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Habitat amount drives the functional diversity and nestedness of anuran communities in an Atlantic Forest fragmented landscape

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Abstract

Natural environments disturbed by human activities can suffer from species extinctions, but some can still harbor high taxonomic diversity. However, disturbances may have impacts beyond the species level, if the species lost represent unique functions in the ecosystem. In this study, we evaluated to what extent the amount of habitat can determine the functional diversity and nestedness of amphibian communities in an Atlantic Forest fragmented landscape in Brazil, and if there is a threshold of habitat amount beyond which there is severe loss of functional diversity. As species responses may depend on their habitat type, we performed the analyses for three different sets of species: all species, forest-dependent species, and generalist species. We also evaluated the relative importance of turnover and nestedness components to total functional dissimilarity among sites. Habitat amount affected functional diversity of frogs, especially for forest-dependent species where a linear reduction was detected. The functional dissimilarity among sites was mostly explained by the nestedness component. The reduction of functional diversity was mediated by an ordered loss of traits, leading to a functionally nested metacommunity. These sensitive traits were closely related to habits and reproductive modes that depend on rivers and streams. The maintenance of functional diversity of frogs in fragmented landscapes must rely on the conservation of both terrestrial and aquatic environments, as some species and their traits can disappear from remnants of native vegetation lacking some specific habitats (e.g. streams).

Abstract in Portuguese is available with online material.

KEYWORDS

amphibia, conservation, functional diversity, functional nestedness, habitat loss

1 | INTRODUCTION

The conversion of natural environments to anthropogenic landscapes is the most important threat to biological diversity, with negative effects on different taxa worldwide (Almeida-Gomes, Vieira, Rocha, Metzger & De Coster, 2016; Arroyo-Rodríguez, Rojas, Saldaña-Vásquez & Stoner, 2016; Díaz, Pérez-Tris, Tellería, Carbonell & Santos, 2005; Leal, Filgueiras, Gomes, Iannuzzi & Andersen, 2012; Wang, Thornton, Ge, Wang & Ding, 2015; Zee & Fukami, 2015). Besides the loss of species, ecological traits can also disappear or be replaced as result of landscape changes (De Coster, Banks-Leite & Metzger, 2015; Farneda et al., 2015; Lindenmayer et al., 2015; Magnago et al., 2014). Even though disturbed habitats can maintain a significant portion of regional taxonomic diversity (Gibson et al., 2011), it remains unclear whether functional diversity—the extent of functional differences among the species in a community (Petchey & Gaston, 2002)—follows this trend or whether it is more affected than taxonomic diversity (Flynn et al., 2009; Hevia et al., 2016; Mumme, Jochum, Brose, Haneda & Barnes, 2015). The loss of functional diversity due to anthropogenic habitat disturbances is essential information for conservation planning (Cadotte, Carscadden & Mirotchnick, 2011; Gagic et al., 2015; Mace, 2014), and to evaluate potential ecosystem resilience (Standish et al., 2014).

Although most studies about habitat loss have focused mainly on species richness and composition, functional diversity can also be negatively affected by habitat loss (Farneda et al., 2015; Flynn et al., 2009; Tscharntke et al., 2008). Moreover, the loss of functional diversity due to habitat loss might not be random: some ecological functions can be more prone to disappear because of disturbance, creating functionally poor communities. In this case, communities subjected to a gradient of disturbance intensity may be functionally nested, with the set of functional traits of species in disturbed communities being a subset of those present in less disturbed ones. For instance, Matthews et al. (2015) used a recently proposed nestedness index (treeNODF; Melo, Cianciaruso & Almeida-Neto, 2014) in a meta-analysis of bird community data from 18 fragmented landscapes and found that communities were functionally nested with regard to decreasing patch area. The possibility of nestedness in the functional structure of communities must be evaluated for other organisms and contexts, especially to determine ecological traits that are more prone to disappear in human-impacted landscapes.

The habitat amount hypothesis proposed by Fahrig (2013) states that the total amount of habitat can be used to predict the number of species in fragmented landscapes, replacing the two classic measures of patch size and isolation derived from the Theory of Island Biogeography (MacArthur & Wilson, 1967). However, the relationship between habitat amount and species richness requires appropriate definition of habitat and selection of species group to make sure that only species that use predominantly the same habitat type are included in the species richness estimate. For example, Vieira, Almeida-Gomes, Delciellos, Cerqueira and Crouzeilles (2018) used forest cover as a proxy of habitat amount and then selected only forest species of non-volant small mammals to test the habitat amount hypothesis. Indeed, there is evidence of a positive relationship between species diversity and total amount of habitat in fragmented landscapes (Andrén, 1994; Melo, Sponchiado, Cáceres & Fahrig, 2017; Pardini, Bueno, Gardner, Prado & Metzger, 2010; Püttker, Bueno, Barros, Sommer & Pardini, 2011; Smith, Fahrig & Francis, 2011), but also of the existence of fragmentation thresholds or regime shifts in the relationship between the amount of habitat and the number and composition of species (Andrén, 1994; Banks-Leite et al., 2014; Pardini et al., 2010). However, comparatively, fewer studies have aimed to test how the reduction in amount of habitat in fragmented landscapes affects functional diversity and, most importantly, whether the relationship is linear or includes thresholds of habitat loss where function diversity reduces more sharply.

