Tropical forest loss drives divergent patterns in functional diversity of forest and non-forest birds

Maísa A. Matuoka | Maíra Benchimol | José Carlos Morante-Filho

Abstract
Tropical forests have been facing high rates of deforestation driven by multiple anthropogenic disturbances, with severe consequences for biodiversity. However, the understanding of such effects on functional diversity is still limited in tropical regions, especially considering different ecological groups responses. Here, we evaluated the functional responses of birds to forest loss at the threatened Brazilian Atlantic forest, considering the complete assemblage, and both forest-dependent and non-forest-dependent species. Birds were surveyed in 40 forest sites with a forest cover gradient, located in two regions showing different land use types. We tested different models to assess the responses of functional diversity indices to forest loss in these sites. Although functional diversity did not differ between regions, forest and non-forest birds showed divergent responses to forest loss. Deforested landscapes presented an increase in functional richness (SESFRic) and evenness for forest species and an increase of functional dispersion for non-forest birds. Additionally, forested landscapes harbor birds presenting lower body mass and wing length, and non-forest species with lower tarsus length. The maintenance of some functional metrics through forest loss resulted from a compensatory dynamic between forest and non-forest birds, indicating that only evaluating the complete assemblage may mask important idiosyncratic patterns of different ecological groups. Although non-forest species are relatively capable to maintain bird functional diversity in deforested landscapes, forest birds are facing a drastic ongoing collapse in these sites, representing an alarming signal for the maintenance of forest ecosystem function.

Keywords
Atlantic forest, bird assemblage, Brazil, deforestation, ecological traits, forest functioning, functional diversity, land use change

1 | INTRODUCTION

Tropical realms harbor nearly 45% of forest areas (Keenan et al., 2015) and over half of species on Earth (Wright, 2005), ensuring the provision of key ecosystem processes to maintain biodiversity (Naeem, Duffy, & Zavaleta, 2012). Yet tropical forests are facing severe anthropogenic pressures through a wide variety of disturbances, such as agriculture, overexploitation (i.e., logging, hunting),
and urbanization (Gardner et al., 2009; Laurance, Sayer, & Cassman, 2014). Together, these anthropogenic drivers contribute to the highest deforestation rates on Earth (Keenan et al., 2015), leading to high levels of biodiversity loss (Maxwell, Fuller, Brooks, & Watson, 2016) and compromising the functioning of tropical forests (Johnson et al., 2017). Therefore, balancing the exploitation of natural resources and maintaining biodiversity in tropical forests is one of the major challenges to ensure ecosystem functioning in human-modified tropical landscapes (HMTLs) in the long term (Laurance et al., 2014).

Although many studies have assessed the impacts of anthropogenic disturbances on biodiversity, most of them are still focused on patterns of species richness (Gibson et al., 2011), a metric only related to taxonomic diversity (Naeem et al., 2012). Conversely, the comprehension of changes in functional diversity (i.e., ecological trait variation of organisms; see Tilman, 2001) is relatively limited in tropical forests, despite its relevance for understanding ecosystem functioning (Naeem et al., 2012). In addition, several studies propose that phylogenetic metrics (i.e., the breadth of evolutionary history) can be used as surrogates for functional metrics (Srivastava, Cadotte, Macdonald, Marushia, & Mirotschnick, 2012). This is largely based on the hypothesis that if species traits reflect their shared evolutionary history, their phylogeny should act as a useful tool for unmeasured and unmeasurable traits (Winter, Devictor, & Schweiger, 2013). However, prioritizing only taxonomic or phylogenetic diversity can represent a great risk for biodiversity conservation, given that this strategy does not necessarily guarantee high functionality (Mazel et al., 2018). For example, previous studies have detected distinct patterns between taxonomic and functional components of diversity in response to environmental changes (Prescott et al., 2016).

Furthermore, studies in HMTLs have demonstrated that the functional diversity of different organisms (e.g., plants, beetles, amphibians, birds, and mammals) can show contrasting responses following a disturbance, such as logging (Ernst, Linsenmair, & Rödel, 2006), agriculture expansion (Edwards et al., 2014), and urbanization (Coetzee & Chown, 2016). Particularly related to deforestation, functional diversity can either decrease (García-Morales et al., 2016), increase (Pessoa et al., 2017), or even be maintained (De Coster, Banks-Leite, & Metzger, 2015) through the gradient of forest loss. This wide variety of responses among studies mostly depends on species pool, perturbation level, and functional index chosen.

