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Causes and processes determining the structure of anuran assemblage in an Atlantic Forest fragmented area

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Índice

General abstract

Understanding causes and processes behind differences in species composition between areas can be useful in understanding how the degradation of natural environments affects the structure of communities. Beta diversity can explain changes between communities by partitioning two components: nestedness and turnover. In addition, it is to being a tool to infer about the role of deterministic and stochastic processes in determining community structure along ecological gradients. In this thesis, we evaluated in the Chapter 1 the importance of the two beta diversity components (nestedness and turnover) between continuous forest patches, forest fragments and pasture matrix; in the Chapter 2, we assessed whether the differences in communities obey deterministic or stochastic patterns in this local fragmented landscape in the state of RJ. We found that habitat amount in the region mediates the strength of nestedness and turnover, but their relative importance depends on which type of environments are being considered in the comparison. We also observed the prevalence of stochastic processes driving the difference in species composition between forest fragments and matrix pastures. These results highlight the importance of evaluating which mechanisms are generating beta diversity patterns and the need of considering a gradient of land cover (including matrix areas) in biodiversity analysis to have a better understanding on biodiversity patterns in fragmented landscapes.

Resumo geral

Entender as causas e processos por trás das diferenças na composição de espécies entre áreas pode ser útil para entender como a degradação de ambientes naturais afeta a estrutura das comunidades. A diversidade beta pode explicar as mudanças entre as comunidades, dividindo-a em dois componentes: aninhamento e substituição (turnover). Além disso, ela é uma ferramenta para inferir o papel de processos determinísticos e estocásticos na estrutura da comunidade ao longo de gradientes ecológicos. Nesta tese, avaliamos no Capítulo 1 a importância dos dois componentes da diversidade beta (aninhamento e *turnover*) entre ambientes de mata contínua, fragmentos florestais e matriz de pastagem; no Capítulo 2, avaliamos se as diferenças nas comunidades obedecem a padrões determinísticos ou estocásticos em uma paisagem fragmentada no estado do RJ. Descobrimos que a quantidade de habitat influencia a relevância do aninhamento e turnover, mas sua importância relativa depende de qual tipo de ambiente está sendo considerado na comparação. Também observamos a prevalência de processos estocásticos conduzindo a diferença na composição de espécies entre fragmentos florestais e matrizes de pasto. Esses resultados destacam a importância de avaliar quais mecanismos estão gerando padrões de diversidade beta e a necessidade de considerar um gradiente de cobertura vegetal (incluindo áreas de matriz) na análise da biodiversidade para ter um melhor entendimento dos padrões de biodiversidade em paisagens fragmentadas.

General introduction

The human-induced disturbance in natural areas leads to the reduction of native landcover patches and increases the insulation among these fragmented areas (Fahrig 2003), providing a land cover gradient of closed and open habitats (Verdú et al. 2000, Taboada et al. 2006) that affects directly how the organisms use the landscape and influence the richness and abundance of species in fragmented habitats (Andrén 1994). Hence, the aforementioned conversion of natural habitats may cause local extinction and changes in composition of communities in degraded areas (Hanski 2015, Bogoni et al. 2016) and ecological services (Birkhofer et al. 2018).

Species diversity in natural environments can be measured at three different levels: (1) in a specific habitat or community (alpha diversity); (2) in all habitats in a given region (gamma diversity); or (3) by the difference in species composition between habitats (beta diversity) (Whittaker 1960, Koleff et al. 2003). Beta diversity can be defined as the extent of change within a community (Whittaker 1960) and understood as the replacement or change in species composition between locations (Koleff et al. 2003). The beta diversity indexes provide values for how different one community is from others, and can provide answers on the drivers of such differentiation. Therefore, it is important to distinguish the two phenomena behind beta diversity patterns: nestedness and the spatial substitution of species (turnover) (Baselga 2010).

Nested communities result from non-random species loss, emerging poorest communities that represent subsets of richer original communities (Ulrich et al. 2009, Baselga 2010, Almeida-Neto et al. 2012). However, when replacement of species occurs in a fragmented habitat, this pattern is assigned by the spatial turnover (Qian 2009, Baselga 2010), indicating that some areas lose and gain groups of organisms. Spatial turnover occurs more markedly in environments where there is greater intensification of land use, possibly due to the increased risk of extinction of specialist species caused by conversion of natural areas (Stofer et al. 2006, Questad et al. 2011), since generalists have more amplitude in resource utilization (Harrison et al. 1992). Thus,

disentangling these two components in the evaluation of species composition becomes important for understanding the causes of differences between communities (loss or replacement of species), which is not possible by using indices that do not make this distinction (e.g., Whittaker, Jaccard or Sorensen). Thus, by separating these components, we can associate the different patterns of species composition variation with their potential triggers (Baselga 2012).

Beta diversity analysis is also a useful tool for inferring the importance of deterministic (niche-based) and stochastic (neutral) processes for community structure along ecological gradients (Chase 2010, Anderson et al. 2011). As the two are fundamentally intertwined, unveil the importance of these processes with different local or regional factors requires a careful analysis of the factors influencing beta diversity (Chase & Myers 2011).

Deterministic processes (environmental filters and species interactions, for example) have traditionally been seen as the most important in a community. For example, Püttker et al. (2015) reported a non-random species extinction in small mammal communities in fragmented Atlantic Forest landscapes, and suggested that habitat loss and other anthropogenic disturbances are filters that increase the importance of deterministic processes in a community. On the other hand, several ecologists suggest that stochastic processes, such as random extinctions and ecological drifts, are more important in certain cases for natural communities' structure due to the difficulty of detecting the influence of niches when there are numerous stochastic processes emerging from local and biogeographic factors (Vellend 2010, Chase & Myers 2011). However, the strength of these two factors probably varies in relation to time and space and depends on the taxonomic group under study (Vellend 2010), and the abiotic conditions, in addition to environmental disturbances. This set of aspects have been seeing as important triggers of deterministic and stochastic processes in communities (Trexler et al. 2005, Chase 2007, Vellend 2010).

It is also important to highlight that the variations in species composition within communities are induced by factors that limit the presence of species in a certain habitat. In this scenario, the type of matrix surrounding natural fragments in a landscape is an important factor

for species composition, since characteristics such as quality and complexity of the matrix act as filters in the movement of the species (Zollner 2000, Prevedxello & Vieira 2010). The capacity of a specie moving across the matrix is determinant for its permanence in a fragmented landscape, so that species with higher mobility and more tolerant to the matrix have more chances to survive and to avoid local extinction (Antongiovanni & Metzger 2005, Harper et al. 2008).

The Brazilian Atlantic Forest is the second largest domain in South America (Galindo-Leal & Câmara 2003) and, despite being a biodiversity hotspot (Mittermeier et al. 2011), remains only 16% of the original vegetal cover (Ribeiro et al. 2009). Much of the remaining biome is composed of small isolated fragments, with different human influence histories and wide variety of environmental conditions (Ribeiro et al. 2009; Melo et al. 2013; Ferraz et al. 2014). Understanding the causes (loss or replacement of species) of differences in species composition between communities and determining the processes (deterministic or stochastic) behind these changes can be critical to understanding how habitat loss and fragmentation affects species composition in this biome with high endemism and species diversity.

In this work we sought to understand how the process of land use change affects the beta diversity of biological communities at a local landscape scale. To do so, in the Chapter 1 we assessed differences in amphibian communities among continuous areas of forest, forest fragments and pasture matrix, and verified whether these differences are caused by species loss or replacement. In the Chapter 2, we used null models to verify whether these differences in amphibian species composition between forest fragments and pasture matrix are the result of deterministic or stochastic processes.

Chapter 1 – Habitat amount mediates the strength of nestedness and turnover in anuran communities in an Atlantic Forest area

Abstract

Changes in community structure after anthropogenic disturbances (e.g., habitat loss) can be evaluated through a beta diversity analysis. The two components of beta diversity, nestedness and turnover, may act simultaneously, but local and spatial features may change their relative importance. Applying a Structural Equation Model (SEM), we compared species composition between continuous forest areas and forest fragments, and between forest fragments and matrix areas, assuming that continuous forest and matrix areas represent two extremes of the same gradient of habitat amount (forest cover). We found a predominance of nestedness comparing continuous forest sites and forest fragments, indicating that more species are lost than replaced when the forest cover is reduced and fragmented. We also found a predominance of turnover comparing forest fragments and matrix areas, indicating that more species are replaced than lost when the land cover changes from forest fragments to pasture areas. Our results support the importance of maintaining large areas of continuum forest to preserve amphibian biodiversity. By disentangling nestedness from species turnover, we were able to show empirically that species loss happens mostly due to habitat loss and fragmentation of former continuous forest areas.

Resumo

Mudanças na estrutura da comunidade após distúrbios antropogênicos (por exemplo, perda de habitat) podem ser avaliadas através da análise da diversidade beta. Os dois componentes da diversidade beta, aninhamento e substituição (turnover), podem agir simultaneamente, mas as características locais e espaciais podem mudar sua importância relativa. Aplicando um Modelo de Equação Estrutural (SEM), comparamos a composição de espécies entre áreas florestais contínuas e fragmentos florestais, e entre fragmentos florestais e áreas de matriz, assumindo que floresta contínua e áreas de matriz representam dois extremos do mesmo gradiente de quantidade de habitat (cobertura florestal) . Encontramos uma predominância de aninhamento comparando áreas florestais contínuos e fragmentos florestais, indicando que mais espécies são perdidas do que substituídas quando a cobertura florestal é reduzida e fragmentada. Também encontramos uma predominância de substituição comparando fragmentos florestais e áreas de matriz, indicando que mais espécies são substituídas do que perdidas quando a cobertura vegetal muda de fragmentos florestais para áreas de pastagem. Nossos resultados apoiam a importância de manter grandes áreas de floresta contínua para preservar a biodiversidade de anfíbios. Ao separar o aninhamento da substituição de espécies, fomos capazes de mostrar empiricamente que a perda de espécies ocorre principalmente devido à perda de habitat e fragmentação de antigas áreas de floresta contínua.

Introduction

The conversion of natural habitats into anthropogenic areas has been acknowledged as the main cause of the world biodiversity crisis, especially in the humid tropics (Kim et al. 2015, Hossain et al. 2020). These tropical areas sustain the majority of biodiversity (Slik et al. 2015), but suffer from increased rates of land use change and deforestation (Asner et al. 2009, Hansen et al. 2013, Kim et al. 2015). Habitat loss and fragmentation create landscapes characterized by a heterogeneous mosaic of land cover, with native forest patches immersed in different types of anthropogenic matrix (Fahrig 2003). These landscape changes can directly affect patterns of species diversity and ecological processes, resulting in local extinctions and changes in species composition (Andrén 1994, Pardini et al. 2010, Bitar et al. 2015).