We assessed effects of habitat amount on three aspects of amphibian diversity, namely taxonomic species richness, functional diversity, and functional nestedness, with three main goals. First, we evaluated the relationship between total amount of forest habitat, and functional diversity and taxonomic species richness in a fragmented landscape. More forest habitat in local landscapes will provide higher heterogeneity of conditions, thus higher species richness and functional diversity, at least for forest-dependent species. Further, we evaluated whether those relationships were gradual and linear, or nonlinear, with thresholds of functional diversity or species richness loss. Second, we investigated whether the total functional dissimilarity was explained mostly by the nestedness or by the turnover component. We hypothesized that the functional dissimilarity among sites was due to the nestedness component rather than the turnover component. Third, we determined whether the communities we studied were functionally nested by the amount of forest habitat. Based on previous evidence of trait-mediated loss due to habitat loss (Almeida-Gomes & Rocha, 2015; Bregman, Sekercioglu & Tobias, 2014; Newbold et al., 2013), our hypothesis was that some ecological traits are present only in local landscapes with high amount of habitat, and that progressive habitat loss causes non-random loss of ecological functions.

To test these hypotheses, we used a dataset obtained during the largest empirical study (in terms of number of fragments and range of fragment sizes) ever conducted in tropical forests with amphibians (Almeida-Gomes, Vieira et al., 2016). Amphibians are considered key indicators of landscape changes (Cushman, 2006; Schneider-Maunoury et al., 2016), and there is evidence that some species and some ecological traits (especially reproductive modes) are more prone to disappear in the environments outside large remnants in fragmented forest landscapes (Almeida-Gomes & Rocha, 2015; Almeida-Gomes, Vieira et al., 2016; Fonseca et al., 2013).

2 | METHODS

2.1 | Study site

Our sampling was carried out between July 2007 and March 2014 in an Atlantic Forest fragmented landscape, in the municipality of Cachoeiras de Macacu, state of Rio de Janeiro, Brazil. The vegetation is classified as dense evergreen forest and the climate as mild–humid–mesotermic (Vieira et al., 2009). The landscape has fragments of different sizes, degrees of regeneration and isolation, immersed in different matrices (mainly pastures). We sampled three sites within the continuous forest of the Reserva Ecológica de Guapiaçu (CF1–CF3), which comprises a forested area of over 7000 ha, and 21 forest fragments, ranging between 1.9 and 619 ha, that were near the reserve (F1–F21) (Figure S1). All sampled fragments were surrounded mostly by a matrix of pasture. For more details about the study area, see Almeida-Gomes, Vieira et al., (2016).

2.2 | Frog sampling

Anurans were detected by visual encounter surveys (VES; Crump & Scott, 1994) at nighttime (19:00–24:00 hr), using headlamps. Different habitat types were systematically inspected, such as tree trunks, branches, forest floor leaf litter, rocks in streams, bromeliads, and puddles. This method is acknowledged as the best for assessing frog species richness and abundance in tropical areas (e.g., Almeida-Gomes & Rocha, 2014; Doan, 2003) because it enables a thorough search of all environments available in each area and, consequently, the recording of many species usually not detected by other methods (e.g., pitfall traps and plots). Sampling effort ranged from 21 to 118 h for forest fragments, and from 66 to 92 h for sites in continuous forest, with sampling effort proportional to the size of the sampled area (total effort = 1,244 h) (Table S1).

2.3 | Functional traits and species classification

According to Flynn et al. (2009), a functional trait can be described as a measurable aspect of an organism that somehow determines its interaction with the environment where it lives. Three functional traits were used to perform the analyses on functional diversity; one continuous—frog body size (mm), and two categorical—habit and reproductive mode. The frog species found presented a wide range in their body sizes, from nearly 20 to 180 mm. The habit displayed by frogs was classified according to Haddad et al. (2013) in three categories: arboreal, terrestrial, and rheophilic. We used reproductive mode as an ecological trait for two reasons. First, the Brazilian Atlantic Forest is known as the biome that harbors the highest diversity of frog reproductive strategies worldwide (Haddad & Prado, 2005), and some of them are found only in large protected areas (Almeida-Gomes & Rocha, 2015). Second, the type of reproductive strategy encompasses information on developmental mode (aquatic larvae vs. terrestrial development), the microhabitat where the eggs or tadpoles are laid (e.g., leaf litter on the ground, leaves on trees, streams), and the source of food for tadpoles (endotrophic vs. exotrophic). Accordingly, reproductive modes summarize a range of important life history characteristics. Amphibians are mostly involved in ecosystem functions such as productivity, nutrient cycling, and energy flows (Hocking & Babbitt, 2014). Therefore, our selected traits can represent the extent that frogs use the available resources in the environment, and for which type of predators, they can be used as a food source.

