

## RESEARCH ARTICLE

# Random placement models explain species richness and dissimilarity of frog assemblages within Atlantic Forest fragments

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## Abstract

1. Understanding the effects of random versus niche-based processes on biodiversity patterns is a central theme in ecology, and an important tool for predicting effects of habitat loss and fragmentation on biodiversity. We investigated the predictive power of random processes to explain species richness and species dissimilarity of amphibian assemblages in a fragmented tropical landscape of the Atlantic Forest of South America.
2. We analyzed a large database of amphibian abundance and occupancy, sampled in 21 forest fragments ranging in size from 1.9 to 619 ha. We compared observed species richness and species dissimilarity with the outcomes of two null (random placement) models: 1- the traditional Coleman's area-based model and 2- an abundance-based model (based on the number of individuals observed in each fragment). We applied these models for all species combined, and separately for forest-dependent and habitat-generalist species.
3. The abundance-based model fitted the observed species richness data better than the area-based model for all species, forest-dependent species, and generalist species. The area-based and the abundance-based models were also able to significantly explain species dissimilarity for all species and for generalists, but not for forest dependent species.
4. The traditional area-based model assigned too many individuals to large fragments, thus failing to accurately explain species richness within patches across the landscape.
5. Although niche-based processes may be important to structuring the regional pool of species in fragmented landscapes, our results suggest that part of the variation in species richness and species dissimilarity can be successfully explained by random placement models, especially for generalist species. Evaluating which factors cause variation in the number of individuals among patches should be a focus in future studies aiming to understand biodiversity patterns in fragmented landscapes.

**KEYWORDS**

anura, beta diversity, human-modified landscapes, niche processes, null model, random processes, species distribution

## 1 | INTRODUCTION

Understanding variation in community structure is a central challenge in ecology. For example, the species-area relationship (SAR)—the increase in species richness with the increase in island or habitat area—is one of the most robust and pervasive patterns in ecology (Arrhenius, 1921; Fattorini et al., 2017; Preston, 1960; Sutherland et al., 2013). However, the underlying mechanisms behind variation in community structure are still under debate (Gotelli & Graves, 1996; Hubbell, 2001; Prevedello et al., 2016). Several niche-based processes have been proposed to explain variation in community structure across patchy systems, including SARs (e.g. Banks-Leite et al., 2010; Henneron et al., 2019). Large patches may support more species than small patches because of their higher habitat heterogeneity (Williams, 1943), which allows occupation by more species with distinct niche requirements. For example, the species richness of rock-savanna plants in neotropical inselbergs was mainly explained by the size of vegetation patches, and this size effect was mediated by an increase in terrestrial-habitat diversity (Henneron et al., 2019). An alternative to the habitat diversity hypothesis is that local extinctions are more likely to occur in small patches because they usually support smaller population sizes than large patches (MacArthur & Wilson, 1967). For example, Gibson et al. (2013) found a near-complete extinction of native species of small mammals on small islands 5 years after their isolation by a dam.

On the other hand, variation in community structure across patchy systems can also be generated by random processes (Gotelli & Graves, 1996; Hubbell, 2001; Prevedello et al., 2016). It is well known that species richness tends to increase as a function of the number of individuals in the community, which may vary depending on patch size or other factors (Gotelli & Colwell, 2001). For example, large patches can have more species than small patches because they are likely to receive more individuals from the regional species pool, a hypothesis known as passive sampling (Coleman et al., 1982). Passive sampling effects may be estimated through random placement models, in which individuals or species are randomly placed in patches (Bidwell et al., 2014; Gotelli & Graves, 1996; Guadagnin et al., 2009). In Coleman's (1981) original model (hereafter, "area-based model"), the number of individuals assigned to each patch is directly proportional to patch size or area, and the area of each patch is treated as a fraction of the total habitat area in the landscape. Therefore, the higher the number of individuals received by

a patch, the greater the species richness. This model explained relatively well species richness of terrestrial birds on islands in reservoirs (Coleman et al., 1982) and of marine invertebrates on intertidal boulders (McGuinness, 1984), but not species richness of waterbirds in wetlands (Guadagnin et al., 2009) or of duck communities in ponds (Bidwell et al., 2014).

One possible explanation for the poor fit of the area-based model found by previous studies (Bidwell et al., 2014; Guadagnin et al., 2009) is that large remnants might support fewer individuals than one could expect by their areas alone. In other words, the area-based model may assign too many individuals to large patches, leading to overestimation of species richness on these patches. To account for differences among patches in the actual number of individuals they contain, a complementary approach would be the use of an abundance-based random placement model, in which total abundance on each patch is constrained to its observed value (Bidwell et al., 2014; Guadagnin et al., 2009). In this case, it is not necessary to estimate species abundance for each patch, differently from the area-based model. Although this abundance-based null model also failed to explain waterbird species richness in wetlands (Guadagnin et al., 2009), it was suitable to explain species richness of ducks in ponds (Bidwell et al., 2014), suggesting that SARs can be caused by a combination of niche-based and random processes.