Anthropogenic disturbances can also affect species differently, with those exhibiting particular ecological traits (e.g., specialization in habitat use) are likely to present higher vulnerability than others (Clavel, Juliard, & Devictor, 2011; Gardner et al., 2009). Although scientific research on functional diversity has greatly increased, studies examining different ecological groups’ responses separately are still scarce, despite their importance in elucidating the patterns for the entire assemblage (but see Bregman et al., 2016). In particular, it is recognized that taxonomic and phylogenetic diversity can be maintained in deforested landscapes through compensatory dynamics, in which forest-dependent species losses are balanced by the non-forest-dependent species gains (Banks-Leite et al., 2014; Morante-Filho et al., 2018). Yet, considering that different species can present similar traits (i.e., high functional redundancy, see Mayfield et al., 2010), assessing species responses from a functional point of view can provide additional knowledge on the consequences of deforestation to forest functioning in HMTLs. For instance, the maintenance of species richness within a forest remnant does not necessarily imply in the maintenance of ecological functions (Mayfield et al., 2010). Additionally, even when functional diversity is maintained for the complete assemblage is essential to distinguish forest and non-forest species responses, given that these groups perform different ecological functions (De Coster et al., 2015).

In this study, we examine the influence of landscape forest cover on the functional diversity of birds in a large set of forest sites in the threatened Brazilian Atlantic forest. Specifically, we evaluated the responses of forest-dependent and non-forest-dependent species, as well as the complete bird assemblages, recorded in 40 forest sites distributed along a gradient of forest loss embedded in two regions with contrasting land use change patterns. We expected that the functional diversity of the complete bird assemblages would be maintained across forest loss gradient through a compensatory dynamic, that is, a replacement of functional traits between forest and non-forest species would be likely to occur, assuming therefore that non-forest species could occupy the same amount of functional space than forest species (De Coster et al., 2015). This hypothesis is supported by previous studies conducted in the same forest sites that detected the maintenance of bird taxonomic (Morante-Filho, Faria, Mariano-Neto, & Rhodes, 2015) and phylogenetic diversity (Morante-Filho et al., 2018) in deforested landscapes due to compensatory dynamics. However, as forest species present specific functional traits (i.e., high habitat adaptation), we expected that forest loss would act as an ecological filter affecting the more specialized species, and therefore directly leading to a decrease in functional trait diversity of forest-dependent species (Flynn et al., 2009). Conversely, given that different non-forest species are prone to share similar trait values (i.e., functional redundancy) (Clavel et al., 2011), we predict that this group will not suffer expressive changes on functional diversity (Mayfield et al., 2010) with forest loss in HMTLs.

2 | METHODS

2.1 | Study area

We conducted this study in forest remnants located in southern Bahia Atlantic Forest, in Brazil (Figure 1). This region is characterized by a mosaic of forest remnants in different successional stages, inserted in matrices primarily composed of pastures, rubber trees, eucalyptus, and cocoa plantations (Pardini et al., 2009). Yet, according to the Köppen classification, the climate of the region is characterized as type Af, with no dry season (Alvares, Stape, Sentelhas, Gonçalves, & Sparovek, 2014) and annual average temperature and precipitation of 23–24°C and 1500–1750 mm, respectively (Amorim et al., 2009). Additionally, we used high-resolution satellite images (i.e., Quick Bird and World View, both from 2011, and Rapid Eye from 2009–2010;
with resolutions of 0.6 m, 0.5 m, and 5 m, respectively) to acquire cloudless images for the study region. Then, we classified and digitalized land-cover features through ArcGIS software (ESRI, 2012) at 1:10,000 scale, which is adequate for identifying patches based on the visual inspection of color, texture, shape, location, and context. Forest types were classified following the Instituto Brasileiro de Geografia e Estatística (IBGE, 2006) typologies, and after intensive ground-truthing (Rocha-Santos et al., 2017), we developed a digital map that covered an area of 3,500 km² (central coordinates—15°28′S and 39°15′W). Although the mapped area presents similar soil, topography, and floristic characteristics (Benchimol et al., 2017), the northern region harbors greater amount of continuous native forest (approximately 50% of total forest cover), with a highly heterogeneous matrix composed of cacao and rubber tree plantations (Figure 1), while the southern region is more deforested (only 30% of forest cover), with a homogeneous matrix predominantly comprised of cattle pastures (Morante-Filho, Arroyo-Rodriguez, & Faria, 2016).