Frog species were classified as forest-dependent and generalists according to their habitat use, as habitat loss and fragmentation can affect differently habitat specialist and generalist species (Almeida-Gomes, Prevedello & Crouzeilles, 2016). We considered forest-dependent species as those that are mainly found in forest areas even if some of them are occasionally found in matrix areas (Almeida-Gomes & Rocha, 2014; Almeida-Gomes, Vieira et al., 2016; Haddad et al., 2013). Generalist species were those found in both forest and matrix areas, most of them being common in disturbed habitats (Almeida-Gomes, Rocha & Vieira, 2016). This classification relies on previous samplings in pasture matrix in the same study area (Almeida-Gomes & Rocha, 2014; Almeida-Gomes, Rocha et al., 2016) and available information for Atlantic Forest frogs (Haddad et al., 2013). Analyses were performed for forest and generalist species separately as we expect they respond differently to forested habitat amount. Additionally, we repeated analyses with the two groups pooled. Although partially redundant to the analyses done separately, this is the most common form of analyses and allow us to explicitly assess the potential masking effect of including species that likely respond differently to human disturbances (Fahrig, 2013). For details about trait data and species categorization, see Table S2.

2.4 | Habitat amount

Forest cover, here used as a proxy for amount of habitat, was calculated from the central point of each sampling site (continuous forest sites and forest fragments) as the percentage of forest cover included in a circular area defined by a given radius. We used a multi-scale analysis as proposed by previous studies (Fahrig, 2013; Holland, Bert & Fahrig, 2004; Jackson & Fahrig, 2015) to find the spatial scale with a maximum fit of the species richness–habitat amount relationship (the “scale of effect”). This was done by estimating forest cover within circles of different radius centered at sampling sites and recording the explained variance of the species richness–habitat amount relationship. The highest explained variation was found for a radius of 200 m for all species and generalist species, and 1,400 m for forest-dependent species. We adopted the same procedure for functional diversity and the highest explained variation was found for a radius of 1,000 m for all species, and 1,400 m for both forest-dependent and generalist species (Figures S2 and S3).

2.5 | Species richness and functional diversity

To evaluate a possible effect of sampling effort on our results, we compared observed with estimated species richness given by Chao 1 estimator in EstimateS (Colwell, 2013). Sample completeness (Magurran, 2004) for each site was indicated by the number of observed species divided by the number of species predicted by Chao 1 estimator. There was no significant correlation between sampling effort and sample completeness (r Pearson = 0.27; $p = 0.19$). Therefore, we used the observed species richness in our analyses. Functional diversity (FD) was quantified using the Rao's quadratic entropy (RaoQ), which incorporates both the relative abundances of species and the functional distinctiveness of pairs of species (Botta-Dukát, 2005). Moreover, Weigelt, Schumacher, Roscher and Schmid (2008) characterized RaoQ as “a continuous measure of functional diversity including information about the evenness of the distribution of functional traits within a community.” RaoQ is one of the most used FD indices, and it is only weakly influenced by species richness (Dias et al., 2013; Laliberté & Legendre, 2010; Pavoine & Bonsall, 2011). We used the Gower distance to estimate FD as it accommodates quantitative and categorical variables in a single measure (de Bello et al., 2010; Podani & Schmera, 2006). This analysis was performed using the R package FD (Laliberté, Legendre & Shipley, 2014).

2.6 | Linear versus threshold models

To investigate the existence of thresholds in the relationship between species richness and the amount of habitat for the three sets of species mentioned above (all species, forest-dependent species, and generalist species), we employed piecewise regression models using the R package *segmented* (Muggeo, 2008). This approach uses more than one line to fit data and a break point to unite the regression lines (Toms & Lesperance, 2003; see continuous piecewise model in Matthews, Steinbauer, Tzirkalli, Triantis & Whittaker, 2014). These breakpoints may allow inferences on regime shifts in the relationship between the species richness and amount of habitat, making possible the identification of a possible fragmentation threshold (Andrén, 1994; Pardini et al., 2010). We also used piecewise regression models to investigate the existence of thresholds in the relationship between functional diversity and the amount of habitat for the three sets of species. To evaluate the best fit between species richness and FD with habitat amount, we used the Akaike Information Criterion corrected for small samples (AICc) and a model selection approach (Burnham & Anderson, 2002) to compare linear and threshold (segmented) models. The best model was chosen based on the lowest AICc value. We performed the model selection analyses using the function model.sel in "MuMIn" package (Barton, 2016).

2.7 | Total functional dissimilarity and its components

We assessed the relative importance of turnover and nestedness to total functional dissimilarity among sites using the approach popularized by Baselga (2010) and extended by Leprieur et al. (2012) to functional/phylogenetic relationships of descriptors. We used presence–absence of all species to obtain the total functional dissimilarity and its two components using the Jaccard family. The functional dendrogram used to obtain dissimilarities included all species and was built using the Gower distance matrix cited above and the UPGMA linkage method. We used the function *as.phylo()* in the *ape* R package (Paradis, Claude & Strimmer, 2004) to convert UPGMA dendrograms into tree objects. The functional dissimilarities were obtained using the *betapart* package (Baselga, Orme, Villeger, Bortoli & Leprieur, 2018). The three dissimilarity matrices were summarized using Principal Coordinate Analysis.