However, both area-based and abundance-based random placement models have been used in attempts to explain only species richness in habitat patches. To our knowledge, no study has ever tested whether these models are able to also explain dissimilarity in species composition, which is increasingly recognized as a central community parameter to understand community structure in patchy systems (Banks-Leite et al., 2012; Bernard & Fenton, 2007; Collins et al., 2017). Several neutral and niche-based processes have been proposed to explain patterns of species dissimilarity in patchy systems. For example, a clear pattern is that larger patches are more similar to each other in terms of species composition than when they are compared to small patches, for birds (Banks-Leite et al., 2010), frogs (Almeida-Gomes & Rocha, 2014a), and lizards (Almeida-Gomes & Rocha, 2014b). The potential process behind these dissimilarity patterns could be attributed to edge effects: small patches tend to be more strongly affected by edge effects, which can result in changes in environmental conditions (e.g. increased forest desiccation and light levels) and species composition through a replacement of specialist species by generalist species (Banks-Leite et al., 2010; Filgueiras et al., 2016; Laurance et al., 2018). A second explanation is based on the observation that community similarity usually decreases with increasing geographic distance, reflecting in part spatially autocorrelated environmental variables (Gavish &

Ziv, 2016; Jacquemyn et al., 2021). In the absence of autocorrelated environmental variables, limited dispersal in a neutral model can also cause changes in species association and composition among sites (Ulrich, 2004).

In the absence of dispersal limitation or environmental gradients, purely random processes could potentially explain species dissimilarity in habitat patches, because most indices of species association (which reflect differences in species composition) are highly correlated with species richness (Ulrich et al., 2018). Species dissimilarity could reflect, at least partially, the number of individuals and species in patches randomly sampled from a larger regional source pool of species. For example, two large patches could receive a high and similar number of individuals from a regional pool, thus sampling higher number of species and potentially increasing their species richness and similarity in species composition (Chao et al., 2005), especially if the regional pool is small. Therefore, it remains an open question the degree to which random processes alone may explain patterns of species dissimilarity in patchy systems.

Here, we used area-based and abundance-based random placement models to test whether simple random processes explain species richness and species dissimilarity in tropical forest fragments. To do so, we used a large empirical dataset of frogs from the Brazilian Atlantic Forest, one of the most threatened world's biodiversity hotspots (Laurance, 2009). In a previous study using this dataset, we showed that larger forest fragments had more similar communities compared to continuous forest than smaller fragments (Almeida-Gomes, Vieira, et al., 2016). These patterns were previously attributed to the higher diversity of reproductive sites in larger fragments (Almeida-Gomes & Rocha, 2015; Almeida-Gomes, Vieira, et al., 2016). Here we tested a simpler hypothesis: that the variation in both species richness and species dissimilarity among patches is a simple consequence of variation in abundance per patch. To do so, we evaluated the outcomes of the area-based and abundance-based models. If both models were able to explain community structure (i.e. species richness and/or dissimilarity), it would suggest that the distribution of individuals and species across forest fragments is random. On the other hand, if both models failed to explain community structure, it would suggest that ecological factors not included in the models are important. If only the abundance-based model explained community structure, it would indicate that species abundance is a good predictor of species richness and dissimilarity, and that the area-abundance function used to estimate abundance is inaccurate. Finally, if only the area-based model was able to explain species richness and dissimilarity, it would suggest that patch size is a good predictor of species abundance, and that this predicted abundance is better to explain community structure than the observed abundance obtained in the field sampling. Alternatively, a better fit of the area-based model could indicate the presence of niche processes associated to patch area, such as habitat diversity. As species with different habitat requirements may respond differently to niche and neutral processes (Almeida-Gomes et al., 2019; Morante-Filho et al., 2016), we also tested these predictions separately for forest-dependent and habitat-generalist species.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

Fieldwork to obtain the dataset we used in the present study was carried out between July 2007 and March 2014 in an Atlantic Forest fragmented area in Cachoeiras de Macacu, Rio de Janeiro state, Brazil. The region is characterized by a mosaic of fragments of different sizes embedded in different matrix types, mainly pastures (Vieira et al., 2009). We sampled 21 forest fragments ranging from 1.9 to 619 ha, selected to encompass the largest possible variation in patch size (Figure 1). In a previous study, Almeida-Gomes and Rocha (2015) found that larger fragments had more types of reproductive sites for frogs than smaller ones. For example, small streams were found mostly in large fragments and were absent in most small fragments. For more details about the study area, see Almeida-Gomes, Vieira, et al. (2016).