Patches surrounded by a matrix are compose the most important landscape elements in determining biodiversity patterns in fragmented landscapes (Forman 1995). The size, spatial arrangement, habitat heterogeneity, and quality of patches can have strong importance in determining patterns of biodiversity in fragmented landscapes. In such human-induced disconnection between patches, i.e., habitat split, is expected the decreasing of populations' size and occupancy rates, and negatively affect richness of local communities due to the change in habitat structure (Becker et al. 2007). For example, Almeida-Gomes and Rocha (2015) found that only continuous forest sites had specific habitats for anurans (e.g., large rivers), and that the smaller the fragment, the lower the diversity of reproductive sites. A same model is also observed for taxonomic and functional avian diversity, where has been verified a "biodiversity-area relationship" (e.g., Ehlers Smith et al. 2018, Muller et al. 2020) that include important biological landscape metrics, such as matrix permeability (da Silva et al. 2015). The matrix is usually the most ubiquitous and connected landscape element type, playing an essential role in landscapes worldwide (Forman & Godron 1986, Prevedello & Vieira 2010). These areas act as a filter for the movement of individuals and their ability in moving across the matrix determines its persistence in fragmented landscapes (Prevedello & Vieira 2010, Boesing et al. 2018). An example of the

importance of matrix in the biological flow is the fact that different groups of animals vary in their overall response to the fragmentation, where the matrix linking patches can affect positively or negatively to the dynamics and composition of species assemblages (Gascon et al. 1999).

Several ecological processes may be responsible for the variation in species composition (beta diversity) in fragmented landscapes. For example, dispersal limitation implies that not all suitable habitats will be occupied by a given species (Ehrlen & Eriksson 2000). Patterns of beta diversity in fragmented landscapes are influenced by factors such as environmental gradients, species dispersal and spatial connectivity between sites (Moritz et al. 2013, Hill et al. 2017). For example, forest-dependent species may be recorded only in large habitat remnants due its high structural complexity (Ehlers Smith et al. 2018), the presence of required food (Si et al. 2015) and specific habitats (Almeida-Gomes & Rocha 2015). Furthermore, it is expected an increase in the diversity of higher mobile species when the fragmentation of habitats also increases and higher rates of beta diversity for taxonomic groups with lower dispersal ability (Tilman et al. 1994, Thomas 2000, Silva et al. 2016).

Patterns of beta diversity in fragmented landscapes can be caused by loss (nestedness) or replacement (turnover) of species (Baselga 2010). Although these two regulatory phenomena act simultaneously to total beta-diversity among assemblages, local and spatial attributes of the environment may influence their relative importance (Brendock et al. 2015, Tonkin et al. 2016). Nested assemblages resulted from non-random species loss, with poorest communities representing subsets of richer original communities (Ulrich et al. 2009, Baselga 2010, Almeida-Neto et al. 2012). For example, several studies found that small patches usually represent a subset of the species recorded in larger patches (e.g., Bittencourt-Silva & Silva 2014; Goded et al. 2019; Dardanelli & Bellis 2021). On the other hand, there may be a predominance of turnover in environments where there is greater intensification of human activities, possibly due to the increased risk of extinction of specialist species caused by conversion of natural areas (Stofer et al. 2006, Questad et al. 2011), since generalists have more amplitude in resources utilization

(Harrison et al. 1992). Therefore, separating these two different components of dissimilarity brings more accurate information about ecological processes in fragmented landscapes.

Here, we assessed the contribution of nestedness and turnover to explain differences in anuran species composition in an Atlantic Forest fragmented area. We predict that there would be a predominance of nestedness when forest cover is lost and fragmented into smaller patches and a predominance of turnover when forest patches are converted into open matrix areas, assuming that continuous forest and matrix areas represent two extremes of the same gradient of habitat amount (forest cover). To perform the analyses, we used one of the largest datasets of amphibians in tropical fragmented landscapes, which includes samples in continuous forest sites, forest fragments and pasture matrix areas (Almeida-Gomes et al. 2016b).

Methods

Study area

We carried out the frog sampling between July 2007 and March 2014 in a fragmented Atlantic Forest landscape in the municipality of Cachoeiras de Macacu, state of Rio de Janeiro, Brazil. This municipality holds the Reserva Ecológica de Guapiaçu (REGUA) (22°24'S, 42°44'W), which contains nearly 7600 ha of Atlantic Forest, ranging from secondary forests to areas of relatively non-disturbed forests (Almeida-Gomes et al. 2016b). The surrounding landscape is composed of forest patches immersed in different matrices, mainly pastures (Vieira et al. 2009). We sampled three continuous forest sites (CF1-CF3), 21 forest patches ranging from 1.9 to 619 ha (F1-F21) and 21 pasture matrix areas (M1-M21) (Fig. 1), covering a gradient of habitats usually present in fragmented landscapes (e.g., Pardini et al. 2009).

Figure 1 - Study area, indicating continuous forest sites (CF1–CF3), forest fragments (F1–F21), and matrix areas (M1-M21) sampled in the Brazilian Atlantic Forest, Rio de Janeiro, Brazil.
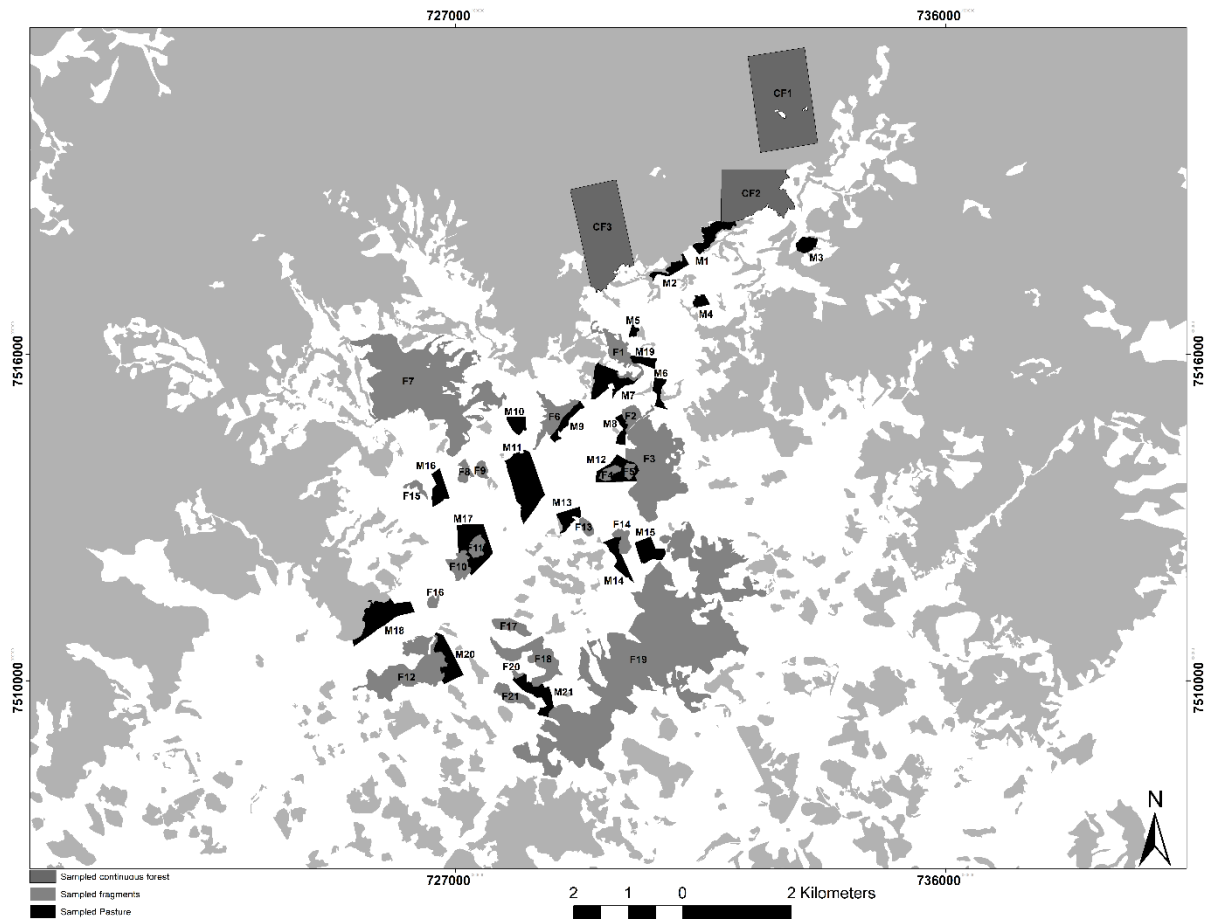
Data collection and frog assemblages

We recorded anurans by visual encounter survey (VES; Crump & Scott 1994) at nightime from 19:00 to 00:00 h, using headlamps. This method is regarded as the best to detect the highest number of anuran species, including arboreal species that usually are not detected by pitfalls or plots (Almeida-Gomes et al. 2014). We conducted VES in eight periods: July-September/2007, December/2007-March/2008, July-September/2008, January-March/2009, July-September/2009, and January-March/2010, January-December/2013, and January-February/2014. During frog sampling, we inspected different habitat types such as tree trunks, branches, leaf-litter, rocks in the streams, bromeliads and puddles, in order to record anuran species with different habitat requirements. Sampling effort varied between 66 and 92 h (median = 86 h) for continuous forest sites, 21 and 118 h (median = 36 h) for forest fragments and 9 and 27 h (median = 14 h) for pasture matrix (Table 1 in Appendix 1). Sampling coverage (proportion of observed richness relative to richness estimated by Chao 1) varied between 0.54 to 1 among all sites, and there was no significant correlation between sampling effort and sampling coverage (r Pearson = -0.08; P = 0.601). Since most biodiversity samplings tend to be incomplete, the empirical species-rank abundance distribution (RAD) can overestimate the true relative abundance of the set of detected species because it ignores the set of undetected species (Chao et al. 2015). Thus, we used the Jade algorithm (Joint species-rank Abundance Distribution/Estimation package; Hsieh and Chao, 2014) to generate the rank abundance curves with undetected species. The analysis suggested that our data was satisfactorily sampled, presenting a small tail in all land use categories of undetected species in our study system (Fig. 1 in Appendix 1). We also assessed the diversity of anurans by comparing the iNEXT rarefaction/extrapolation curves for the Hill numbers, which is a standardized method to quantify and compare species diversity across multiples assemblages (Hsieh et al. 2016) and represents an alternative to other diversity indices (Chao et al. 2014) (Fig. 2 in Appendix 1).