2.8 | Functional nestedness

We used the treeNODF index to estimate functional nestedness (Melo et al., 2014). It is an extension of the NODF index (Nested Overlap and Decreasing Fill) used to quantify taxonomic nestedness (Almeida-Neto, Guimarães, Guimarães, Loyola & Ulrich, 2008). NODF assesses the proportion of species present in species-poor assemblages that are present in species-rich assemblages. Similarly, treeNODF assesses the proportion of functional diversity present in functionally poor assemblages that are present in functionally rich assemblages. Functional diversity is estimated as the sum of branch lengths in a functional dendrogram connecting species present in an assemblage (Petchey & Gaston, 2002). The treeNODF index can be partitioned into two components. S.Fraction is the fraction of treeNODF that would be observed if all species were equally related and thus the relationship among them would be represented by a star dendrogram (all branches of the same size and originating in the root). The topoNODF is the fraction of the treeNODF value due to the topology of the dendrogram, that is, the functional differences between species (Melo et al., 2014).

A distinctive advantage of NODF and its extension treeNODF is the capability of accommodating a specific hypothesis to be tested. These indexes are computed in a pair-wise manner, but always distinguishing which sample in the pair should be nested in the other sample. This distinction is given by the order of rows (samples) entered in the data matrix, with rows at the bottom being hypothetically nested subsets of those above. Accordingly, the last row is hypothesized to be the least diversified (in terms of species richness or functional diversity, respectively, for NODF and treeNODF), and a nested subset of all other rows above. The penultimate row is nested in all rows above, but not the row below, and so on until the first row, which is the most diversified and not nested in the other rows. We took advantage of this possibility and ordered the rows of our studied sites-species matrices according to our hypothesis of the decreasing amount of habitat on the generation of nestedness. This contrasts with many previous studies in which rows are ordered by decreasing diversity, which maximizes nestedness, but that precludes a straightforward interpretation of mechanisms generating nestedness.

The statistics produced by NODF and treeNODF should be tested against a null distribution of expected values. This distribution may be generated using null models (Gotelli, 2000). Despite the popularity of null models, they have been severely criticized since its introduction in the ecological literature, for instance, by generating too artificial matrices or inability to detect a pattern when it is very strong (Connor & Simberloff, 1984; Gotelli, 2000). We circumvented this problem by using a permutation test, a possibility allowed by the inclusion of a hypothesis to order rows (Melo et al., 2014). For instance, in case we order rows by decreasing diversity, the observed statistics would be highest and all randomized values lower than or equal to the observed ones. The permutation test consisted simply in the permutation of rows in the matrix to break any nested pattern present, computation of the statistics for the permuted matrix, and repetition of this procedure 999 times. In contrast to null models, the permutation procedure maintains the original matrix intact as values in the cells are not shuffled (it always remains associated to the same site and species). The functional dendrogram was the same used to obtain the functional Jaccard dissimilarities. Both treeNODF and the permutation test were computed using the *CommEcol* R package (Melo, 2016).

All analyses were conducted in R 3.3.1 (R Development Core Team, 2014). As we used a functional dendrogram built from traits in the treeNODF, we refer to the method traitNODF hereafter.

3 | RESULTS

We recorded 2,839 individuals of 50 anuran species belonging to 11 families (Table S2). The most abundant species in continuous forest sites was *Haddadus binotatus* (18.4%), and we detected 32 species in these areas (13 exclusive to continuous forest areas). On the other hand, *Adenomera marmorata* (30.6%) was the most abundant species in forest fragments, where we detected an overall richness of 37 species (18 of which were only found in forest fragments). We found a total of 15 reproductive modes among anuran species in all areas (continuous forest sites and forest fragments). However, six reproductive modes (40%) were found only in continuous forest areas (modes 3, 6, 8, 19, 25, and 36; see Table S3, for the description of these reproductive modes), three of them being related to streams and rivers inside the forest (modes 3, 19, and 25). Regarding habit types, the rheophilic species were found only in continuous forest sites. Other frog species, arboreal or terrestrial, which are closely related to streams inside the forest, were found only in continuous forest areas (e.g., *Ololygon albicans*) or mostly inside continuous forest areas and large forest fragments (e.g., *Aplastodiscus eugenioi*).

The linear model for species richness was more plausible for forest-dependent and generalist species, whereas for all species, the threshold model was as plausible as the linear model (ΔAICc < 2, Table 1). For all species, the species richness decreased sharply as forest cover was reduced from 100 to 73.1%, when there was a smoothing in the loss of species richness (Figure 1). Likewise, the relationship between FD and habitat amount was better described by a linear model than by a threshold model for forest-dependent species, whereas for generalist species and all species together, the threshold model was as plausible as the linear model (ΔAICc < 2, Table 1). Considering all species, the FD decreased as forest cover was reduced from 100 to 21.3%, when there was an inflexion and the FD increased as the amount of habitat decreased (Figure 1).

The functional composition represented by the Jaccard dissimilarity and summarized in the Principal Coordinates Analysis indicated a clear separation of the three continuous forests from the fragments (Figure 3). This separation was mostly due to nestedness (or differences in functional diversity). In fact, the functional dissimilarity component based on turnover scored continuous forests in the middle of the cloud formed by fragments (Figure 2).