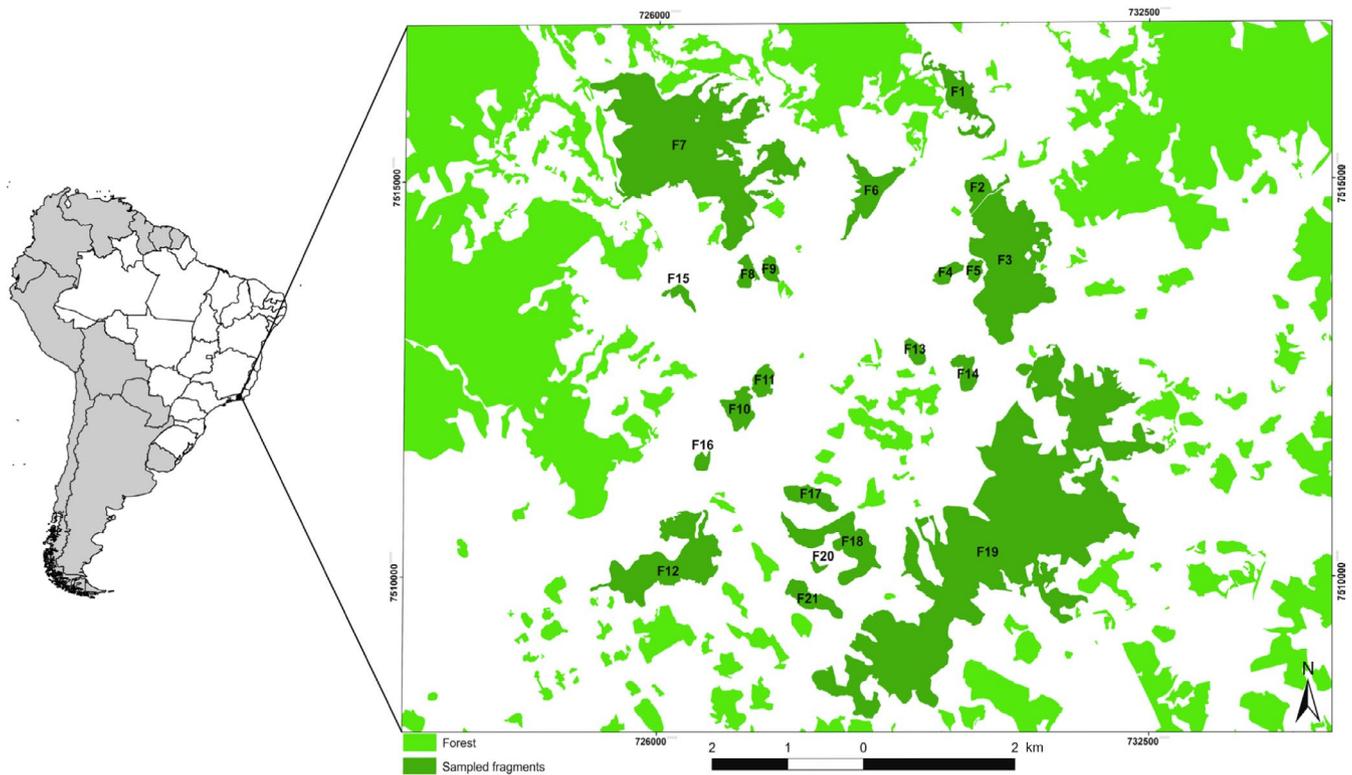
### 2.2 | Frog sampling

Anurans were recorded by visual encounter survey at nighttime (19:00 to 00:00 hr), using headlamps. This method is acknowledged as the best to detect the highest number of anuran species, including species with arboreal habits that usually are not detected by using other traditional methods, such as pitfalls or plots (Almeida-Gomes, Vieira et al., 2016). Within each patch, we inspected different habitat types (e.g. tree trunks, branches, leaf-litter, bromeliads and puddles) in order to record as many anuran species as possible. Each fragment was visited at least four times (range four-14 visits) and sampling effort was scaled according to fragment size and logistic constraints (e.g. access to the area) and ranged from 21 to 118 hr (Table S1 in Appendix 1). Therefore, as planned, there was a strong and positive correlation between sampling effort and fragment size (Pearson's correlation:  $r = 0.84$ ,  $n = 21$ ,  $p < 0.001$ ).

To avoid counting the same individual frog more than once, we always accessed forest fragments by different locations on each visit. Moreover, some studies in tropical areas found a low recapture rate for anurans (e.g. Del Lama et al., 2011; Funk et al., 2003; Grafe et al., 2004). To assess our sampling efficiency, we compared iNEXT (Hsieh et al., 2016) rarefaction/extrapolation curves for each fragment by using the exponent  $q = 0$  for the Hill numbers, which corresponds to simply species richness and puts more weight on rare species. This analysis showed that most fragments were adequately sampled, as extrapolated values of species richness were similar to observed values (Figure S1 in Appendix 1). All capture and handling protocols were conducted in accordance to ICMBio/SISBIO (license 13088-1) and the study did not require ethical approval.

### 2.3 | Species classification

It is well known that habitat-specialist and habitat-generalist species can be affected differently by habitat loss and fragmentation



**FIGURE 1** Study area including the 21 forest fragments (F1–F21) sampled in the Brazilian Atlantic forest in Cachoeiras de Macacu, Rio de Janeiro, Brazil

(Almeida-Gomes, Prevedello, et al., 2016). Therefore, we classified frog species as “forest-dependent” and “generalists”, according to their habitat use (Table S2 in Appendix 1). Forest-dependent species are those mainly found in forested areas, although some of them can also be able to occasionally use matrix areas near forest remnants (Almeida-Gomes & Rocha, 2014a; Almeida-Gomes, Rocha, et al., 2016; Haddad et al., 2013). Generalist species are usually common and abundant in disturbed habitats, being found in both forest and matrix areas (Almeida-Gomes, Rocha, et al., 2016). Frog species were classified in forest-dependent and generalist based on previous samplings in the same study area (Almeida-Gomes & Rocha, 2014a; Almeida-Gomes & Rocha, 2015; Almeida-Gomes, Vieira, et al., 2016; Almeida-Gomes, Rocha, et al., 2016) and on available information for Atlantic Forest frogs (Haddad et al., 2013).

## 2.4 | Observed frog species richness and dissimilarity

Species richness was defined as the cumulative number of frog species observed in multiple censuses of each patch. To quantify the dissimilarity among fragments in terms of species composition, we used the Simpson dissimilarity index, which calculates the dissimilarity between a pair of areas controlling for differences in species richness (Baselga, 2010; Simpson, 1943). This index represents the turnover component of Sørensen dissimilarity or spatial turnover (Baselga, 2012).

We created a distance matrix with the Simpson index of dissimilarity, using the function *ecol.dist* in the *FOSSIL* package (Vavrek, 2011), where a value of 1 is assigned to pairs of sites with no species in common and a value of 0 is assigned to pairs of sites with identical communities.