Habitat amount and geographical distance

We used, as a continuous variable, the amount of forest cover as a proxy of habitat amount, as it can be used to predict patterns of species diversity in fragmented landscapes (Fahrig 2013). We calculated the amount of forest cover surrounding the centroid of each sampling site (continuous forest sites, forest fragments, and pasture areas). To do so, we used two buffer sizes taking into account the minimum and maximum expectation of anurans' dispersal ability: 500 and 1000 m, respectively. (Almeida-Gomes et al. 2016a, Sinsch 2010), despite of some highly vagile frogs can move 1000-1600 m or more (Semlitsch & Bodie 2003, Sinsch 2010). However, as the results and main conclusions were quite similar irrespective to the buffer size we used (Appendix 2), we presented only the results using a 500 m-radius. Forest cover ranged from 90% to 98% in continuous forest sites (mean = 95%), from 6% to 96% (mean = 38%) in forest fragments, and from 0% to 51% (mean = 23%) in pasture matrix areas.

We also measured the Euclidean distance among the centroids in sampling sites. Because both response variables (beta components) and one predictor variable (geographical distance) were distance matrices, we also transformed the vector of habitat amount in a distance matrix based on simple pairwise differences of observed values. Habitat amount (forest cover) and geographical distance were measured using *raster* and *rgeos* packages available in R.

Beta diversity partitioning

We partitioned the anuran beta diversity into two components: $\beta_{nestedness}$ and $\beta_{turnover}$, which depicts changes in biological assemblages driven by species loss and species replacement, respectively (Baselga 2010). Because our dataset included species abundance, we estimate these aforementioned components using abundance-based dissimilarity matrices (Baselga 2013) based on Euclidean distance, in *betapart* R package (Baselga 2012). We split our dataset into two site-species matrices: one including exclusively sites from continuous forest and forest fragments and another considering only sites from forest fragments and pasture matrix. For each scenario, we

partitioned the beta diversity, resulting in two pairwise matrices holding $\beta_{nestedness}$ and $\beta_{turnover}$ values.

Hypothesis testing

To measure the effect of two drivers (geographical distance and habitat amount) on beta diversity components (nestedness and turnover), we were required to address four statistical challenges: First, the two beta components are intrinsically and inversely correlated. Second, we are interested in the effects of habitat amount on beta diversity components, but geographical space itself should also cause changes in beta diversity, mainly in turnover (direct confounding effect) (Kraft et al. 2011). Third, environmental gradients (e.g., forest loss) are usually also spatially structured; this means closer sampling sites should have more similar landscape structure. Therefore, geographical space could input indirect confounding effects in the environmental gradient. Fourth, the pseudo-replicated nature of our response variable, i.e., pairwise comparison matrices of beta diversity indexes, precludes the use of standard general linear modeling.

To address these analytical challenges, we applied a Structural Equation Model (SEM). It allowed us: to include a correlation structure between beta diversity components (1st challenge – arrow between nestedness and turnover components); to disentangle the effect of habitat amount and geographical distance on beta components (2nd challenge – arrows from habitat amount and from geographical distance to beta components); to measure the spatial structure of landscape, and to estimate the indirect effect of space on beta components via landscape structure (3rd challenge - arrow from geographical distance to habitat amount). Finally, to circumvent the pseudoreplication held in our distance matrices (4th challenge), we applied a bootstrapping procedure (10^4 replications) while running the SEM. For each replication, we sampled the sampling sites with replacement, reran the SEM and stored the estimated coefficients. We assessed the significance of coefficients by checking that the quantile between 2.5% and 97.5% of bootstrapped coefficients did not include zero. Estimated coefficients were z-standardized to

allow comparisons of importance among variables. Boostrapping of SEM was performed separately for each dataset (continuous forest sites vs. forest fragments and forest fragments vs. matrix areas) using the *lavaan* package available in R. Model fit, which quantifies the global model fit to the population covariance structure, was checked through the baseline model Chi-square test ran for each bootstrapping replication. Direct, indirect and total effects were estimated following Grace (2008).

Results

We recorded 5745 individuals of 56 anuran species from 12 families (Table 2 in Appendix 1). We found 478 individuals of 32 species in continuous forest sites, 2361 individuals of 37 species in forest fragments, and 2906 individuals of 32 species in pasture matrix areas. The most abundant species in continuous forest sites, forest fragments, and pasture areas were *Haddadus binotatus* (18.4%), *Adenomera marmorata* (30.6%), and *Leptodactylus latrans* (23.3%), respectively.

Global model adequately fit the observed covariance structure (Chi-square = 11.95 [CI95% = 6.40-20.76], df=12, p = 0.50 [CI95% =0.10-0.94]). As expected, nestedness and turnover components were inversely correlated (Fig. 2; r_1 = - 0.55 and r_2 = - 0.54) (P<0.05). Furthermore, habitat amount was structured in space for both comparisons (β_1 = 0.42 and β_2 = 0.19), which means that closer sampling sites presented more similar levels of forest cover. Geographic distance influenced species turnover both in the comparison between continuous forest sites and forest fragments (β_3 = 0.18, P<0.05), and the comparison between forest fragments and matrix areas (β_4 = 0.11, P<0.05), mainly in the former (Fig. 2).

However, we found marked differences between the importance of nestedness and turnover components. When comparing continuous forest sites and forest fragments, differences in habitat amount produced nestedness (β_5 = 0.21, P<0.05), but not turnover (P>0.05; Fig. 2a). That means that the higher the difference in habitat amount between areas, the larger the nestedness and that the direction of nestedness was from areas of continuous forests to forest

fragments. However, the opposite was found in the comparison between forest fragments and matrix areas, where differences in habitat amount resulted in turnover ($\beta_6 = 0.19$, $P<0.05$), but not nestedness (($P>0.05$; Fig. 2b).

Figure 2 – Path analysis showing the direct and indirect effects of geographical distance and habitat amount on beta components, using a 500 m-radius buffer. (a) Comparison between continuous forest sites and forest fragments, and (b) comparison between forest fragments and matrix areas. Solid and dashed lines depict significant (P < 0.05) and nonsignificant (P >= 0.05) coefficients, respectively. Regression coefficients, correlation coefficients and coefficient of determination were depicted by b, r and R^2, respectively.
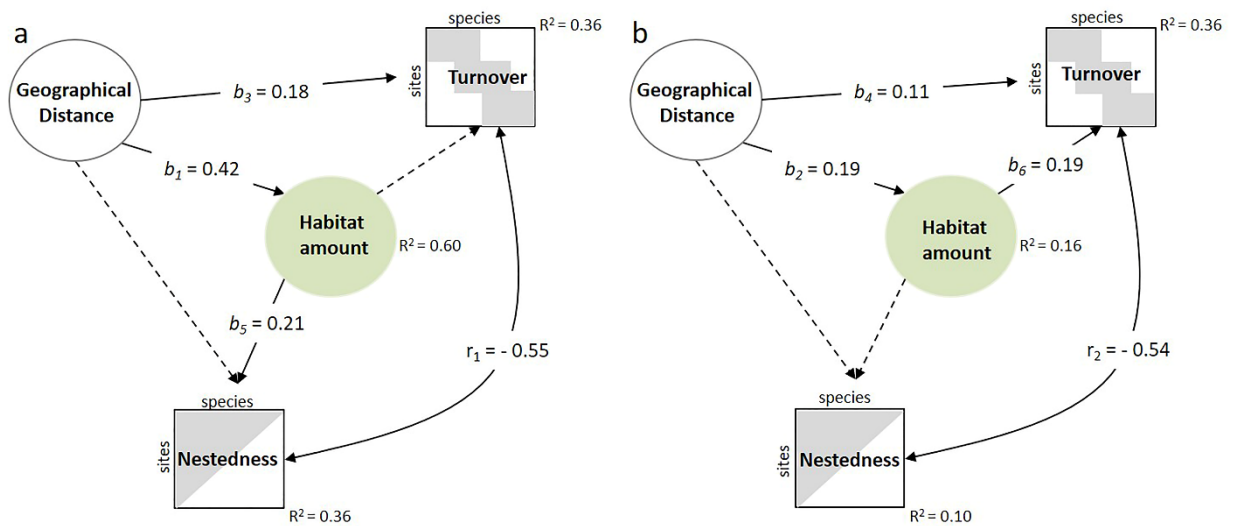
Because habitat amount is spatially structured, geographic distance also had indirect effects on beta components, increasing the nestedness even more in the comparison between continuous forest sites and forest fragments ($\beta_{1*}\,\beta_5 = 0.09$) and the turnover in the comparison between forest fragments and matrix areas ($\beta_{2*}\,\beta_6 = 0.03$). Overall, beta diversity in the comparison between continuous forest sites and forest fragments was strongly influenced by nestedness because if we change one standardized unit of the predictor variables, we should observe about 1.7 times more nestedness ($\beta_{total} = \beta_{5} + [\beta_{1*}\,\beta_5] = 0.30$) than turnover ($\beta_{total} = \beta_3 = 0.18$). On the other hand, in the comparison between forest fragments and matrix areas, a shift of one standardized unit of the predictor variables should trigger only turnover ($\beta_{total} = \beta_{4} + [\beta_{2*}\,\beta_6] + \beta_6 = 0.33$), with higher contribution of habitat amount ($\beta_6 = 0.19$) than geographical distance ($\beta_{2} + [\beta_{4*}\,\beta_6] = 0.14$).

As we found species turnover in the comparison between forest fragments and matrix areas, we conducted a PCoA to identify which species contributed to the shifts in the community. We found two distinct groups where the areas of forest fragments were dominated by *Adenomera marmorata* and *Scinax* aff. *x-signatus*, and the matrix areas were dominated by *Leptodactylus latrans*, *Scinax alter* and *Dendropsophus meridianus* (Appendix 3).

Discussion

Our results showed that different components of beta diversity were responsible for changes in anuran species composition in an Atlantic Forest fragmented landscape. The beta diversity partitioning showed that changes in species composition between continuous forest sites and forest fragments are caused by the loss of species (nestedness), while changes in assemblages between forest fragments and matrix areas are mostly driven by turnover. Habitat amount in the region mediates the strength of nestedness and turnover, but their relevance depends on which environments are being considered in the comparison. These results highlight the importance of evaluating which mechanisms are generating beta diversity patterns and the need of considering a gradient of land cover (including matrix areas) in biodiversity analysis to have a better

understanding on biodiversity patterns in fragmented landscapes, assuming that forest and matrix areas represent two extremes of the same gradient of habitat amount.