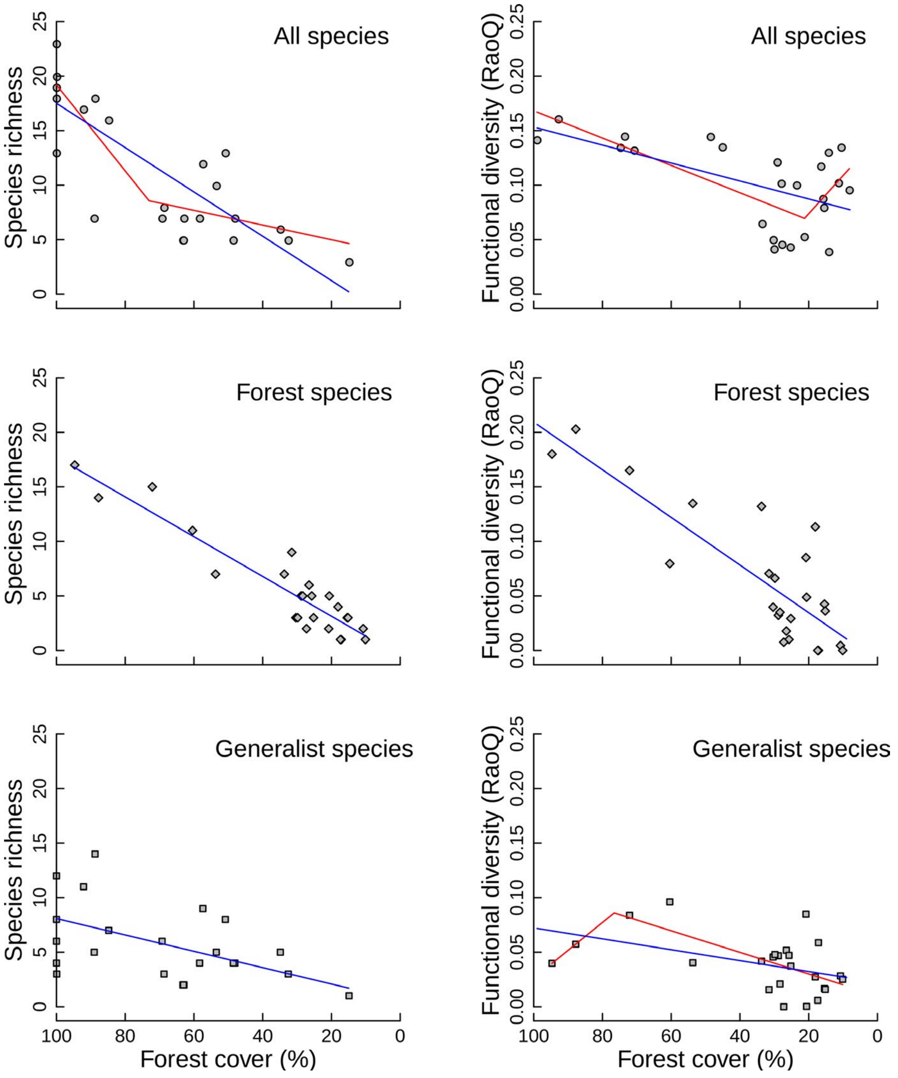
The functional dendrogram grouped the species mainly in terms of their habits (terrestrial, arboreal, and rheophilic) and reproductive modes (Figure 3). Considering all species, the observed traitNODF value ordered by the amount of habitat was significantly higher than expected by chance (Table 2). The observed traitNODF value was mostly represented by the S.Fraction or the species composition component (73.0%) rather than the topoNODF or the dendrogram topology component (27.0%). For forest-dependent species, the observed traitNODF value ordered by the amount of habitat was also significantly higher than expected by chance (Table 2). Similarly, the traitNODF value was mostly represented by the S.Fraction (93.8%) rather than the topoNODF (6.2%). In contrast, the observed

TABLE 1 Model selections comparing linear and threshold models of the relationship between species richness (SR) and functional diversity (FD) with habitat amount

Response variable	MODEL	K	LL	AICc	ΔAICc	w_i	R^2_{adj}
SR all species	**Threshold**	**5**	**−61.691**	**136.700**	**0.000**	**0.601**	**0.70**
SR all species	Linear	3	−65.166	137.500	0.820	0.399	0.63
SR forest-dependent species	**Linear**	**3**	**−45.251**	**97.700**	**0.000**	**0.952**	**0.86**
SR forest-dependent species	Threshold	5	−45.173	103.700	5.980	0.048	0.85
SR generalist species	**Linear**	**3**	**−60.411**	**128.000**	**0.000**	**0.942**	**0.24**
SR generalist species	Threshold	5	−60.131	133.600	5.570	0.058	0.18
FD all species	**Threshold**	**5**	**51.942**	**−90.600**	**0.000**	**0.563**	**0.40**
FD all species	Linear	3	48.623	−90.000	0.510	0.437	0.28
FD forest-dependent species	**Linear**	**3**	**45.745**	**−84.200**	**0.000**	**0.942**	**0.63**
FD forest-dependent species	Threshold	5	46.086	−78.600	5.580	0.058	0.60
FD generalist species	**Linear**	**3**	**57.250**	**−107.300**	**0.000**	**0.633**	**0.17**
FD generalist species	Threshold	5	59.773	−106.200	1.090	0.367	0.26

Note: The best models for each model selection are in bold format; K, number of parameters; LL, model log likelihood; w_i, Akaike weights.