## 2.5 | Random placement models

To investigate whether overall frog abundance could explain frog richness and dissimilarity, we used two main null models, namely an area-based model and an abundance-based model. Both models were based on sampling with replacement, which allows making more general inferences regarding the regional species pool, including unsampled fragments. The first main model, referred as the “area-based model”, corresponds to Coleman’s (1981) original random placement model. In this model, the total number of individuals in each fragment ( $Z_i$ ) is proportional to its area, as follows:

$$Z_i = N * a_i.$$

Where  $N$  is the total number of individuals sampled in the regional species pool (the total number of individuals found in all sampled fragments), and  $a_i$  is the relative area of the fragment  $i$  (i.e. area of the fragment divided by the sum of all sampled areas), which corresponds to its probability of receiving a given individual of the regional pool. For example, a forest fragment with an area corresponding to 10%

of the overall fragment areas (the sum of all sampled areas) would receive 10% of the total number of individuals from the sampled regional species pool ( $N$ ).

We tested two alternative versions of the main area-based model, to assess whether the fit of this model may be improved with two simple adjustments. In these two alternative versions, the abundance estimated for each patch differs from the main area-based model (compare red, blue and green points in Figure S2 in Appendix 1), which could lead to different predictions of species richness and dissimilarity. First, because sampling effort varied among patches, we tested a model taking into account both area and effort. In this “area-and-effort-based model”, we calculated  $Z_i$  as  $N * a_i * e_i$ , where  $e_i$  was the proportional effort spent in each fragment (i.e. effort spent in fragment  $i$  divided by total effort spent in all sampled fragments). This model returned similar results as the traditional area-based model, as both models had similar intercept, slope, and  $R^2$  for species richness and similar values of correlation for observed and predicted distance matrix of species dissimilarity (Tables S3 and S4; Figure S3 in Appendix 1). Secondly, we applied a log transformation to patch areas, in an attempt to better meet the assumption that the number of individuals increases linearly with area (Coleman, 1981), as the observed area-abundance relationship we found was not linear (black points in Figure S2 in Appendix 1). In this “log(area)-based model”, the total number of individuals on each fragment ( $Z_i$ ) was proportional to its log-transformed area, as follows:

$$Z_i = N * La_i.$$

Where  $N$  is the total number of frog individuals sampled in the regional species pool, and  $La_i$  is the relative area of the fragment  $i$  calculated after applied a log-transformation to all areas (i.e.  $\log(\text{area})$  of the fragment divided by the sum of the logarithms of all sampled areas), which corresponds to its probability of receiving a given individual of the regional pool. This model, had a similar fit compared to the main area-based model for species richness, as can be seen by the  $R^2$  values, and similar values of correlation for observed and predicted distance matrix of species dissimilarity (Tables S3 and S4; Figure S4 in Appendix 1). Therefore, we applied only the main area-based model (without effort and without a log-transformation) for the analyses separating forest-dependent and habitat-generalist species (see Section 2.6).

For the second main model, the abundance-based model, we retained the total frog abundance observed in the field for each fragment, but the species identities were shuffled, and their relative abundances could vary. Therefore, for each fragment  $i$ , we drew (with replacement)  $Z_i$  individuals from the sampled regional pool, where  $Z_i$  was the same number of individuals sampled on each fragment.

Because some species may not have been detected in some fragments during our field sampling, we also tested a modified version of the abundance-based model that incorporates detection error. Prior to the randomizations, we followed the approach proposed by

Chao et al. (2015) to obtain a corrected estimate of the abundance of each frog species in the regional pool, while accounting for detection error. To do so, the relative abundances of the regional species pool were corrected, through the adjustment of the relative abundances for the set of species detected in the sample and the estimation of the relative abundances for the set of species undetected in the sample (see details in Chao et al., 2015). The few (three) undetected species were disregarded, and the proportions of the remaining (detected) species were rescaled, to obtain a corrected estimate of their abundances. Then, the same procedures of the abundance-based model were applied to sample from this corrected regional species pool. This model generated similar results to those of the simpler abundance-based model (Tables S3 and S4; Figure S5 in Appendix 1), suggesting that detection error was low or negligible in our study.

Finally, to test the sensitivity of the results to the type of sampling (i.e. with or without replacement), we also repeated the same procedures described for the two main models (area-based model and abundance-based model), but using sampling without replacement (as in Bidwell et al., 2014; Guadagnin et al., 2009). When sampling without replacement, both the area-based and the abundance-based models simply shuffled the sampled regional pool of individuals across fragments, limiting inferences only to the sampled fragments. These alternative versions of our models (without replacement) returned similar results to those using all species and sampling with replacement (Table S5; Figure S6 in Appendix 1).

Our models are null models in the sense that they only incorporate the variables area (area-based models) or abundance (abundance-based models). We know that many other factors can affect the community structure in fragmented landscapes, such as habitat quality (Krämer et al., 2012), edge effects (Banks-Leite et al., 2010), and isolation (Boscolo & Metzger, 2011). However, our aim was to test whether observed patterns deviate from null models predictions across habitat patches, as potential deviations could indicate which ecological or methodological factors are indeed important in shaping such patterns (Gotelli & Graves, 1996).