2.2 Study design

Based on the map and field investigations, we identified 58 potential sampling sites and subsequently excluded those with limited access, within indigenous lands, or in mountainous forest (above 500 m a.s.l.). Thus, we randomly selected 40 forest sites, embedded along a

FIGURE 1 Study area map highlighting the distribution of the 40 sampled sites (black dots) inserted in the (a) northern (50% of remaining forest cover) and (b) southern (30% of remaining forest cover) regions of southern Bahia, Brazil. In (c) are exhibited six landscapes embedded within a wide range of landscape native forest cover and land-cover classes from both regions.
gradient of native forest cover (i.e., excluding cacao plantations and rubber trees) distributed in both regions (Figure 1). Each site was spaced by at least 1 km from one another and exhibited medium to advanced stages of secondary succession according to previous floristic surveys (Rocha-Santos et al., 2017). Forest cover at the landscape scale was chosen given it has been widely recognized to be a key driver of biodiversity patterns in fragmented landscapes and has been positively related to habitat amount and landscape connectivity for a wide range of species (Fahrig, 2003). Based on our previous analysis (Appendix S1), we detected that 600 m was the most appropriate radius, so it was used for forest cover estimates for subsequent data analyses. The gradient of forest cover ranged from 7% to 98% at the landscape scale, specifically with a mean forest cover amount (±standard deviation) of 69.2% (±20%) and 38.3% (±28.5%) in the northern region and southern region, respectively.

2.3 | Bird surveys

We sampled bird assemblages in three field seasons (January–April, 2013; May–September, 2013; and October, 2013–April, 2014), using point counts. In each forest site, four 50 m radius sampling points were established, at least 100 m away from edges and 150 m distant from each other. In each point, we recorded all birds seen and heard during 15 min at sunrise (06:00 to 09:00 a.m.) and 15 min at sunset (3:00 to 5:00 p.m.), totaling 6 hr in each site (see detailed information in Morante-Filho et al., 2016; Morante-Filho et al., 2015). Birds that were flying over the forest and that could not be located precisely were excluded from the data. The richness and abundance of each species in each site were estimated by, respectively, summing the presence of all species and the number of individuals recorded during the three field seasons at the four-point counts (following Edwards et al., 2011).

Based on information available on the literature (Bregman, Sekercioglu, & Tobias, 2014; Stotz, Fitzpatrick, Parker, & Moskovits, 1996), and our own extensive personal knowledge about the ecology of species, we classified birds either as forest-dependent or non-forest-dependent species (hereafter, forest birds and non-forest birds, see more details of species classification in Appendix S2). The former comprises bird species highly specialized on forest resources, encompassing Atlantic forest endemic species and forest interiors dwellers. In contrast, non-forest birds do not depend directly on forest resources and comprised those species recorded in a variety of habitat types such as early-successional forest and forest edges, open vegetation, and anthropogenic areas (e.g., cocoa agroforestry plantations).

2.4 | Functional diversity

We carefully selected 11 broadly employed bird traits that are mainly related to resource acquisition and sensitivity to disturbances: diet, foraging stratum, habitat, body mass, beak length, beak depth, gape width, tarsus length, tail length, Kipp’s distance, and wing length (see more details on Appendix S3). We chose to combine these feeding, foraging, and locomotion traits because they are directly related to both the species capacity to respond to disturbances (Luck, Lavorel, McIntyre, & Lumb, 2012) and to ecological functions performed by birds, such as pollination and seed dispersal (Pigot et al., 2020). Traits such as diet, foraging stratum, and body mass were obtained through EltonTraits database (Wilman et al., 2014), whereas morphological traits (i.e., beak length and depth, gape width, wing length, Kipp's distance, tarsus, and tail length) were collected from preserved specimens of the ornithological collection of the Zoological Museum from the Universidade de São Paulo (Appendix S4).