We also observed that fragments may represent a subset of species found in continuous forest areas. Similar results in previous studies also evidenced habitat loss originating nestedness assemblages (e.g., Vallan, 2000, Pineda & Halffter 2004), which was related to intrinsic organisms' traits, such as frequency of dispersal events, environmental heterogeneity and biotic interactions (Soininen et al. 2018). We believe that different ecological processes might explain this difference in community composition between continuous forest area and forest fragments. First, the habitat heterogeneity tends to be higher in continuous forest areas than in forest fragments. For example, Almeida-Gomes et al. (2016) found that 40% of the frog species and 46.7% of their reproductive modes were found only in continuous forest sites, probably because of the higher diversity of reproductive sites (e.g., rivers, streams, and bromeliads). Therefore, we may expect in most forest fragments the loss of some species that depend on these habitats. Furthermore, there may be a dispersal limitation for some species, preventing the colonization of new patches and the rescue effect. For example, several species of mammals (Laurance 1991), birds (Neuschulz et al. 2013), and frogs (Almeida-Gomes & Rocha 2014) may not be able to disperse from continuous forest areas to forest fragments, either because these areas are beyond the perceptual range of species (e.g., Prevedello et al. 2010) or because they do not tolerate the matrix conditions (e.g., Silva et al. 2012). Therefore, the spillover effect from continuous forest sites to forest fragments is possibly restricted to more generalist species, that are able to either stand the matrix conditions or to disperse by long distances (Boesing et al. 2021). In fact, generalists tend to be better dispersers compared to specialist species (Li et al. 2020).

On the other hand, we found that the variation in community composition between forest fragments and matrix areas is mostly driven by species replacement (turnover). Recent studies have shown that species turnover is the component of beta diversity that better explain the variation in species composition among assemblages (e.g., Soininen et al. 2007 Soininen et al.

2018). For example, Beca et al. (2017) found that species turnover was the main mechanism of total beta diversity for mammals in fragmented landscapes dominated by matrixes of sugarcane plantation. The evidence of turnover we found may be explained by compensatory dynamics, where the extinction of forest-dependent species is compensated by the proliferation of non-forest species (Morante-Filho et al. 2018). In fact, several forest-dependent species we found in forest fragments (e.g., *Aplastodiscus eugenioi*, *Ischnocnema guentheri*, *Haddadus binotatus*) were absent from pasture matrix areas. Conversely, some species usually found in disturbed habitats were present only in pasture matrix areas (e.g., *Leptodactylus fuscus*, *Sphaenorhynchus planicola*). These compensatory dynamics may occur at taxonomic and phylogenetic levels (Morante-Filho et al. 2018), sustaining the diversity in disturbed areas by adopting strategies aiming at reducing the extinction risk for a phylogenetically diverse set of species, and taking into account the conservation value of sites in more deforested landscape as important reservoirs of phylogenentic diversity (Morante-Filho et al. 2018).

Extensive deforestation in landscape acts as an environmental filter that contribute to configure a spatial gradient of land use and cover, ranging from large forest remnants to different matrix types, as agriculture and pasture areas (Umetsu et al. 2008, Rocha-Santos et al. 2020). Here we argue that, in a perspective of fragmented landscapes, nestedness and turnover represent a continuum of changes in assemblage composition (Si et al. 2016, Ehlers Smith et al. 2018). Our results represent a general process not only for amphibians in the Atlantic Rainforest, since the landscape that we studied is typical of the most current landscapes of this biome, even presenting equivalent ecological processes and dynamics. In the current scenario of global conversion of continuous natural areas into several remnant patches, we believe that our results depict the processes driving biodiversity patterns for different taxa in different landscapes. This contrasting turnover and nestedness components show that their relative importance depends on the amount of habitat remnants in the landscape and how much of the original habitat was converted to other habitats, such as the conversion of forest to pasture. Moreover, partitioning beta diversity into

nestedness and turnover components can help to elucidate the patterns of variations in regional biodiversity (Baselga 2010, Baselga 2012, Si et al. 2015) and to infer the processes driving the assembly composition (Meynard et al. 2011). For instance, beta diversity of amphibians in large scale showed a pattern of spatial turnover in low latitudes, while the nestedness-resultant dissimilarity was more pronounced at high latitudes (Baselga et al. 2012). Such overview of land cover was essential to perceive that the components of beta diversity do not act alone in a landscape with a gradient of decreasing habitat amount, resulting in contrasting turnover and nestedness-resultant components.

Here we support the importance of maintaining large areas of continuum forest to preserve amphibian biodiversity, since intensive land use led to a decrease in beta diversity due to the spatial uniformity only tolerated by a small subset of abundant native species (Gabriel et al. 2006, Solar et al. 2015, Socolar et al. 2016). The novelty in the present study is that we assessed a complete gradient of land cover, ranging from continuous forest sites to matrix areas, which allow a holistic understanding of the ecological processes operating in the community assembly. To our knowledge, this is the first study evaluating patterns of beta diversity in fragmented landscapes using both the partitioning of beta diversity and a gradient of land cover, and we strongly recommend that further studies consider the gradient of land use, and hence increasing the potential of viewing overall patterns and processes structuring the assemblage composition. Ultimately, understand beta diversity patterns is crucial to assist conservation planning and effectively conserve the gamma diversity (Gardner et al. 2013). In addition, it aids to helping in the still current conservationist debate for the SLOSS (whether single large reserve will conserve more species than several small; Abele & Connor 1979). Some forest species are able to persist in forest fragments, but eventually are replaced by generalists or species of open areas when the forest is completely converted to pastures or other types of habitats.

Appendix 1

Table 1 Number of hours of Visual Encounter Survey (VES) in continuous forest sites (CF1-CF3), forest fragments (F1-F21), and pasture matrix areas (M1-M21), municipality of Cachoeiras de Macacu, state of Rio de Janeiro.

	TOTAL (hours)
F1	60
F2	42
F3	96
F4	36
F5	36
F6	60
F7	114
F8	30
F9	30
F10	42
F11	42
F12	66
F13	28
F14	28
F15	21
F16	28
F17	30

F18	41
F19	118
F20	22
F21	30
CF1	92
CF2	86
CF3	66
M1	27
M2	21
M3	16
M4	16
M5	14
M6	9
M7	27
M8	14
M9	10
M10	10
M11	27
M12	18
M13	11
M14	14
M15	15
M16	12

M17	18
M18	27
M19	14
M20	13
M21	14

Table 2 Anuran species recorded during Visual Encounter Surveys in continuous forest sites (CF), forest fragments (F), and matrix areas (M), municipality of Cachoeiras de Macacu, state of Rio de Janeiro, Brazil.

AMPHIBIA: ANURA	AREAS
Brachycephalidae	
Ischnocnema guentheri	CF/F
Ischnocnema octavioi	CF/F
Bufonidae	
Dendrophryniscus	*CF*
brevipollicatus	
Rhinella icterica	CF/M
Rhinella ornata	CF/F/M
Rhinella margaritifera	F
Centrolenidae	
Vitreorana sp.	CF
Craugastoridae	
Euparkerella brasiliensis	CF/F
Haddadus binotatus	CF/F
Cycloramphidae	
Cycloramphus brasiliensis	CF
Thoropa miliaris	CF
Hemiphractidae	
Fritziana goeldii	CF

Hylidae

Aplastodiscus eugenioi	CF/F
Boana albopunctata	M
Boana faber	CF/F/M
Boana pardalis	M
Boana secedens	CF
Boana semilineata	CF/F/M
Bokermannohyla circumdata	CF
Dendropsophus anceps	F/M
Dendropsophus berthalutzae	F/M
Dendropsophus bipunctatus	F/M
Dendropsophus decipiens	F/M
Dendropsophus elegans	CF/F/M
Dendropsophus giesleri	F
Dendropsophus meridianus	F/M
Dendropsophus microps	M
Dendropsophus minutus	F/M
Dendropsophus pseudomeridianus	M
Dendropsophus seniculus	CF/F/M
Itapotihyla langsdorffii	F
Phrynobatrachus albomarginatus	CF/F/M

Phyllomedusa burmeisteri	CF/F/M
Pithecopus rohdei	F/M
Ololygon albicans	CF
Ololygon argyreornata	CF/F/M
Ololygon humilis	CF/F/M
Ololygon v-signata	CF
Scinax alter	F/M
Scinax cuspidatus	F/M
Scinax cf. *similis*	F
Scinax aff. *x-signatus*	CF/F/M
Sphaenorhynchus planicola	M
Trachycephalus mesophaeus	CF/F
Trachycephalus nigromaculatus	F/M
Hylodidae	
Crossodactylus aeneus	CF
Hylodes pipilans	CF
Leptodactylidae	
Adenomera marmorata	CF/F/M
Leptodactylus fuscus	M
Leptodactylus latrans	CF/F/M
Leptodactylus mystacinus	F/M
Leptodactylus spixi	F/M
Physalaemus signifer	CF/F/M