## 2.6 | Data analysis

Each model was run 1,000 times, the same number of randomizations employed by previous studies (Bidwell et al., 2014; Guadagnin et al., 2009). At each run, we recorded the frog species richness for each fragment and a distance matrix for all fragments (based on Simpson index of dissimilarity, with the data transformed to presence-absence). For each fragment, we averaged species richness (as in Bidwell et al., 2014; Guadagnin et al., 2009) across the 1,000 iterations, thus obtaining a single (average) predicted value. Furthermore, we also averaged the pairwise dissimilarities (e.g. the dissimilarity value between fragments 1 and 2 and between fragments 1 and 3) across the 1,000 iterations, thus obtaining a single (average) predicted distance matrix. We compared observed and predicted frog species richness through linear models. To obtain a better visualization of the SAR predicted by each model, as well

as the observed SAR, we log-transformed fragment areas. We performed a Mantel correlation test (Mantel, 1967) between observed and predicted distance matrix, using 10,000 permutations and the function *mantel* in VEGAN package (Oksanen et al., 2018).

Analyses of the two main models (area-based and abundance-based) were performed for (a) all species combined, (b) forest-dependent species only, and (c) habitat-generalist species only. Analyses of the alternative versions of these two main models (i.e. the area-and-effort-based model, the log(area)-based model, the abundance-based model with detection error, and the models without replacement) were restricted to the first group only (i.e. all species combined; see Supporting Information).

For models with a significant ( $p < 0.05$ ) relationship between observed and predicted values of species richness, we further used a Student's *t* test to test the significance of slope = 1 and intercept = 0 null hypotheses (Piñeiro et al., 2008). This approach enabled us to verify if predicted richness was biased and whether the bias depended on the level of species richness. If the slope does not differ statistically from 1, but the intercept differs from 0, there is a constant bias, in which observed species richness differs from predicted by a simple offset. If the slope differs from 1, then the degree of the bias depends on the level of species richness. If the slope does not differ from 1 and the intercept does not differ from 0, the model predictions are unbiased. Higher  $R^2$  values indicate greater precision of the predictions. All simulations and analyses were performed in R version 3.6.3 (R Core Team, 2020).

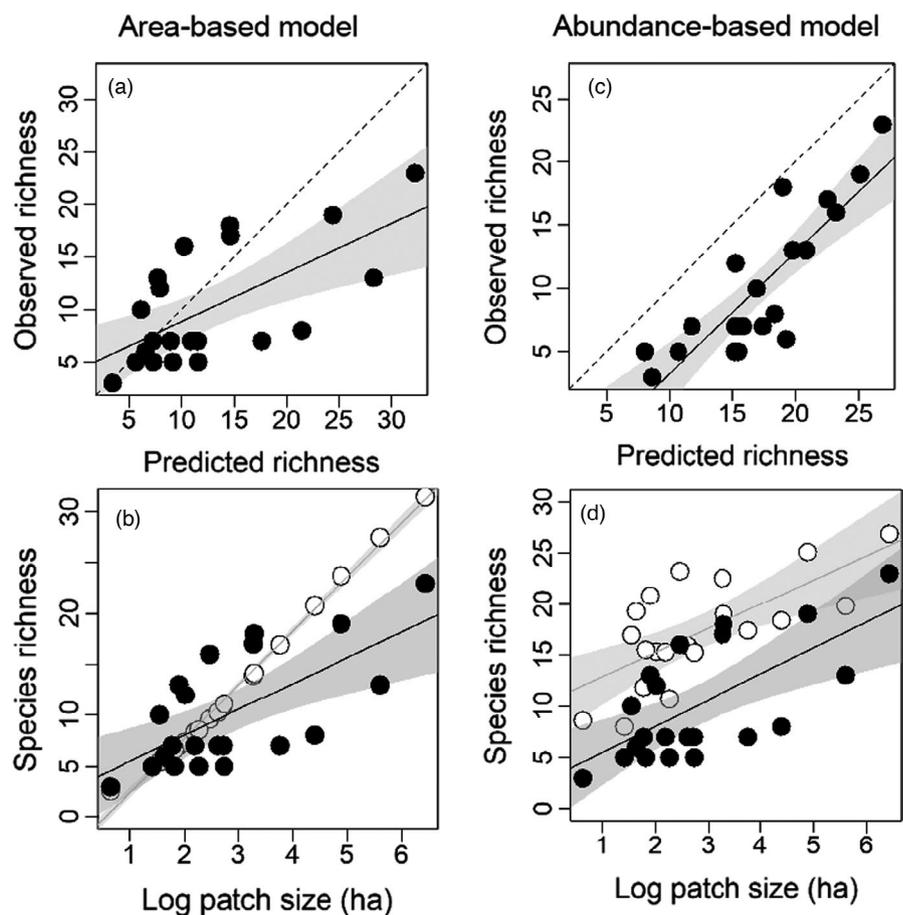
### 3 | RESULTS

In total, we sampled 2,361 frog individuals from 37 species in the 21 forest fragments (Table S2 in Appendix 1). Observed abundance and species richness per fragment varied from 15 (F16) to 425 (F19) individuals and from 3 (F20) to 23 (F19) species, respectively. The three most abundant species were *Adenomera marmorata* ( $N = 723$ ; 30.6%), *Scinax aff. x-signatus* ( $N = 274$ ; 11.6%), and *Euparkerella brasiliensis* ( $N = 240$ ; 10.1%).