Functional diversity indices are calculated from a community (sites × species abundances) and a trait (species × traits) matrix. However, as our data are composed of both continuous and qualitative traits (all with equal weights), we first computed a distance measure (Gower) from the trait matrix, resulting in a distance matrix (species × species), which in turn, is analyzed through a principal coordinates analysis (PCoA). The resulting matrix (species × PCoA axes) represents species distribution in a functional space with reduced uncorrelated dimensions (i.e., PCoA axes are not correlated). Then, combining these species coordinates and the community matrix, we obtained the functional diversity indices values for each of 40 forest sites (Villéger, Mason, & Mouillot, 2008).

For each site, we measured five functional diversity indices widely used in ecological studies—functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), and functional uniqueness (FU). These indices measure different aspects of functional diversity and are based on a multidimensional trait space occupied by the species of a community (Laliberté & Legendre, 2010; Villéger et al., 2008). FRic calculates the volume of functional space, with higher values indicating that species occupy a higher amount of space, meaning a more complete use of resources (Mason, Mouillot, Lee, & Wilson, 2005). Both FEve and FDiv are related to how species are distributed in the functional space weighted by their abundances, with FEve measuring the uniformity of the distribution of abundances or distances among species, and FDiv considering the species distances to the center of this functional space. Therefore, high FEve indicates a regular arrangement of species while high FDiv can be observed when the most abundant species are distant to the center (i.e., higher niche differentiation, hence, lower competition), both indicating a higher resource use efficiency (Mason et al., 2005). FDis measures the mean distance of species to the centroid of the functional space, weighted by their abundance (i.e., the spread of the species in the functional space; Laliberté & Legendre, 2010). Lastly, FU measures the mean functional distance of species to its nearest neighbor in the functional space occupied by all species of the regional pool. Thus, FU evaluates the degree of species’ isolation in the functional space, being inversely associated to functional redundancy (Grenié, Denelle, Tucker, Munoz, & Violette, 2017).
To minimize the influence of species richness on functional richness (Appendix S5), we calculated the Standardized Effect Size Functional Richness (SESFric). This metric is calculated as: (Observed FRic value – Mean of randomized FRic values/SD of randomized FRic values) where positive and negative values indicate higher and lower functional diversities than expected by chance, respectively. Positive SESFRic also indicates low functional redundancy, whereas negative values indicate high redundancy (Petchey, Evans, Fishburn, & Gaston, 2007; Plass-Johnson, Taylor, Husain, Teichberg, & Ferse, 2016). Additionally, to specifically evaluate the relationship of each trait for forest loss, we also calculated community-weighted mean trait value (CWM), which consists of a one-dimensional metric that quantifies the mean values of a trait weighted by species relative abundances (Ricotta & Moretti, 2011). All functional diversity analyses were conducted in R software (R Development Core Team, 2013), using FD package (“dbFD” function) (Laliberté & Legendre, 2010) to calculate indices and picante package (Kembel et al., 2010) to calculate SESFRic (functions provided by Plass-Johnson et al. (2016)).

2.5 Statistical analysis

To account for spatial autocorrelation effects on the functional responses of birds, despite inter-site independence found by Morante-Filho et al. (2015) for species richness and abundance (both metrics used for functional diversity calculation), we performed a Mantel test between the geographical distance and all functional diversity indices dissimilarity matrices among pairs of sampling sites. Our results showed that, although spatial correlation was statistically significant for few indices, such relationships were mostly weak, indicating that most variation in functional diversity of birds is not related to intersite geographic distances (Appendix S6). For each assemblage (i.e., complete, forest, and non-forest species), we thus evaluated the relationship between each functional diversity index and forest cover through four models widely used by studies in fragmented tropical forest landscapes (see Banks-Leite et al., 2014; Benchimol et al., 2017; Morante-Filho et al., 2018)–null (constant), linear, power law (non-linear), and ANCOVA (analysis of covariance) considering the region (north and south) as a categorical factor. We subsequently used Akaike information criterion corrected for small samples (AICc) and Akaike weights (i.e., the normalized relative likelihood of each model) to select the best model for each index. The model presenting the lowest AIC value was considered the most plausible one, and all models presenting a lower than two units difference in AIC with similar Akaike weights were considered parsimonious. Furthermore, the number of parameters were taken into consideration, with smaller models (less parameters) being chosen over more complex models. Following these criteria, the order of choice when the AICc values and weights were similar was null, linear, power law, and ANCOVA (Anderson, 2008). Additionally, we used generalized linear models to evaluate the relationship between each CWM and forest cover amount. We carried out all statistical analyses and graphics in R Software using AICcmodavg (Mazerolle, 2017) and bblme (Bolker, 2017) packages.