Microhylidae

Chiasmocleis carvalhoi   F

Stereocyclops parkeri   F

Odontophrynidae

Proceratophrys boiei   CF

Figure 1 – Estimator of complete RAD of anurans in our study system in a fragmented Atlantic Forest landscape. We combined the adjusted relative abundances for detected species (red line) and the estimated part for undetected species (green line). (A) RAD for overall study system; (B) RAD for Continuous Forest; (C) RAD for Forest Fragments; and (D) RAD for Matrix sites.
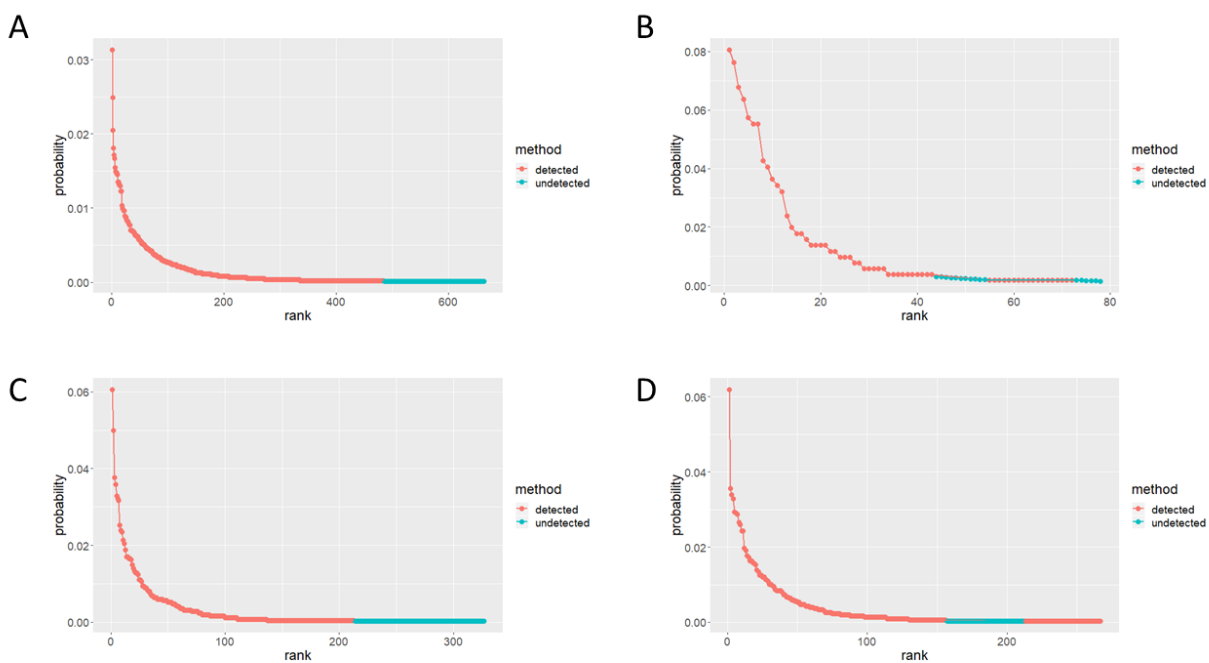
Figure 2 – Comparison of Rarefaction (solid segment) and extrapolation (dashed segment) sampling curves for the three land use categories in our study area (CF = Continuous Forest, red line; F = Forest Fragments, green line; M = Matrix, blue line), by using the iNEXT function. The shaded area represents the 95% confidence interval. The curves are separated by diversity orders (Hill numbers), q = 0 (species richness, A), q = 1 (Shannon diversity, B) and q = 2 (Simpson diversity, C). Solid symbols refer to the reference samples (the number of species found on each sample site).
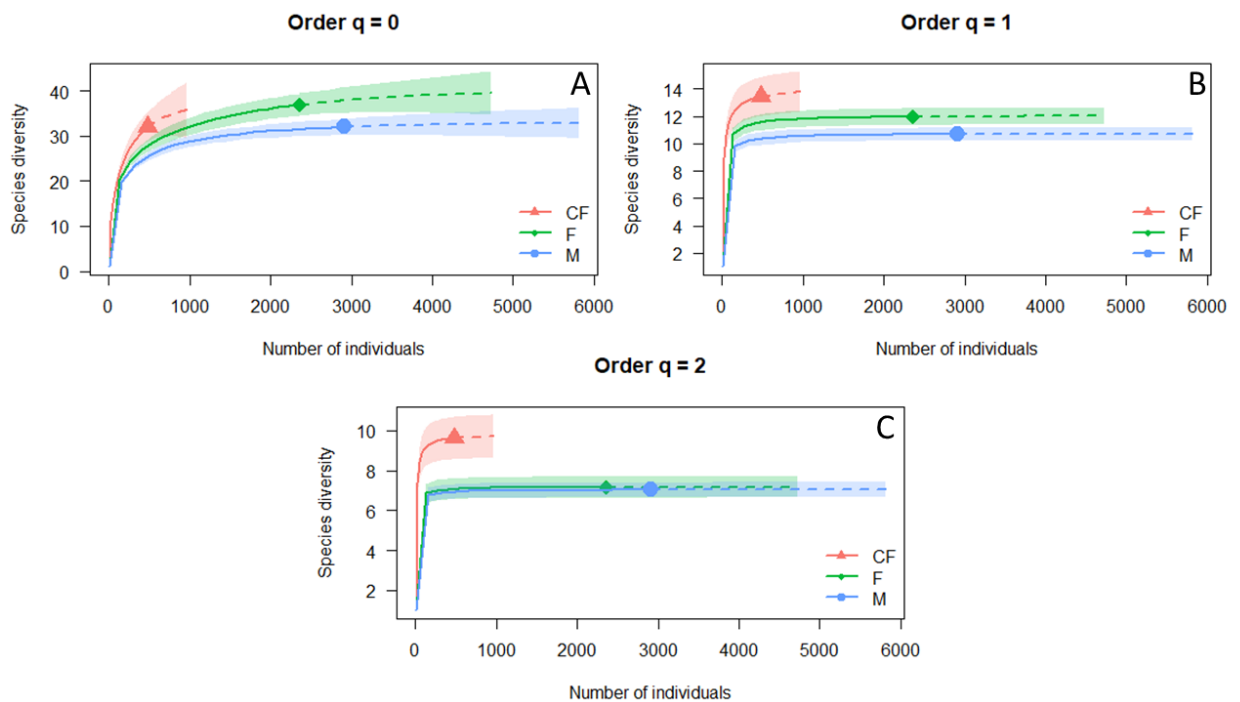
Appendix 2

Figure 1 – Path analysis showing the direct and indirect effects of geographical distance and habitat amount on beta components, using a 1000 m-radius buffer. (a) Comparison between continuous forest sites and forest fragments, and (b) comparison between forest fragments and matrix areas. Solid and dashed lines depict significant (P < 0.05) and nonsignificant (P >= 0.05) coefficients, respectively. Regression coefficients, correlation coefficients and coefficient of determination were depicted by b, r and R^2, respectively.
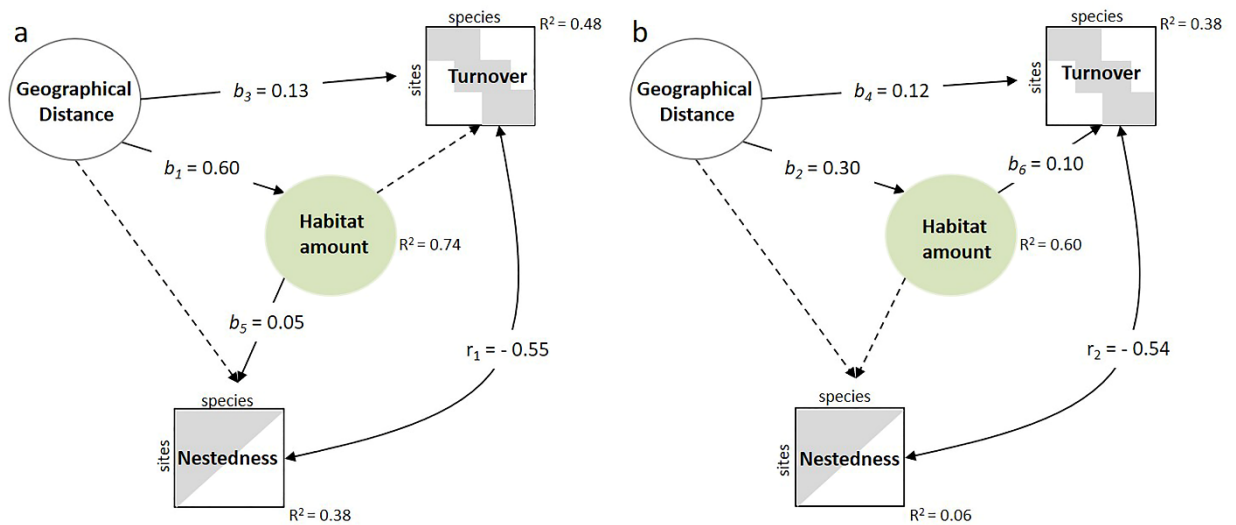
Appendix 3

Figure 1 – PCoA-plotting identifying the species that most contributed to turnover (over 40% of correlation) in comparison between forest fragments (open circles) and matrix sites (solid circles). Lpt.ltr = *Leptodactylus latrans*; Scn.alt = *Scinax altus*; Dnd.mrd = *Dendropsophus meridianus*; Bon.alb = *Boana albopunctata*; Dnd.bpn = *Dendropsophus bipunctatus*; Dnd.elg = *Dendropsophus elegans*; Dnd.brt = *Dendropsophus berthalutzae*; And.mrm = *Adenomera marmorata*; Scn.sgn = *Scnax x-signatus*.
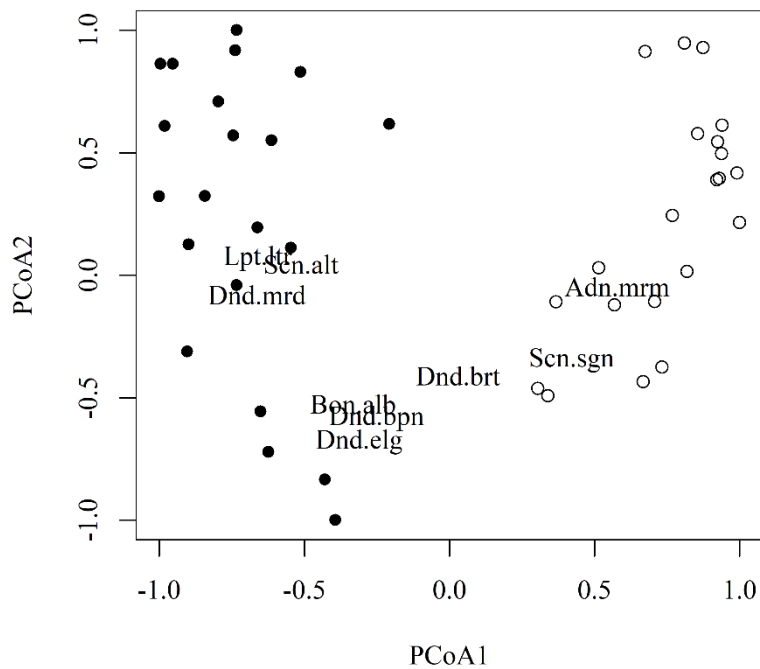
Chapter 2 – Anuran beta-diversity in a local Brazilian Atlantic Forest fragmented landscape: disentangling deterministic vs. stochastic processes

Abstract

Variation in species composition within communities is induced by factors that limit the presence of species in certain habitats. These patterns of beta diversity can be linked to stochastic or deterministic processes. Some studies have claimed that stochastic (neutral) processes satisfactorily explain beta diversity patterns, however, deterministic (niche-based) processes have been acknowledged as the main driver of variation in species composition for several taxa across the globe. We aimed to disentangle the contributions of deterministic and stochastic processes in structuring amphibians' assemblages in an Atlantic Forest fragmented landscape in Brazil, and to verify how homogenized is the community. To do so, use a null-model approach to calculate beta diversity and a Raup-Crick metric of dissimilarity (β_{RC}) to compare communities from forest fragments and pasture matrix. We found that stochastic processes are structuring the amphibians' assemblage and that the community of the studied local landscape is not biotically homogenised. This implies that land cover not always is the main cause of differences among assemblages. We also claim for the importance in considering stochastic processes acting together with deterministic processes, to better establish conservation strategies.

