similarity.

Differences in abundances between vertebrates and invertebrates were pronounced. Although $\beta_{\text{RC-abund}}$ of vertebrates declined markedly as habitat amount decreased, $\beta_{\text{RC-abund}}$ of invertebrates did not differ among classes of habitat amount. In fact, similarity in invertebrates was slightly (nonsignificant) higher in forested than in deforested landscapes. Nonetheless, our observed increase in $\beta_{\text{RC-occur}}$ and the absence of an impact of habitat loss on $\beta_{\text{RC-abund}}$ of invertebrates contrasts with the findings of Barreto et al. (2023) and Filgueiras et al. (2019) who studied butterflies and dung beetles, respectively, in the Brazilian Atlantic Forest, which suggest biotic differentiation increases as habitat loss increases. According to these authors, a possible explanation is that habitat loss can lead to an increase in diversity and abundance of habitat generalists, mainly due to the proliferation of forest edges, which provide distinct habitat for new species, thereby compensating or even exceeding species losses. Although our results do not corroborate this hypothesis, the variance in $\beta_{\text{RC-abund}}$ for invertebrates indicated a high dependency of different invertebrates on other factors than habitat loss. Our results on invertebrates should be interpreted with caution given the limited number of datasets (16%) and the generally higher uncertainty in abundance estimates for this group. Methods to collect data on the number of invertebrate individuals are likely more prone to flaws compared with those used for vertebrates (Hausmann et al., 2020; Montgomery et al., 2021).

Finally, community composition of plants did not differ significantly as habitat amount decreased. However, the substantial increase in confidence intervals when relying on abundance data indicated highly variable responses of β diversity across datasets, especially in highly deforested landscapes. This variability underscores the detection of decreases and increases in similarity of plant communities as habitat amount declined, which is consistent with previous studies that show biotic homogenization in Brazilian Atlantic Forest (Lôbo et al., 2011) and differentiation in Mexican and Amazonian tropical forests (Arroyo-Rodríguez et al., 2013; Solar et al., 2015, respectively). Our results suggest that rather than being solely influenced by landscape-wide habitat amount, plant community responses seem to be strongly contingent on study-specific factors. Given their sessile nature, plants respond strongly at local scales (Pyles et al., 2022), with landscape-scale responses varying according to functional groups (Metzger, 2000). Moreover, plants can be influenced by variables related to habitat configuration, such as density of nearby forest patches, forest edges (Magnago et al., 2015), and level of contrast with matrix habitat (Filgueiras et al., 2021; Mangueira et al., 2021). Therefore, plant responses to habitat loss at the landscape scale may not be dependent directly on habitat amount, but rather on changes in landscape configuration and connectivity correlated with habitat amount, as well as the quality of the surrounding matrix. Another potential factor influencing plant communities that we did not investigate is the likely time lag in community responses. The majority of our plant datasets were for trees (10 of 12), which are typically longer-living organisms compared with vertebrates and invertebrates. Thereby, trees might respond primarily to past habitat amounts (or other predictors) where the time required for community extinction debts to be paid off has not yet been reached (Halley et al., 2016).

Our results likely represent a conservative estimate of the effect of habitat loss on community composition, given our study design. Because we grouped landscapes according to classes of habitat amount, a landscape with low amounts of habitat is not necessarily surrounded by other landscapes of the same class or even by landscapes with high amounts of habitat (e.g., forest fragments in the vicinities of continuous habitat) (Figure 1b). Accordingly, the probability of species sensitive to habitat loss occurring in landscapes with low amounts of habitat may be positively influenced by colonization and immigration from nearby source areas. Thus, in highly deforested regions (i.e., regions containing predominantly local landscapes with low amount of habitat), the increase in community similarity may be even stronger than we detected.

Our β diversity index results differed from those of other similar studies (e.g., Baeten et al., 2012; Karp et al., 2012; Vázquez-Reyes et al., 2017). Because differences in α diversity among sites are common in the context of habitat loss (Watling et al., 2020), particularly in species-rich ecosystems like the Atlantic Forest, we adopted modified Raup−Crick β diversity indices. This approach compares the observed compositional similarity among 2 sites relative to the random distribution expectation without the influence of differences in α diversity. Thus, possible reasons for a discrepancy between our results and those found in previous studies (Filgueiras et al., 2016; Laurance et al., 2007; Sfair et al., 2016) could be influenced by a methodological artifact resulting from the lack of control for differences in species richness among sampling sites. The importance of controlling for variation in α diversity when investigating patterns of β diversity is underscored by studies in the Brazilian Atlantic Forest. For instance, Lôbo et al. (2011) and Püttker et al. (2015) found increased species similarity in the most deforested landscapes when α diversity was controlled. Similarly, Barreto et al. (2023), Karp et al. (2012), and Petsch et al. (2017) observed distinct patterns in their results before and after accounting for species richness differences among sites. Thus, the difference between β diversity indices in terms of controlling or not for the variation in α diversity among sampling sites might be important when investigating biotic homogenization and differentiation.

Conservation implications

Brazilian Forest Code, the main legislation regulating land use and management on private properties, obliges landowners to preserve at least 20% of native vegetation on their rural property in the Atlantic Forest and defines permanently protected areas, which are environmentally sensitive areas, such as riparian forest, hilltops, high elevation areas, and steep slopes (Brasil, 2012; Soares-Filho et al., 2014). Although other studies show a disproportionate decrease in species richness at a threshold

of around 30% of landscape-wide habitat amount (Banks-Leite et al., 2014; Estavillo et al., 2013; Pardini et al., 2010), our results call attention to the potential and commonly overlooked process of decreases in β diversity, indicating biotic homogenization at those below-threshold landscapes. Thus, compliance with 20% forest cover as dictated by Brazilian law will likely not be enough to avoid possible consequences of biotic homogenization of faunal communities, including decreasing functional diversity (Liang et al., 2019; Rivera et al., 2023), reduction of ecosystem services (Clavel et al., 2011; Marcacci et al., 2021), decreased ecosystem resilience (Olden et al., 2004), and potential proliferation of infectious diseases in wildlife, which may affect human health and well-being (Wilkinson et al., 2018). In 2021, about 24% of the total Brazilian Atlantic Forest area was covered by forest (Projeto MapBiomas, 2022) and amounts of forest varied among landscapes and regions (Rezende et al., 2018). Therefore, it appears essential to prioritize the maintenance of highly forested landscapes that still contain sufficient habitat amount and thereby provide refuge areas for forest specialists (Arroyo-Rodríguez et al., 2020). These landscapes then can function as sources for colonization of deforested areas to maintain or decrease species similarity (Rozendaal et al., 2019). Further, reforestation efforts to increase habitat amount in deforested landscapes may not only prevent drastic species loss (Banks-Leite et al., 2014; Pardini et al., 2010), but also prevent biotic homogenization, as suggested by our results.

Our results showed that habitat loss in the Brazilian Atlantic Forest led to an increase rather than a decrease in community similarity of faunal communities and had variable effects on plants. Given that such results may indicate a process of biotic homogenization throughout the Brazilian Atlantic Forest, we stress the importance of maintaining at least 30% of forest cover in Brazilian Atlantic Forest landscapes (Banks-Leite et al., 2014). This exceeds the threshold of habitat required by the existing Brazilian Atlantic Forest legislation. Because the Brazilian Atlantic Forest shares a myriad of characteristics with other subtropical and tropical regions (e.g., high diversity, widespread land use change, large agricultural and urban areas), it is likely that biotic homogenization is a common but rarely investigated community response to habitat loss in other regions, which calls for investigations of within-landscape community β diversity in human-modified landscapes elsewhere.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.