3 RESULTS

3.1 Overview

We recorded a total of 5,931 individuals belonging to 184 species across all 40 forest sites, including 103 forest species (n = 3,715) and 81 non-forest species (n = 2,216; Appendix S2). The most abundant species were Cacicus cela, Tolmomyias flaviventris, Machaeropterus regulus, Thamnophilus ambiguous (all forest species), followed by Tangara palmarum, Pitangus sulphuratus, Megarynchus pitangua, and Coereba flaveola (all non-forest species), representing nearly a quarter (24.6%) of all records.

3.2 Patterns of functional diversity driven by forest loss

Overall, the association between forest cover and each functional index did not differ between regions, as the ANCOVA was rarely the most parsimonious model (Table 1). Considering the complete bird assemblage, except for FEve and FDiv, forest loss led to an increase in functional diversity indices, mostly predicted by linear models (Table 1, Figures 2 and 3). Furthermore, forest and non-forest birds showed contrasting responses to forest loss for all functional indices, for instance, FRic considerably decreased for forest species and increased for non-forest species (but just for the southern region, see Figure 2). Additionally, we detected a decrease in SESFRic and functional uniqueness (FU) of forest birds with increasing forest cover amount, indicating lower functional redundancy in deforested landscapes (Figure 3). Conversely, non-forest birds presented relatively constant SESFRic and uniqueness and, thus, functional redundancy maintenance throughout the forest cover gradient (Figure 3). Besides, FEve in deforested landscapes was maintained in non-forest species but presented a slight increase in forest species. In contrast, the opposite pattern was observed for FDiv, with forest loss causing an increase in non-forest species, but not affecting forest species (Figure 2). Additionally, we detected that forest loss led to a decrease in FDiv for both non-forest and forest species, yet the latter exhibited divergent patterns between regions, with higher values in the north sites (see differences in intercept in the ANCOVA model; Figure 2). We also observed by CWM analyses that more forested landscapes retain species with smaller body mass and wing length, regardless of bird group evaluated. Finally, non-forest birds present smaller tarsus length in landscapes within lower amount of forest cover (Appendix S8).

4 DISCUSSION

Our study revealed that functional diversity of birds exhibited divergent patterns among different ecological groups in response to
forested areas, and these patterns can both be related to the proliferation of the non-forest species in agricultural landscapes (Bregman et al., 2016). Indeed, forest and non-forest species exhibit distinct patterns of biodiversity, as indicated by a decrease in functional richness of non-forest species with forest loss (i.e., less than 40%–30% of forest cover). In addition, the increase in functional richness of non-forest species with forest loss was only evident in the southern region, with a matrix predominated by cattle pastures and lower proportion of forest cover, which can be distinctly affected by anthropogenic disturbances (Bregman et al., 2016). Indeed, forest and non-forest species exhibit distinct traits, adaptations, and thus sensitivities to human disturbances in the tropics (Clavel et al., 2011; Gardner et al., 2009). Therefore, disentangling the responses at different group-level contributes to enhancing our understanding on the effects of deforestation on patterns of functionality provided by birds, and presumably on forest integrity in HMTLs.

In accordance with patterns of species richness observed in our region (Morante-Filho et al., 2015), we detected positive and negative relationships of FRic with forest cover for forest and non-forest species, respectively. Yet, it is worth mentioning the alarming low values of FRic for forest species in severely deforested landscapes (i.e., less than 40%–30% of forest cover). In addition, the increase in functional richness of non-forest species with forest loss was only evident in the southern region, with a matrix predominated by cattle pastures and lower proportion of forest cover, which can both be related to the proliferation of the non-forest species (Morante-Filho et al., 2016). On the other hand, we detected a negative relationship between SESFRic and forest cover for forest birds, indicating that although the number of species decreases in forest cover loss, confirming previous results focused on taxonomic and phylogenetic diversity within the same region (Morante-Filho et al., 2015, 2018). By combining a wide set of ecological traits and robust functional diversity metrics in our study, we revealed that the maintenance of some metrics along the gradient of forest reduction results from a compensatory dynamic between forest and non-forest species (Banks-Leite et al., 2014; Morante-Filho et al., 2018).