Resumo

A variação na composição de espécies dentro das comunidades é induzida por fatores que limitam a presença de espécies em certos habitats. Esses padrões de diversidade beta podem ser associados a processos estocásticos ou determinísticos. Alguns estudos afirmam que os processos estocásticos (neutros) explicam satisfatoriamente os padrões de diversidade beta; no entanto, os processos determinísticos (baseados em nicho) têm sido reconhecidos como o principal fator de variação na composição das espécies para vários táxons em todo o mundo. Objetivamos desvendar a contribuição dos processos determinísticos e estocásticos na estruturação das assembleias de anfíbios em uma paisagem fragmentada da Mata Atlântica no Brasil, e também verificar o quão homogeneizada é essa comunidade. Usamos uma abordagem de modelo nulo para calcular a diversidade beta e a métrica Raup-Crick de dissimilaridade (β_{RC}) para comparar comunidades de fragmentos florestais e matriz de pastagem. Descobrimos que os processos estocásticos estão estruturando a assembleia de anfíbios e que a comunidade da paisagem local estudada não é bioticamente homogeneizada. Isso implica que a cobertura do solo nem sempre é a principal causa das diferenças entre os conjuntos. Também destacamos a importância de se considerar processos estocásticos atuando em conjunto com processos determinísticos, para melhor estabelecer estratégias de conservação.

Introduction

The conversion of natural ecosystems into anthropogenic areas is the main cause of the biodiversity crisis worldwide (McGill et al. 2015, Newbold et al. 2015). The human-induced landscape changes cause the loss and fragmentation of habitats and hence, the reduction of patches of native cover and the increase of the isolation between them (Fahrig 2003). Such changes directly affect the distribution of species in fragmented areas (Andrén 1994), having profound effects on the structure of communities. As a result, we can observe changes in community composition in human modified-landscapes (Pardini et al. 2010, Almeida-Gomes et al. 2016).

Variation in species composition within communities are induced by factors that limit the presence of species in certain habitats (Villéger et al. 2010, Dirzo et al., 2014). For example, due to the loss of specialist species (loser) and its replacement by generalist species (winners), some patches can have distinct communities from those found in continuous forest areas (Arroyo-Rodríguez et al. 2020, Filgueiras et al. 2021). This is especially true for smaller forest patches (Si et al. 2015), due to the alterations in abiotic conditions related to edge effects or lack of specific habitats (Almeida-Gomes & Rocha 2015, Banks-Leite et al. 2012). In addition, the type of matrix in a landscape is an important factor for determining the persistence of species in fragmented landscapes. Recent studies have shown that matrix areas can share some species with forest remnants, although most of them are generalists (Almeida-Gomes and Rocha 2014, Beca et al. 2017, Kennedy et al. 2010). Thus, the quality and complexity of the matrix surrounding forested areas act as filters for the species movement (Prevedello & Vieira 2010, Zollner 2000), so the matrix itself, not only native habitat remnants, should be taken into account areas when assessing patterns of species diversity in fragmented landscapes (Revilla et al. 2004, Umetsu et al. 2008, Verbeylen et al. 2003).

Beta diversity, or the variation in species composition among sampling units, is a prominent method to quantify the biodiversity changes in human-disturbed landscapes (Barlow et

al. 2007, Gardner et al. 2009, Anderson et al. 2011) and can provide insights on processes that maintain such site-to-site diversity of species (Kraft et al. 2011). Patterns of beta diversity can be linked to deterministic (niche-based) or stochastic (neutral) processes. Some studies have claim that stochastic processes (i.e., dispersal, speciation and random extinction) satisfactorily explain beta diversity patterns (Clark 2012, Hubbell 2001). On the other hand, deterministic processes (i.e., climate or land use changes) has been acknowledged as the main driver of variation in species composition for several taxa across the globe (Hillebrand et al. 2010, Lindstrom et al. 2013). These deterministic processes are linked to abiotic factors that filter the establishment or persistence of species in a given location and select species that are unable to tolerate certain conditions (Kraft et al. 2015). For instance, Püttker et al. (2015) found that a non-random extinction of small mammal species after habitat loss led to a strong biotic homogenization in high deforested Atlantic Forest areas.

Despite the emphasis given to deterministic vs. stochastic processes (i.e., niche vs. neutral processes), both can simultaneously drive the dynamics of assemblages and metacommunities (Guo et al. 2018) and may vary with the spatial scale (Viana et al. 2016), habitat quality (Chang et al. 2013), and the taxonomic group (Vergnon et al. 2009). A useful alternative to assess the importance of theses neutral and niche-based processes is the evaluation of beta diversity patterns across space (Püttker et al. 2015). Chase et al. (2011) and Chase and Myers (2011) claimed for the relevance of null-models in assessing the relative importance of deterministic and stochastic processes by comparing the observed similarity in an assemblage to that expected assuming a random assemblage. Due to its independence from species richness, the approach described by Raup & Crick (1979; hereafter called β_{RC}) can be useful for analysing biotic homogenization (Baeten et al. 2012, Lôbo et al. 2011).

Special attention has been given to anthropogenic-induced landscape changes as the principal source of biotic homogenization, which leads to an increase in the similarity of communities for both animals and plants over space and time (Olden 2006, Solar et al. 2015). For

example, Pauchard et al. (2013) found that communities of generalist's alien plants homogenize matrix areas surrounding parks in South-Central Chile and are prone to invade these protected areas. Hidasi-Neto et al. (2019) also predicted that the biodiversity of mammals from Brazilian Cerrado hotspot may become biotically homogenized driven by an expansion of exotic and generalist species due human interference. Beyond the taxonomic similarity, the biotic homogenization can also lead to functionally (e.g., Marr et al. 2013, Smith et al. 2009) and phylogenetically similar communities (e.g., Shaw et al. 2010, Toyama et al. 2015).

The Brazilian Atlantic Forest is the second larger domain in the South America (Galindo-Leal and Câmara, 2003). This biome has only 16% of the original vegetation cover (Ribeiro et al. 2009), and it is considered one the most important biodiversity hotspots (Myers et al. 2005). The biome is mostly composed by small-isolated fragments, with different historic of human interference and a huge variety of environmental conditions and structures (Ribeiro et al. 2009, Melo et al. 2013, Ferraz et al. 2015). Since habitat loss has been considered the most important driver of the current increase in extinction rates (Pereira et al. 2010), the high biodiversity, endemism rates, and the extension of forest loss and fragmentation make the Brazilian Atlantic Forest a suitable biome to understand how changes in landscape affect the composition of communities. Therefore, unveiling the processes driving changes in species composition after landscapes changes has profound theoretical and practical implications (Legendre et al. 2005, Socolar et al. 2016).

Here we aim to assess whether anurans' assemblages in an Atlantic Forest fragmented area in Brazil are structured by deterministic (niche-based) or stochastic (neutral) processes. To do so, we used a dataset obtained from a large empirical study conducted with amphibians (Almeida-Gomes et al. 2016). Anurans are considered key indicators of landscape changes (Cushman 2006, Schneider-Maunoury et al. 2016) and there are evidences that some species are more prone to disappear in the environments outside large remnants in forest fragmented landscapes (Almeida-Gomes & Rocha 2015, Almeida-Gomes et al. 2016, Fonseca et al. 2013).

We evaluated if the process of habitat loss in the landscape resulted in a taxonomic biotic homogenization of anurans' assemblage. Since the habitat loss caused by forest extirpation act as an ecological filter that reduces the beta diversity in forest-fragmented landscapes (e.g., Lobo et al. 2011, Puttker et al. 2015) we predict that deterministic, niche-based processes will structure the anurans' assemblage in the fragmented landscape, leading to a homogenized community.

Methods

Study area

The study was carried out between July 2007 and March 2014, in an Atlantic Forest fragmented area in the municipality of Cachoeiras de Macacu, State of Rio de Janeiro, Brazil. This area is located in the Macacu River watershed and is formed by forest fragments of different sizes and degrees of isolation, immersed in different types of matrices, mainly pastures, due to the intensified fragmentation process initiated in the 1960s by the construction of a major highway, and hence, increasing human settlements (Vieira et al. 2009). We sampled 21 forest fragments (F1-F21) ranging from 1.9 to 619 ha and 21 pasture matrix areas (M1-M21) (Figure 1). The sampling effort varied between 21 and 118 h for forest fragments (median = 36 h) and from nine to 27 h in pasture matrix areas (median = 14 h).

Figure 1 – Map of the studied fragmented landscape, showing the sampled areas in forest fragments (dark green) and matrix pastures (black).
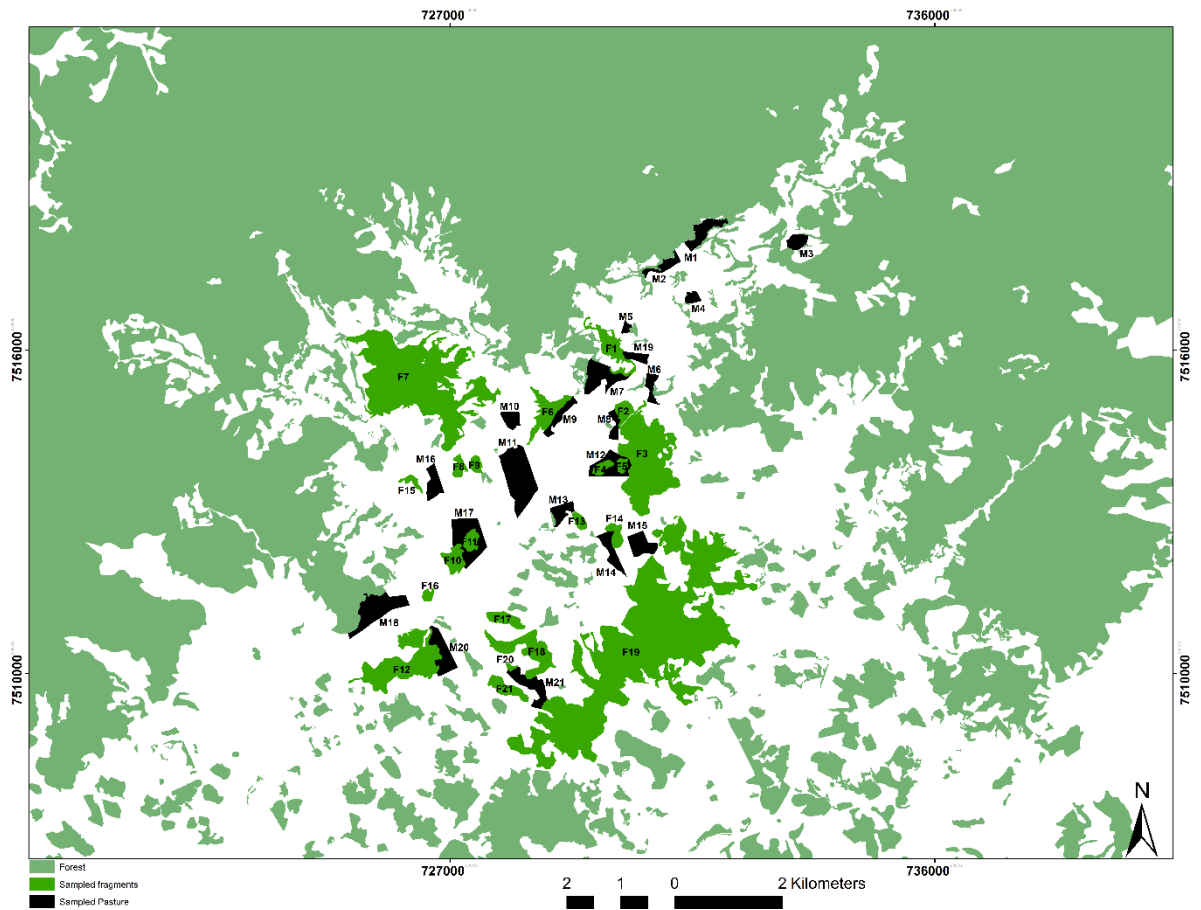
Frog sampling