#### 3.1 | All species combined

##### 3.1.1 | Area-based model

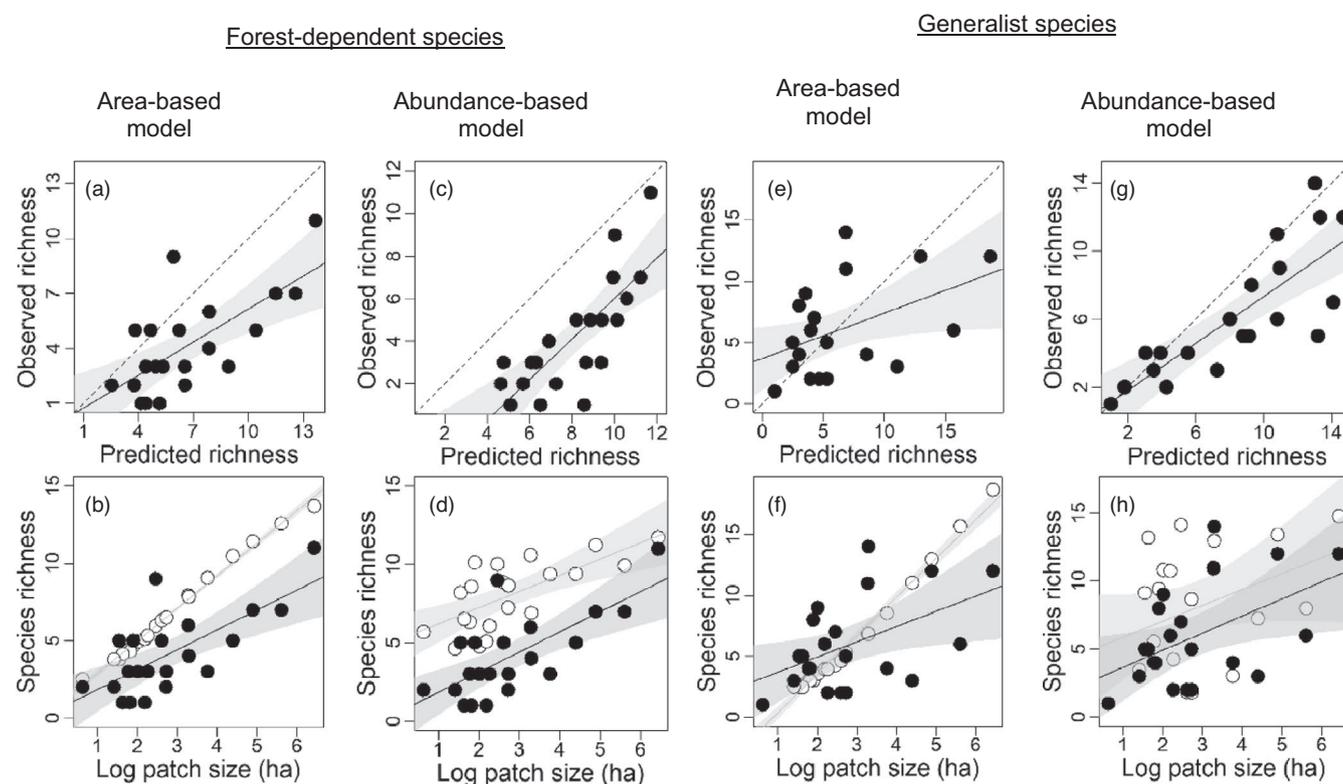
Considering all frog species combined and the area-based model, the relationship between observed and predicted richness was significant ( $R^2 = 0.42$ ,  $p < 0.01$ ; Figure 2a; Table 1a). Intercept and slope of this relationship were different from 0 and 1, respectively, meaning that the degree of bias depended on the species richness of the forest fragment. The model underestimated species richness in smaller fragments, and overestimated richness in larger fragments (Figure 2b). Observed and predicted species dissimilarity were also correlated (Mantel  $r = 0.33$ ,  $p = 0.005$ ; Figure S7 in Appendix 1).



**FIGURE 2** Results from the two random placement models (area-based model and abundance-based model) for all species, using sampling with replacement: (a and c) Observed and predicted species richness. (b and d) Observed (black dots) and predicted (white dots) species-area relationships. In all plots, predicted values represent the average values obtained for each forest fragment across 1,000 iterations of the model, and the shaded polygons delimit 95% confidence intervals. In (b and d), the lines represent the regression between log(patch size) and predicted (gray line) or observed values (black line). Dotted lines in (a and c) depict the 1:1 relationship

**TABLE 1** Parameters of linear regression between observed (response variable) and predicted species richness (explanatory variable). If *t* tests for intercept = 0 and slope = 1 are significant ( $p < 0.05$ ), they are considered different from 0 and 1, respectively

Model	Intercept $\pm$ SE	Slope $\pm$ SE	$R^2$	<i>F</i> overall	<i>p</i>	<i>t</i> for intercept = 0	<i>p</i>	<i>t</i> for slope = 1	<i>p</i>
<b>(a) All species</b>									
Area-based									
Species richness	4.19 $\pm$ 1.85	0.46 $\pm$ 0.12	0.42	14.00	<0.01	-2.26	0.04	4.27	<0.01
Abundance-based									
Species richness	-7.13 $\pm$ 2.49	0.98 $\pm$ 0.14	0.73	51.70	<0.01	2.86	<0.01	0.17	0.87
<b>(b) Forest-dependent species</b>									
Area-based									
Species richness	0.16 $\pm$ 1.06	0.60 $\pm$ 0.14	0.48	17.51	<0.01	-0.15	0.88	2.79	0.01
Abundance-based									
Species richness	-4.18 $\pm$ 1.57	0.97 $\pm$ 0.18	0.61	30.1	<0.01	2.66	0.01	0.16	0.88
<b>(c) Habitat-generalist species</b>									
Area-based									
Species richness	3.45 $\pm$ 1.32	0.36 $\pm$ 0.16	0.22	5.24	0.03	-2.62	0.02	3.98	<0.01
Abundance-based									
Species richness	-0.14 $\pm$ 1.09	0.70 $\pm$ 0.11	0.67	38.98	<0.01	0.14	0.90	2.62	0.01