FIGURE 1 Relationship between forest cover (habitat amount) and species richness and functional diversity (RaoQ), for anuran species. Red line = threshold model; blue line = linear model. Higher values of RaoQ mean higher functional diversity. The threshold model is displayed only when it was considered plausible in the model selection



traitNODF value ordered by the amount of remnant habitat was not higher than expected by chance for generalist species (Table 2). The S.Fraction (68.7%) also comprised the most part of the traitNODF value, compared to the topoNODF (31.3%).

4 | DISCUSSION

Functional diversity tended to be higher for forest-dependent species than for generalist species. Most importantly, functional diversity of forest species was very sensitive to loss of habitat and decreased linearly with the percentage of forest around sampling sites. In contrast, generalist species were less sensitive to forest loss. Total functional dissimilarity was mostly explained by the nestedness rather than the turnover component. Besides, the reduction of functional diversity of forest-dependent species in fragmented landscapes was mediated by an ordered loss of sets of species (S.fraction) and traits (topoNODF), leading to a functionally nested metacommunity. These sensitive traits were related to species closely associated to streams.

The amount of habitat (forest cover) had a generalized effect on the functional diversity of frog species, but this effect was much stronger when we considered only forest-dependent species. As stated by Fahrig (2013), the correct definition of habitat for the species group under evaluation is an essential step to understand how the reduction in the amount of habitat affects the number of species in local landscapes. This approach has been used in other studies, considering only a subgroup of species to conduct analyses for communities (Melo et al., 2017; Pardini et al., 2010; Vieira et al., 2018).

Thresholds of change in functional diversity with habitat loss may occur when all species are considered, but mostly by a replacement of forest dependent by generalist species rather than an acceleration of loss in functional diversity. In our results, the threshold model was as good as the linear model (ΔAICc < 2) when all species were analyzed together, mainly because of the inversion in functional diversity below 25% of forest cover, with an increase in functional diversity after a consistent reduction. This indicates a replacement of species and their ecological traits in landscapes with low amount of forest cover, with a reduction of forest specialists and an increase of generalist species. Studies with other taxonomic

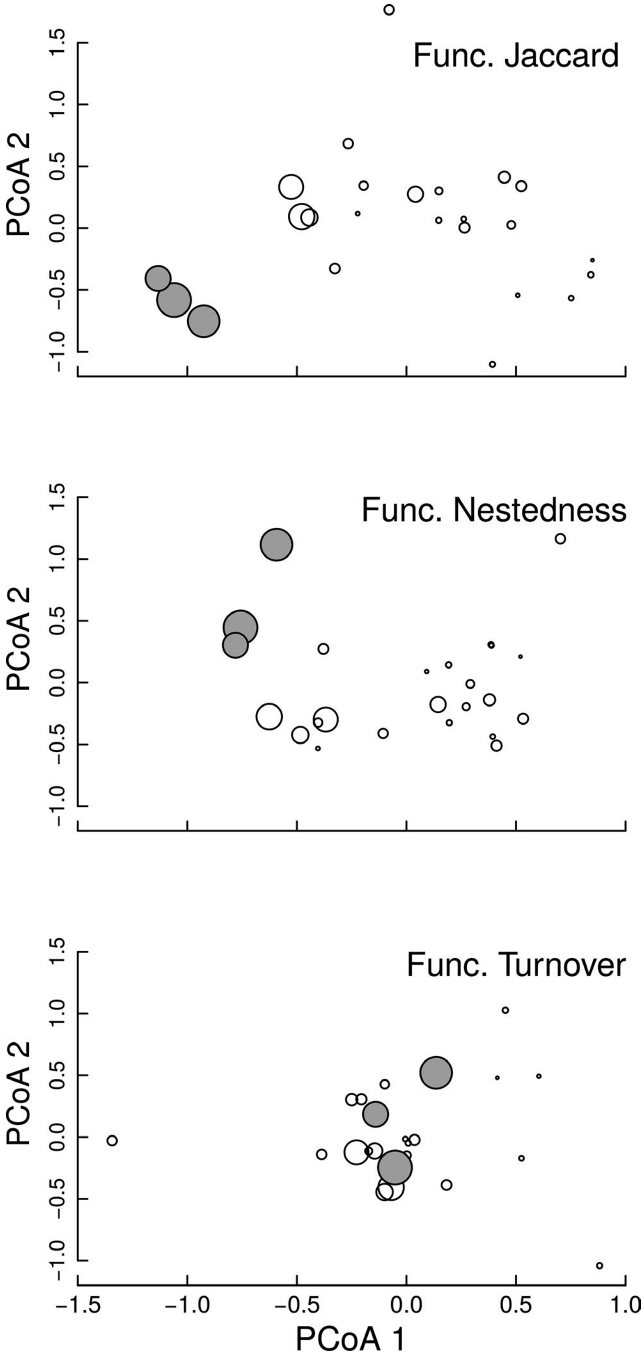


FIGURE 2 Principal Coordinate Analysis showing the total functional dissimilarity among sites and the relative importance of its two components (nestedness and turnover), based on a presence–absence matrix of all species. Gray circles represent the continuous forest sites (*N* = 3), and white circles represent the forest fragments (*N* = 21). Symbols are scaled according to the amount of habitat (forest cover) in a radius of 1,000 m surrounding the central point of each sampling site

groups have obtained similar results, such as birds (De Coster et al., 2015), and the replacement of large-fruited trees by early-successional, small-seeded species at fragment edges (Magnago et al., 2014). The mechanism behind this kind of threshold differs from the usual thresholds of 10-30% for species richness, described for many taxonomic groups and landscapes, but that apply only to habitat-dependent species (Andrén, 1994; Pardini et al., 2010). Species richness thresholds are caused mainly by difficulty of habitat-dependent species to percolate between habitat patches in landscapes with less than ca. 10%–30% of habitat cover. The best supported model for forest-dependent frog species in our landscape is linear, without thresholds, hence, without evidence to support fragmentation thresholds.