We recorded anurans by visual encounter surveys (VES; Crump & Scott, 1994) at nightime from 19:00 to 00:00 h, using headlamps. We inspected different habitat types during VES, such as tree trunks, branches, leaf-litter, rocks in the streams, bromeliads and ponds.

Data analysis

To assess the contribution of deterministic vs. stochastic processes, we used a null-model and a Raup-Crick metric of dissimilarity (β_{RC}) (Raup & Crick 1979) to calculate beta diversity within forest fragment habitats and within pasture matrix habitats. Such approach allows us to assess the role of deterministic and stochastic processes in an assemblage by measuring the deviation from the null expectation that the assemblage is structured by stochastic processes. This approach is recommended when differences in alpha and/or gamma diversity are concomitant with changes in beta diversity (Püttker et al. 2015).

We first defined the species pool as the total number of species that we recorded in forest fragments and matrix areas, since they are potentially able to colonize the sampled areas. Species were then randomly sampled from the pool, with reposition, for 10000 times to generate a null distribution of the expected number of shared species among our sampling areas. However, analyses that rely on presence/absence data might underestimate biotic homogenization (Cassey et al. 2008). We thus evaluated if the anurans' assemblage is biotically homogenized by including abundance information in an additional null model using a pool of individuals to define the regional pool and draw randomly individuals. We used a modified Raup-Crick index ($\beta_{RC\text{-}abund}$) with 1000 randomizations to generate a null distribution of the expected dissimilarity (Püttker et al. 2015).

As reference, we used a scale of β_{RC} values ranging from -1 to 1, proposed by Chase et al. (2011), where two assemblages are more similar than (values close -1), less similar than (values close to 1), or similar as (close to 0) expected by chance. Mean values of β_{RC} that are different from 0 that are close to 1 or -1 indicate deterministic processes in the assemblage, indicating

dissimilarity in species composition between sites. On the other hand, mean values close to 0 indicate an assemblage structured by stochastic processes and a more similar species composition between sites than expected by chance, and hence, accounting for biotic homogenization.

To graphically represent the taxonomic beta diversity, we used a two-dimensional nonparametric multidimensional scaling (NMDS) based on values of β_{RC} and $\beta_{RC\text{-abund}}$. In addition, we tested for spatial autocorrelation in our data proceeding with a Mantel test. All analyses were conducted in R environment, version 3.6.3 (R Core Team 2017), using the package Vegan (Oksanen et al. 2019).

Results

We recorded a total of 2361 individuals of 37 species in forest fragments and 2906 individuals of 32 species in pasture matrix areas. The most abundant species in forest fragments were *Adenomera marmorata* (N = 723; 30.6%), *Scinax* aff. *x-signatus* (N = 274; 11.6%), and *Euparkerella brasiliensis* (N = 240; 10.1%). In pasture matrix areas, the most abundant species were *Leptodactylus latrans* (N = 678; 23.3%), *Dendropsophus meridianus* (N = 623; 21.4%), and *Dendropsophus bipunctatus* (N = 471; 16.2%).

We found that there was no strong variation in beta diversity between forest fragments and between pasture matrix. Mean β_{RC} had similar values within forest fragments and within matrix (-0.44 vs. -0.26, respectively; Figure 2). The NMDS ordination showed no clear separation between the two habitat types, indicating communities composed by a random subset of species (Figure 3A). In addition, despite the negative values, mean β_{RC} were closer to 0, establishing no difference in the observed dissimilarity in comparison with the null expectation, nor sign that the anurans' assemblage is structured by deterministic processes.

However, when we included the abundance data to assess the process of biotic homogenization, mean values of $\beta_{RC\text{-abund}}$ was larger than mean values of incidence β_{RC}, showing an increase in beta diversity in forest fragments and matrix areas with values close to 1 (0.80 and

0.92, respectively), and no clear separation of communities between forest fragments and matrix areas (Figure 3B). Mean values of $\beta_{RC\text{-}abund}$ show communities more distinct than expected by chance, indicating that there is no biotic homogenization process occurring in the anurans' assembly in our study area.

The Mantel test results showed no significant spatial autocorrelation between species composition from forest fragments and matrix areas (Mantel statistic = 0.13, p-value = 0.13).

Figure 2 – Boxplot with the values of taxonomic β_{RC} within forest fragments and within matrix.
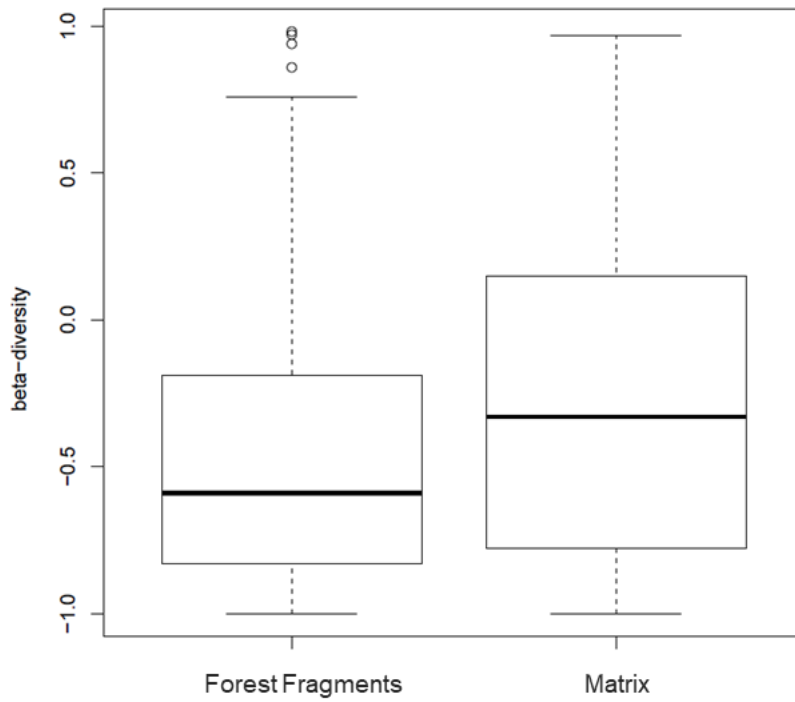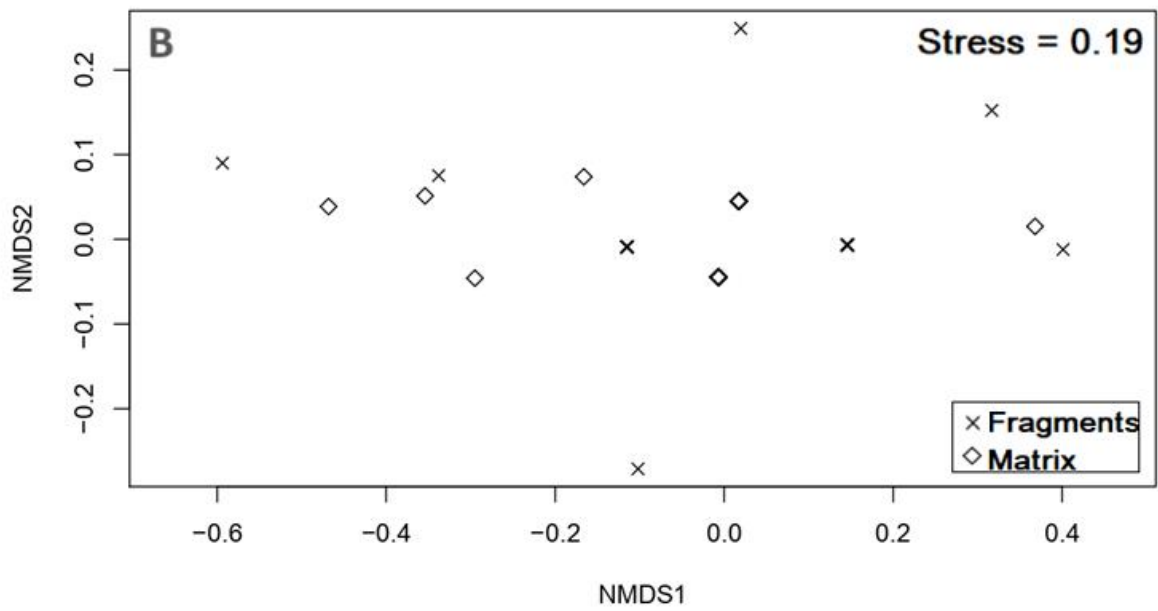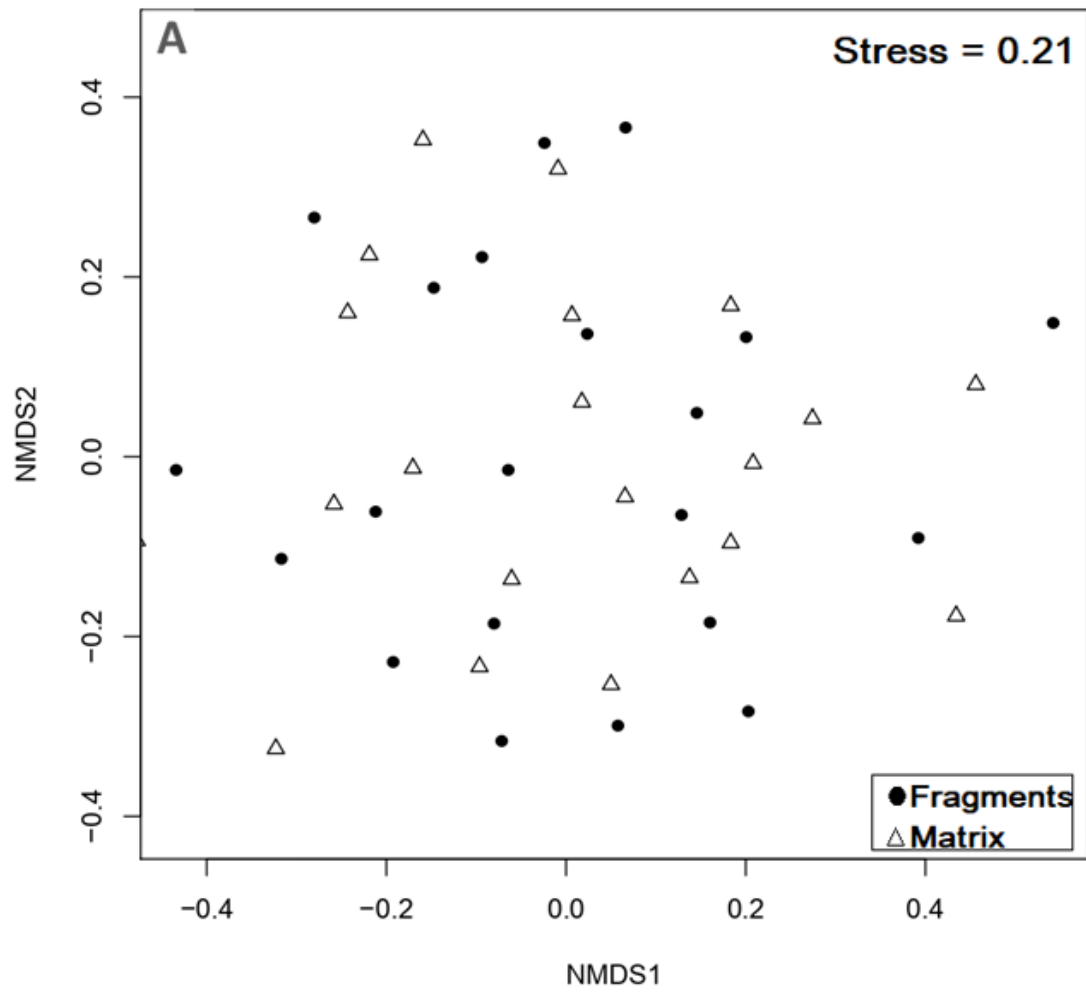