**FIGURE 3** Results from the two random placement models (area-based model and abundance-based model) for forest-dependent and habitat-generalist species, using sampling with replacement: (a, c, e and g) Observed and predicted species richness. (b, d, f and h) Observed (black dots) and predicted (white dots) species-area relationships. In all plots, predicted values represent the average values obtained for each forest fragment across 1,000 iterations of the model and the shaded polygons delimit 95% confidence intervals. In (b, d, f and h), the lines represent the regression between log(patch size) and predicted (gray line) or observed values (black line). Dotted lines in (a, c, e and g) depict the 1:1 relationship

### 3.1.2 | Abundance-based model

Observed species richness was highly correlated to the richness predicted by the abundance-based model ( $R^2 = 0.73$ ,  $p < 0.01$ ; Figure 2c; Table 1a). The slope did not differ from 1, but the intercept differed from 0, indicating a simple offset bias. The model consistently overestimated species richness in fragments of all sizes, predicting  $7.5 \pm 2.9$  (mean  $\pm$  SD) additional species than observed per site (Figure 2d). Similarly, species dissimilarity predicted by this model was significantly related to observed dissimilarity (Mantel  $r = 0.40$ ,  $p < 0.001$ ; Figure S8 in Appendix 1).

## 3.2 | Forest-dependent species

### 3.2.1 | Area-based model

Considering only the forest-dependent species, the relationship between observed and predicted richness was significant for the area-based model ( $R^2 = 0.48$ ,  $p < 0.01$ ; Figure 3a; Table 1b). The slope differed from 1, but the intercept did not differ from 0, indicating that the bias depends on the level of species richness. The model overestimated species richness in all fragments, especially the larger, predicting  $2.5 \pm 2.3$  (mean  $\pm$  SD) additional species than observed per site (Figure 3b). In contrast, observed and predicted species dissimilarity were not correlated (Mantel  $r = 0.08$ ,  $p = 0.283$ ; Figure S9 in Appendix 1).

### 3.2.2 | Abundance-based model

Observed frog species richness was correlated to the richness predicted by the abundance-based model ( $R^2 = 0.61$ ,  $p < 0.01$ ; Figure 3c; Table 1b). The slope did not differ from 1, but the intercept differed from 0, indicating a simple offset bias. The model consistently overestimated species richness in fragments of all sizes, predicting  $4.4 \pm 1.66$  (mean  $\pm$  SD) additional species than observed per site (Figure 3d). Furthermore, frog species dissimilarity predicted by this model was not significantly related to observed dissimilarity (Mantel  $r = 0.17$ ,  $p = 0.064$ ; Figure S10 in Appendix 1).

## 3.3 | Habitat-generalist species

### 3.3.1 | Area-based model

The relationship between observed and predicted frog richness was significant ( $R^2 = 0.22$ ,  $p = 0.03$ ; Figure 3e; Table 1c). Intercept and slope were different from 0 and 1, respectively, meaning that the degree of bias depended on the species richness of the fragment. The model underestimated species richness in smaller fragments, and overestimated richness in larger fragments (Figure 3f). Similarly, observed and predicted species dissimilarity were also correlated (Mantel  $r = 0.29$ ,  $p = 0.012$ ; Figure S11 in Appendix 1).

### 3.3.2 | Abundance-based model

Observed frog species richness was highly correlated to the richness predicted by the abundance-based model ( $R^2 = 0.67$ ,  $p < 0.01$ ; Figure 3g; Table 1c). The slope differed from 1, but the intercept did not differ from 0, indicating that the bias depends on the level of species richness. The model overestimated species richness for larger fragments (Figure 3h). In addition, frog species dissimilarity predicted by this model was significantly related to observed dissimilarity (Mantel  $r = 0.32$ ,  $p = 0.001$ ; Figure S12 in Appendix 1).

## 4 | DISCUSSION

We confirmed that simple random placement models can partially explain patterns of anuran species richness in a fragmented landscape. Moreover, our results show that patterns of species dissimilarity can also be (at least in part) explained by random placement models, especially for habitat-generalist species, an important finding that had not been documented before. These results are robust to methodological issues such as accounting or not for species detectability or applying logarithms to fragment area to linearize the relationship between species abundance and patch size. Therefore, although many ecological factors can affect community structure in fragmented landscapes, our results suggest that simple probabilistic processes can explain not only species richness, but also species dissimilarity, across fragmented landscapes. Our results are consistent with predictions of some neutral models based on demographic stochasticity, species independence, and unlimited dispersal (Hubbell, 2001), but they can also be interpreted more generally as simple sampling effects that influence diversity through sampling effects of abundance and changes in spatial scale (Chase et al., 2018).

In the Coleman's (1981) original area-based model (as well as its slightly-modified version, the log(area)-based model), the relationship between observed and predicted species richness was significant but weak. Previous studies have shown that Coleman's model may explain SARs for different taxa, including birds (Coleman et al., 1982), plants (Miller & Wiegert, 1989; Simberloff & Gotelli, 1984), and sessile organisms of rocky intertidal boulders (McGuinness, 1984). However, the area-based model overestimated anuran species richness in medium-to-large fragments, which has been also documented previously for birds (Bidwell et al., 2014; Guadagnin et al., 2009). The area-based model tends to assign too many individuals to larger fragments, thus predicting too many species (Bidwell et al., 2014; Guadagnin et al., 2009). Therefore, this model may have limited applicability to explain variation in species richness in fragmented landscapes.