Species of frogs were lost at a faster rate than ecological traits when forest cover is reduced, indicating functional redundancy in this species pool. Several studies have shown that the level of functional redundancy drives how ecosystem resilience is affected by species loss (Fonseca & Ganade, 2001; Laliberté et al., 2010; Rosenfeld, 2002). In our study, most species had arboreal habits and shared the same reproductive mode (eggs and exotrophic tadpoles in lentic water). Therefore, some of these frog species sharing the same reproductive mode can go extinct, but the functional trait persists, explaining why we observed a higher loss of species than ecological traits in analyses using all species.

The nestedness analyses indicated that the loss of forest species and their functional traits was non-random but mediated by loss of forest habitat. Previous studies have found evidence of trait-mediated loss of bird species due to habitat loss (Bregman et al., 2014; Newbold et al., 2013) or island/patch size (Matthews et al., 2015). In addition, functional diversity of frogs usually is higher in primary forests compared to exploited forests (Ernst, Linsenmair & Rödel, 2006). The ordered loss of species and traits in our study generated a functionally nested set of communities that differed in the amount of habitat. In addition, the functional nestedness (traitNODF) was driven mainly by compositional nestedness for all three sets of species (all species, forest-dependent species, and generalist species). Forest specialist species usually have a higher requirement of habitat compared to taxonomically similar generalist species (Henle, Davies, Kleyer, Margules & Settele, 2004; Matthews, Cottee-Jones & Whittaker, 2014). In our case, forest-dependent species possess traits related to their habit or reproductive modes that demand specific habitat types (e.g., streams and rivers), only found in local landscapes with high amount of habitat. Therefore, one major implication for amphibian conservation in human dominated landscapes is that the retention of some species and their ecological functions requires the protection of large forest remnants, because of areas with low fractions of habitat availability are unable to hold high levels of functional diversity for amphibians.

Species closely associated with rivers and streams inside the forest seem to be the most affected by habitat loss because most are recorded only inside continuous forest areas and large forest fragments (Almeida-Gomes & Rocha, 2015). In previous studies in the same area, the diversity of frog reproductive modes was much lower in forest fragments compared to continuous forest sites, and there was a trend for larger fragments to harbor both the higher number of types of reproductive sites and diversity of frog reproductive modes (Almeida-Gomes & Rocha, 2015; Almeida-Gomes, Vieira et al., 2016). Indeed, in fragmented rainforests of Madagascar, the presence of