Figure 3 – NMDS ordination between forest fragments and matrix. Figure 3A indicates communities composed by a random subset of species, and Figure 3B shows no clear of communities between forest fragments and matrix areas.

Discussion

Our results indicate that stochastic processes structure the composition of anurans' species in the studied fragmented landscapes. This pattern suggests the occurrence of ecological drift in this community and that the species extinction is completely random, as expected for communities driven by neutral processes. Further, against our predictions, we did not find evidence of a decreasing beta diversity among forest fragments and pasture matrices leading to a biotic homogenization of the anurans' assemblage.

Local communities across the globe have been shown to be dependent on the effects of environmental change, beyond the effects predicted from the null model (Dornelas et al. 2014). However, a critical issue is how to discern the effects of deterministic processes from stochastic processes (Kampichler et al. 2012, Stegen et al. 2013), i.e., how to distinguish the effects of niche processes or neutral dispersal limitation/random local extinction in driving the dissimilarity of assemblages across space (Borcard et al. 1992, Tuomisto et al. 2003, Svenning et al. 2011). Moreover, both processes may simultaneously act in species distribution, in a continuum gradient ranging from purely determinist to purely neutral processes driving the assemblage's composition (Baselga et al. 2015) or even collapse each other (Baselga et al. 2012), which influence patterns of beta diversity.

Land cover change is the most prone deterministic mechanism underlying species distribution at local and regional scales (Pearson et al. 2004, Wilson et al. 2013). Nevertheless, stochastic occupancy dynamics, such as dispersal events and local random extinctions from occupied to non-occupied profitable habitats would result in neutral variation is species composition and be responsible for species' stochastic occupancy (Benedetti-Cecchi et al. 2008). When we reshuffled the regional pool of species and compared to a null model, it showed out that the changes in local assemblages did not significantly differ from null expectations. Hence, we may assume that the changes in land cover, specially comparing forest fragments and its surrounding matrix, were not the main driver of compositional changes of local anuran assemblage.

It is important to highlight that even our results pointed to an assemblage compatible with null models with stochastic variation in the local assemblage in the landscape, we assume that some relevant predictors of land cover not measured in this work may deterministically explain local species distribution, such as fragment size, matrix permeability, distance from continuous forest and distance among fragments. Another plausible explanation for the stochasticity in anuran assemblage is because the spatial scale we used to asses species composition did not encompasses demographic patterns acting in larger scales. (Sirami et al. 2008, Schaub et al. 2012). The same patterns of neutral processes were found by Baselga et al. (2015) in a local-landscape bird assemblage, and the authors state that it would be unlikely to found determinist processes acting in larger scales modifying global heterogeneity of the assemblage, once it would not produce a consistent pattern on the overall heterogeneity among local assemblages. Moreover, the fine scale we used in this work is based on the anuran dispersal ability (500 to 1000 m; Sinsch 1990), therefore, we assume that we would not find deterministic processes driven anuran assemblages in increasing our spatial scale. A second issue raised by Baselga et. (2015) that can mask the effects of deterministic processes is the incomplete sampling, that culminate in a random pattern of species distribution in the landscape. We agree that biodiversity sampling tend to be incomplete. However, our analyses of diversity estimation suggested that our data was satisfactorily sampled, confirmed by the rarefaction/extrapolation curves for the Hill numbers (see Figure 1 and Figure 2 in the Appendix 1 showed in the Chapter 1).

Since we did not find potential deterministic mechanisms for the variation in the anuran species composition, we cannot reject the null hypothesis that the anuran assemblage in the studied fragmented Atlantic Forest landscape is controlled by neutral, stochastic processes. And an ecological implication of this observed pattern is that species appear and disappear from some places without any correlation to our measured variables, i.e., forest fragments vs. pasture matrix (Bonthoux et al. 2013), where plausibly the patchy local landscape formed by several forest fragments could buffer the impact of land cover changes (Lundberg & Moberg 2003). In addition

to the β_{RC} index closer to 0, which establish that observed dissimilarity is not different from the null expectation, we also base this statement on the limited relation of land cover in explain species distribution in this landscape.

No difference in biotic composition in the fragmented landscape

A potential effect of land cover change is the simplification of assemblages' diversity, reducing spatial beta diversity. Moreover, threats to plant diversity, even in small magnitudes, can have significant cascading effects on animals' diversity, which tend lead communities of plant and animals to be phylogenetically and functionally homogenized in the future (Park and Razafindratsima 2019). Nevertheless, the biotic dissimilarity is expected to maintain unchanged under assemblages driven by stochastic processes (Baselga et al. 2015), where random extinctions and dispersal events from occupied to non-occupied habitats would result in neutral shifts in species assemblages through time (Benedetti-Cecchi et al. 2008).

Despite the fact that environmental filtering processes contribute to replacement dynamics (Ernst et al. 2006, Ernst et al. 2012), the inclusion of abundance data for measuring biotic homogenization showed that the changes in species composition did not vary more than expect by chance in species abundance. Using abundance data for investigations on biotic homogenization or heterogenization have important implication for conservationist acts, because only using presence/absence data would more prone to detect homogenization at local scales and to a lesser homogenization at regional scales, while abundance-based analysis would tend to detect heterogenization processes (Puttker et al. 2015, Holting et al. 2016). Therefore, detect shifts in species abundance can be crucial to understand the impacts of human-lead disturbances, since changes in abundance are faster than extinctions that may result from an environmental impact (e.g., extinction debt, sensu Tilman et al. 1994), making it important to detect these early shifts for the efficacy of land management strategies.

Indeed, our finds showed no significantly difference from null expectations when we

compared the random-reshuffled anuran assemblage of the regional pool to a null model. Thus, we assume that: (i) the observed dissimilarity in species composition is due stochastic processes where species populations may randomly appear and disappear from specific localities, and/or (ii) anuran assemblage presents a phenotypic adaptation, allowing them to persist in this region with a historical of anthropogenic disturbance (Baselga et al. 2015). However, even that an overall tendency of absence of biotic homogenization may sound optimistic, it is important to highlight that it is not mean a complete lack of homogenization, since species losses from random extinctions or gains from species introduction may not occur on the same temporal scale (Smith 2006).

Conclusions

Although unmeasured deterministic mechanisms beyond land cover might be driving the anuran composition in this fragmented Atlantic Forest landscape, we reinforce that it is plausible that random emergence/disappearance from specific localities triggered by stochastic processes are influencing the local assemblage. We highlight that is necessary further studies to establish the generality of our findings by experimentally controlling fragmented landscapes. However, we claim for the importance of studies in considering stochastic processes acting together with deterministic processes, and the need of distinguish both processes to not compromise the implementation of conservation strategies (Baselga et al. 2015).

General conclusions

Overall, we found that differences in forest cover between continuous forest and forest fragments induced the species nestedness. On the other hand, due to the difference in land cover, the difference in species composition were better explained by turnover, which was significantly and positively affected by geographic distance. We also observed that, despite the fact that the process of change of land use in the studied landscape occurred for decades, the historic forest fragmentation and anthropogenic interference at the local was not a deterministic process to explain changes in species composition between remnant forest patches and pasture matrices.

We found robust evidence that changes in species composition in fragmented areas might reflect different ecological processes. For example, differences in forest cover positively affects the species nestedness, since closer areas with different forest cover tend to present more similar communities as a subset of richer original assemblages, while distant areas tend to present more distinct communities, hence, higher species turnover. Therefore, it is important to consider a whole gradient of land use for a general viewing of processes structuring assemblages and help in the conservationists' projects. Despite of habitat amount in the studied landscape mediates the strength processes underlying anurans beta diversity, the relevance of each process depends on which environments are being considered in the comparison of species composition between areas. Moreover, if stochastic processes are dominant in the studied area, the ability of correlative and mechanistic models to predict land cover change effects on species composition and thus implement effective conservation strategies would be compromised, since species could appear and disappear from some areas without a strict correlation to fragmentations processes or changes in land use.

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