For instance, when combining all species, no effect of forest loss on the functional divergence or evenness was observed, but when assessing their responses separately, divergent patterns between bird groups were unveiled. This indicates that assessing only the complete assemblage may mask important idiosyncratic patterns of forest and non-forest species, especially because these bird groups can be distinctly affected by anthropogenic disturbances (Bregman et al., 2016). Indeed, forest and non-forest species exhibit distinct traits, adaptations, and thus sensitivities to human disturbances in the tropics (Clavel et al., 2011; Gardner et al., 2009). Therefore,
Deforested landscapes, the functional space is expanded in these areas (Petchey et al., 2007; Prescott et al., 2016). Combined with functional uniqueness response, this result indicates that deforested landscapes harbor species more functionally distinct from each other (i.e., lower functional redundancy), which is an alarming signal for the functioning of forest patches in the long term (see also Prescott et al., 2016), especially considering the drastic increase in FU values below 15%-10% of forest cover, suggesting a threshold under which forest birds might be seriously threatened. As functional redundancy can act as a buffer against future species extinctions, ecosystem functions provided in forest remnant located in deforested landscapes are less resilient facing new disturbances, and thus species loss can easily lead to the discontinuity of services provided by birds in these patches (Flynn et al., 2009; Oliver et al., 2015). Conversely, although the number of non-forest species is higher in severely deforested landscapes (especially in southern region), the SESFRic remains relatively constant. So, additional species do not increase the functional richness, as they are functionally redundant (Mayfield et al., 2010; Prescott et al., 2016).

**FIGURE 2** Relationships between different functional indices (FRric, FEve, FDiv and FDis) and forest cover loss at the landscape scale, considering the complete bird assemblage, forest birds, and non-forest birds. Lines correspond to the best fitting model (see Table 1 and Appendix S7) and panels with two lines represent ANCOVA model, where black circles and continuous lines represent the north region and white circles and dashed lines represent the south region, respectively.
For both complete community and non-forest species, the functional evenness was not affected by forest loss. However, contrary to expected, this metric slightly increased for forest species, corroborating fragmentation effects obtained by Ding, Feeley, Wang, Pakerman, and Ding (2013), which in turn, propose that lower FEve levels can indicate lower functional stability and resilience in more conserved areas. Yet, this result should be interpreted with caution, since species can be evenly distanced from each other, but be irregularly distributed inside the functional space (Schleuter, Daufresne, Fassol, & Argillier, 2010). Indeed, forest patches within deforested landscapes in our region exhibit simplification of vegetation structure (Rocha-Santos et al., 2016), thus reducing niche availability. Therefore, species can be homogeneously distributed within these few remaining niches, which may explain the higher functional evenness despite forest loss (García-Morales et al., 2016; Schleuter et al., 2010). In contrast, for both forest and non-forest birds, the higher levels of functional divergence are observed in patches located in more forested landscapes, which indicates higher niche differentiation and lower competition between bird species, and hence a higher resource use efficacy (Mason et al., 2005).

As forest loss is intensified, functional dispersion is maintained for forest birds, whereas non-forest species become more spread in the functional trait space (i.e., higher FDIs) (Laliberté & Legendre, 2010). This latter pattern was also detected when considering all species together. The expansion in functional space in deforested landscapes, especially for non-forest birds (see Figure S2-C in Appendix S9), is likely caused by the appearance of species with more extreme trait values (Almeida, Green, Sébastien-González, & Anjos, 2018), such as *Caracara plancus*, *Cathartes aura* and *Coragyps atratus*—all non-forest species, which besides presenting extremely high values of body mass and wing length, are also the only three scavenger species recorded in this study. Indeed, these species are often related to disturbed habitats (Barbar, Werenkraut, Morales, & Lambertucci, 2015). Therefore, deforestation may have created new niches that functionally different species, particularly non-forest species, are able to occupy (Boersma et al., 2016).