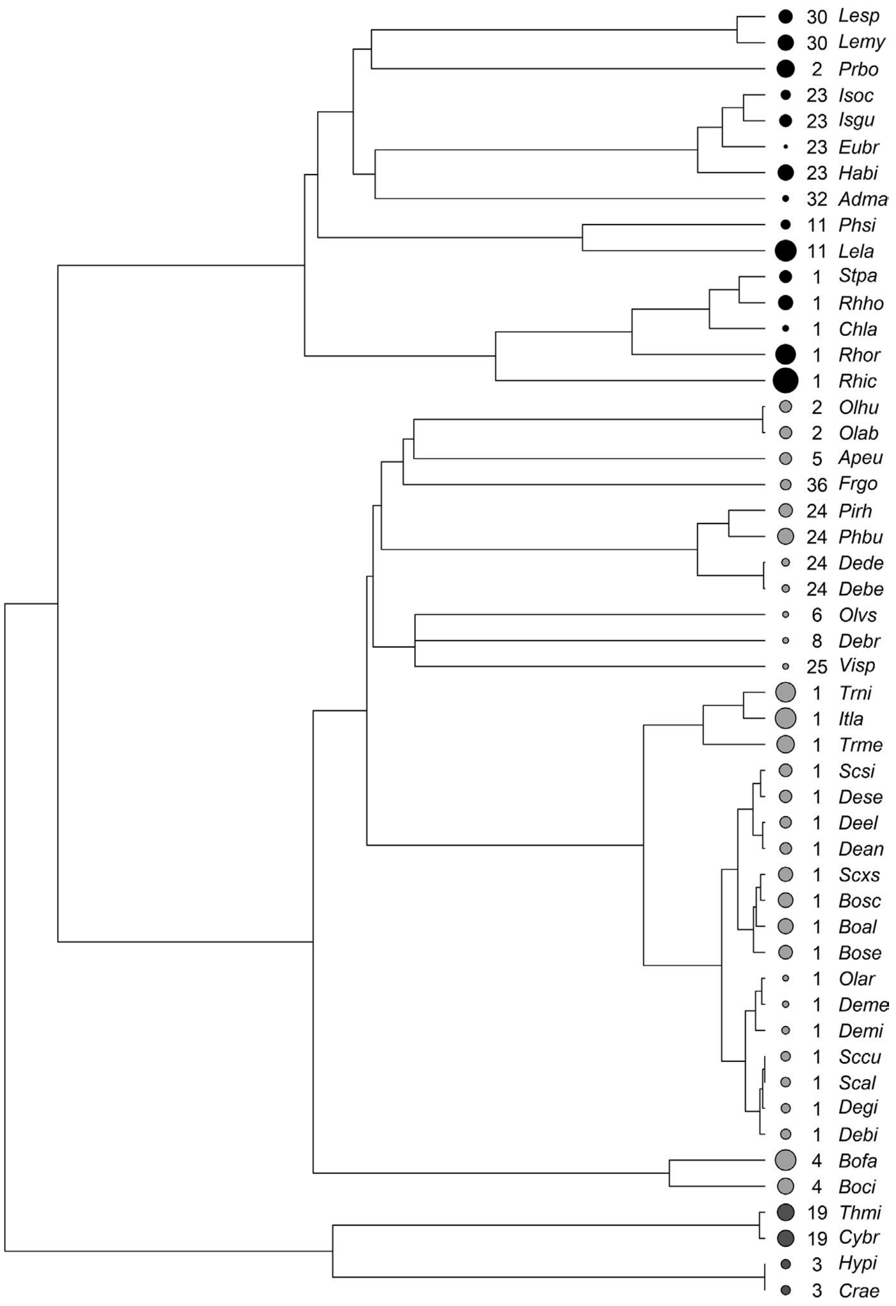


FIGURE 3 Dendrogram showing resemblance among anuran species according to their ecological traits. Circles represent species' body size. Black circles—terrestrial species; light gray circles—arboreal species; dark gray circles—rheophilic species. The numbers represent frog reproductive modes of each species (sensu Haddad & Prado, 2005). The scientific names of the species are abbreviated. The full names are available in Table S2

streams was the factor that most contributed to functional richness of frogs in all land-use categories (Riemann, Ndriantsoa, Rödel & Glos, 2017). The lack of some reproductive environments in most of the fragments we sampled, such as rivers and streams, may preclude the persistence of some species with specific habits (e.g., rheophilic species), or with specific reproductive modes. In addition, species with aquatic larvae might be forced to perform compulsory breeding migrations through unfamiliar and hostile environments, because of the discontinuity between suitable aquatic habitats and the terrestrial habitats used as refuges. Therefore, they are expected to suffer the most from the so-called "habitat split," which can explain the local declines and extinctions of these species in fragmented landscapes (Becker, Fonseca, Haddad, Batista & Prado, 2007; Becker, Fonseca, Haddad & Prado, 2010).

The maintenance of ecosystem function relies on the identification of species and ecological traits that are more vulnerable to disturbances. Our study provides robust empirical evidence that species richness and functional diversity of forest-dependent frogs reduce in direct proportion to total amount of habitat in local landscapes. The order of loss of species and functional traits is non-random, but predictable. This had yet not been explicitly recognized. Species closely related to streams or rivers inside the forest are the most threatened by habitat loss, as these specific environments where they live and reproduce are basically only present in continuous forest areas or large fragments. Policies and strategies to preserve frog species and their ecological traits in fragmented landscapes must consider not only the native cover where they are found, but also the aquatic environments such as

TABLE 2 Functional nestedness among anuran communities in an Atlantic Forest fragmented landscape

	Obs	M.aleat	*SD*.aleat	*Z*	*p*
All species					
traitNODF	66.27	44.35	6.71	3.26	0.001
S.Fraction	48.37	32.60	5.14	3.07	0.001
topoNODF	17.90	11.75	1.93	3.17	0.002
treeNODF	73.33	44.04	6.94	4.22	0.001
Forest-dependent species					
S.Fraction	68.80	41.24	6.68	4.12	0.001
topoNODF	4.52	2.79	0.47	3.65	0.001
treeNODF	47.26	43.70	6.70	0.53	0.302
Generalist species					
S.Fraction	32.49	30.57	5.18	0.37	0.362
topoNODF	14.77	13.13	2.26	0.73	0.249

Note: Functional nestedness was quantified as traitNODF. S.Fraction represents the portion of the traitNODF due to nestedness in species composition and topoNODF the portion due to the functional dendrogram topology. Nestedness values were obtained after ordering rows (sites) by decreasing habitat amount. Analyses were restricted to the rows (sites) of the site by species matrices. Obs = observed statistics. M.aleat (*SD*.aleat) = mean (standard deviation) of the 999 statistics obtained after row permutation. *z* = (Observed − M.aleat)/*SD*.aleat. *p* = probability of obtaining a statistic in row-permuted matrices that is equal or higher than that obtained for the observed data (rows ordered by decreasing habitat amount).

rivers and streams. Refinement of functional groups and traits may further increase our predictive ability, and the identification of species and ecological traits that are more vulnerable to disturbances.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4m0022b (Almeida-Gomes, Vieira, Rocha & Melo, 2019).

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SUPPORTING INFORMATION

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

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