The abundance-based model had a better fit to observed species richness than the area-based model (regardless whether a correction for detecting error is used), as also found for birds in two previous studies (Bidwell et al., 2014; Guadagnin et al., 2009). The reason is simple: the abundance-based model incorporates more accurately variation in the total abundance of individuals among patches, which

seems a strong determinant of species richness. It is a consensus that the number of species increases with the number of individuals sampled (Gotelli & Colwell, 2001). Indeed, in our study we found a strong relationship between the number of sampled individuals and observed species richness in forest fragments ( $R^2 = 0.76$ ,  $p < 0.001$ ).

Despite the better fit of the abundance-based model to our data, this model consistently overestimated species richness for all fragments, considering all species combined, or forest-dependent species only. This limitation does not invalidate the model; rather, we believe it may be illuminating to identify the methodological and ecological factors shaping anuran communities. Three complementary hypotheses can explain why we observed fewer species in the field than predicted by the abundance-based model. First, it is likely that not all species were detected during field samplings, despite the considerable sampling effort employed. Some anuran species have low detectability due to their small body size, rarity, pattern of calling or their ability to camouflage among the leaf litter or underground, making them difficult to detect through visual encounter surveys (de Sá et al., 2019; Lima et al., 2019). However, we highlight that our analysis taking into account imperfect detection returned very similar results, indicating that our sampling effort was reasonably complete in most sites (see Figure S1 in Appendix 1). Second, some species were not found in forest fragments probably because these fragments lacked the specific habitats required by these species. For example, some strictly forest species (e.g. *Aplastodiscus eugenioi* and *Scinax humilis*) depend on streams and pools inside the forest for their reproduction, respectively, and were not found in several forest fragments in the study area lacking these habitats (Almeida-Gomes & Rocha, 2015). Third, some species might not be able to cross the matrix separating forest fragments, either because they do not tolerate the matrix environments or due to dispersal limitation (Hubbell, 2001), preventing rescue effects and resulting in local extinctions. For example, several species we found in the sampled fragments (e.g. *Euparkerella brasiliensis*, *Chiasmocleis lacrimae*, *Ischnocnema guentheri*, *Haddadus binotatus*) are forest-dependent species and were never detected in pasture matrix, the dominant matrix type in the study area (Almeida-Gomes & Rocha, 2014a). Therefore, if the dispersal limitation hypothesis is true, the species richness overestimation in the abundance-based model would be compatible with neutral theory, which includes dispersal limitation as a central parameter (Hubbell, 2001).

Both random placement models significantly explained species dissimilarity for generalist but not for forest-dependent species, suggesting that the relative importance of deterministic versus stochastic processes may vary between the two groups. While generalist species are known to tolerate a broader range of environmental conditions, specialist (e.g. forest-dependent) species are more dependent on specific environments for survival or reproduction (Almeida-Gomes & Rocha, 2015; Almeida-Gomes et al., 2019; Devictor et al., 2008; Morante-Filho et al., 2016; Pardini et al., 2010). As a result, generalist species tend to occupy more sites and be more abundant than specialists (Brown, 1984). For example, Pandit et al. (2009) showed that habitat specialists are primarily affected by

environmental variables, while generalist species are more prone to respond to spatial variables. Moreover, generalists tend to be better dispersers compared to specialist species (Li et al., 2015). This is especially important considering that our models assume no dispersal limitation, which may be particularly true for generalists. Therefore, even acknowledging that there is a large amount of unexplained variance, our results may indicate that forest-dependent species are more affected by niche processes, while habitat-generalist species are more affected by random processes. This finding suggests that random placement models can be particularly useful in explaining distribution and abundance of habitat-generalist species in fragmented landscapes. Moreover, it also suggests that the null models can be useful to detect niche-based processes if the model outputs differ from the observed patterns. Because community dissimilarity is a central parameter to understand how habitat loss and fragmentation affect biodiversity (e.g. Almeida-Gomes & Rocha, 2014a; Banks-Leite et al., 2014; Horváth et al., 2019), we recommend that future studies using a random placement approach also evaluate species dissimilarity in addition to species richness.

## 5 | CONCLUSIONS

Overall abundance of frog individuals detected in the field seems the main variable responsible for the patterns of species richness and dissimilarity we found. Therefore, we believe that the best way to improve understanding of the importance of random processes to explain patterns of biodiversity in fragmented landscapes is to evaluate which factors cause variation in total abundance in fragments. This variation can be caused by a combination of both random (target-effect) and niche processes (higher habitat heterogeneity and suitability). Future studies aimed to understand patterns of biodiversity in fragmented landscapes should consider evaluating the contribution of simple random placement processes in generating these patterns. We suggest treating the two null models (area-based and abundance-based) not as directly alternative models, as the area-based model is an approximation of the abundance-based model. Moreover, other landscape variables beyond patch size can be used in attempts to better estimate species abundance, such as habitat amount, patch isolation, and structural connectivity. Incorporation of such variables in new models would allow testing the relative importance of patch size versus other landscape variables as determinants of species richness and dissimilarity, advancing understanding of the factors shaping community structure in patchy systems.

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## CONFLICT OF INTEREST

We have no conflict of interest to report.

## AUTHORS' CONTRIBUTIONS

M.A.-G. and J.A.P. conceived the idea, performed the data analyses, and led the writing; M.A.-G. defined the sampling design and collected field data; N.J.G. made a substantial contribution to the development of models; all authors commented on drafts and revisions and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data are available at Dryad Digital Repository <https://doi.org/10.5061/dryad.5qfttdz73> (Almeida-Gomes et al., 2022).

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