The overall decrease in body mass and wing length for all species and in tarsus length for non-forest species indicates that landscapes showing greater amount of forest are prone to retain smaller bird species. In fact, we observed a predominance of passerines in these sites, which generally consists of small species (Gaston & Blackburn, 1995). Conversely, the larger species found in deforested landscapes belong to a wide variety of avian orders, ranging from pigeons and parrots to woodpeckers and raptors. Additionally, the whole southern region of Bahia has been losing large bodied species such as cracids (IBAMA, 2004), which are particularly threatened by fragmentation and forest loss allied to strong hunting pressures (Michalski & Peres, 2017). The depletion of large species can lead to the disruption on the provision of functional services they perform consequently reducing the integrality of the ecosystem they inhabit. For example, the loss of large frugivorous birds was a key factor that led to negative consequences of dispersal and regeneration of a palm tree species in Atlantic forest remnants (Galetti et al., 2013).
4.1 | Conclusions and implications

Our study highlights that simultaneously assessing multiple functional aspects through distinct indices leads to a more precise comprehension of the effects of deforestation on ecosystem functioning driven by birds—a key ecological group that performs a large set of ecological functions including seed dispersal, pollination, and invertebrate and vertebrate control. In this sense, our results highlight three important conservation implications that should be considered in future studies. First, we revealed that the greater spread of species in the functional space (i.e., higher FDIs and SESFRic) in deforested landscapes is not accompanied by an increase in FDiv nor FEve. Thus, if only considering the FDIs and SESFRic, one might conclude that due to higher functional diversity, ecosystem functioning is enhanced in deforested landscapes. Therefore, we recommend the use of multiple functional indices in further studies assessing the effects of anthropogenic disturbances on biodiversity patterns, in order to better assess the health of ecosystems and propose conservation mitigation actions.

Second, combined with previous studies on taxonomic and phylogenetic diversity within the same forest sites (Morante-Filho et al., 2015, 2018), the observed patterns of functional diversity indicate that despite forest loss, non-forest species are able to relatively maintain the diversity of bird assemblages. However, caution is needed with this finding, especially because forest and non-forest birds showed conflicting functional responses. For instance, deforested landscapes may reduce niches available for forest species and, at the same time, create new niches for non-forest species. This replacement of forest by non-forest species may involve a loss of trait coevolution between mutualistic species, such as forest frugivorous birds and fleshy-fruited plants, resulting in the loss of specific interactions, which therefore can disrupt seed dispersal of certain species (Dehling et al., 2014). Additionally, this exchange may be detrimental for the functioning of these forest patches in the long term, once forest-dependent species should present more complementary responses (Clavel et al., 2011), and non-forest species may perform different ecosystem functions (De Coster et al., 2015). Therefore, it is possible that although the amount of functions is not reduced, different functions are performed in disturbed areas. This is likely to affect forest functioning in severely deforested landscapes, given that the compensatory dynamic may not involve a true compensation from a functional perspective, since particular functions will be lost (De Coster et al., 2015). Combined with the decrease in functional redundancy of forest species, this pattern may lead to lower resistance and resilience of communities in the face of further disturbances, eventually jeopardizing important ecosystem functions in HMTLs (Olden, Poff, Douglas, Douglas, & Fausch, 2004). Thus, we highlight the importance of future studies to separately assess the responses of different ecological groups, where weak community-level responses to disturbances can potentially be explained by compensatory dynamics, and to directly assess the provision of specific ecosystem functions in order to investigate whether a true functional compensation is possible.

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CONFLICT OF INTEREST

The authors confirm that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHORS’ CONTRIBUTIONS

MAM and JCMF conceived and designed the experiments; JCMF performed the experiments; MAM, JCMF, and MB contributed to data analysis and interpretation; and wrote the paper; MAM wrote original draft.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.ns1rn8ppk (Matuoka, Benchimol, & Morante-Filho, 2020), and the Figshare Repository: https://figshare.com/articles/Data/11933451.

ORCID

Maisa A. Matuoka https://orcid.org/0000-0002-6574-3185
Maira Benchimol https://orcid.org/0000-0002-1238-1619
José Carlos Morante-Filho https://orcid.org/0000-0002-1625-9872

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