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Original article

Fragmentation effects on beta diversity of fragmented and conserved landscapes: insights about homogenization and differentiation processes

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ABSTRACT

Fragmentation is one of the main causes of biodiversity loss in tropical forests through consequences on their different components. Beta diversity patterns across fragments have been studied across multiple spatial scales, but comparisons with intact landscapes and in a variety of vegetation types are scarce. In order to address this issue of anthropogenic landscape disturbance, we tested two hypotheses relating to fragmentation and beta diversity: 1. Floristic homogenization at patch-level scale and 2. Floristic differentiation at landscape-level scale. The study was conducted in the Espinhaço Range biosphere reserve, Brazil. Three landscapes encompassing a broad range of vegetation types were sampled in 115 plots. Two landscapes were fragmented due to mining activities (Sabará and Brumadinho) and one is protected (Parque Estadual Serra do Rola-Moça). Results showed high overall beta diversity both between landscapes (conserved and fragmented) and vegetation types (forest, Brazilian savanna "campos rupestres", ecotone and ironstone "canga") with high turnover and species losses, even in highly disturbed vegetation types. The conserved landscape was most diverse in terms of richness. Thus, fragmentation effects differed from the expected with a main role of differentiation processes, and we argue that high beta diversity is not always a good predictor of ecosystem health.

Keywords: turnover, nestedness, anthropic disturbance, habitat loss, biotic homogenization, beta diversity, fragmentation

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Introduction

Tropical forests are known for high species diversity, but are threatened by anthropogenic land use change. Losses of primary tropical forests reached about 2,5 million hectares in 2016 and 12 million in 2018, of which 1,3 million are just in Brazil, according to Global Forest Watch 2018 (Turubanova *et al.* 2018). The biodiversity is a determining factor of many tropical forest's ecosystem functions like productivity, that is related to the global carbon stocks and uptake (Poorter *et al.* 2015; van der Sande *et al.* 2017). Among all biodiversity benefits, carbon stocks and uptake buffers global climate change like CO_2 increase, which according to The United Nations, Reducing Emissions from Deforestation and Forest Degradation (REDD+) imputes a value in biodiversity conservation (Grainger *et al.* 2009). It is a high priority, therefore, to investigate and understand the impacts of fragmentation on tropical forest biodiversity.

Tropical forests typically exhibit high beta diversity (species turnover) as well as high alpha diversity and gamma diversity (species count). Beta diversity, which refers to the substitution of species as one move across a landscape, may be influenced by ecological processes that operate at both regional (colonization, extinction and dispersion processes) and local (niche structure by biotic and abiotic filters) spatiotemporal scales (Ricklefs 1987; Rosenzeig 1995; Lawton 1999). High substitution rates may be promoted by several processes, including environmental heterogeneity and dispersal limitation (Hubbell 2001; Myers *et al.* 2016). Also, at landscape-level scales, gamma diversity can be positively correlated with beta diversity due random distribution of species among patches (Kraft *et al.* 2011; De Cáceres 2012). However, tropical forests in transition sites are neglected. Beta diversity patterns in several vegetation types (*e.g.*, savanna, forest, ironstone, ecotones) in multiscale approach bring further information to land use change effects on similarity/dissimilarity of fragmented landscapes contrasting heterogeneous perturbed habitats and their evolutionary history.

Biodiversity conservation must be underpinned by an understanding of the ecological processes – at all levels between species and ecosystem – that are affected by anthropogenic disturbance. In this sense, several studies have been developed in order to elucidate the effects of such alterations over fragmented forests (Laurance *et al.* 2007; Laurance *et al.* 2009; Arroyo-Rodríguez *et al.* 2013; Magnago *et al.* 2014; Magnago *et al.* 2015; Collins et al., 2016; Machado *et al.* 2016; Magnago *et al.* 2016; Fahrig 2017). Natural forest sites have been continuously reduced by deforestation, thus leaving isolated remnants across the landscape (FAO 2011; Rosa 2017). Loss of forest cover reduces diversity (Saunders *et al.* 1991; Laurance *et al.* 2006), reduces size and increase isolation of fragments promoting some fragmentation effects like barriers to migration (reducing gene flow) and edge effects (Kramer *et al.* 2008; Laurance *et al.* 2009; Ribeiro *et al.* 2009; Souza *et al.* 2014; Collins *et al.* 2016). According to the landscape divergence hypothesis (Laurance *et al.* 2007), fragments in the same landscape will tend to homogenize over time, leading to the convergence of floristic composition. Such biotic homogenization and simplification occur due to the habitat and land cover type losses and consequent loss of species traits (Smart *et al.* 2006; Tabarelli *et al.*, 2012). The results are new environmental conditions that favor a particular group of species (Smart *et al.* 2006; Tabarelli *et al.* 2012) mainly nonnative species with invasive traits and short-lived pioneer species (*e.g.* seed rain and fast growth) (Mckinney & Lockwoody 1999; Olden & Poff 2003). Thus, fragments consist of small, isolated and homogenized remnants with each fragment containing a reduced group of dominant species (Tabarelli *et al.* 2012; Machado *et al.* 2016).

On the other hand, fragments within different landscapes will diverge in composition (Laurance *et al.* 2007; Machado *et al.* 2016). Homogeneous landscapes over time and geographical distance, with different impoverishment groups of species, undergo the differentiation process (Laurance *et al.* 2007; Machado *et al.* 2016). Fragmentation affects ecological processes linked to important life-history traits like seed dispersal, seedling recruitment, growth and survival (Laurance *et al.* 2007). Thus, the lack of connectivity between isolated patches promotes different successional trajectories and high beta diversity by regeneration in different post fragmentation disturbances, disturbance regime and distance between fragments (Laurance *et al.* 2007; Chazdon 2008). Defaunation process can lead to floristic divergence reducing animal-mediated seed dispersal, mainly middle-fruits and large seeds dispersers, like large mammals, that disperse old-growth tree species sensitive to fragmentation effects changing floristic composition (Canale *et al.* 2012; Carvalho *et al.* 2016). Environmental gradients like altitude and some landscapes and fragments characteristics like size and shape that are related to environmental heterogeneity also increase beta diversity (García-Aguirre *et al.* 2010; Arroyo-Rodríguez *et al.* 2013).

Even for the well-known negative effects of fragmentation on diversity in patch-level scale (Fletcher *et al.* 2018), there is a compile evidence that habitat fragmentation - fragmentation effects controlled by the habitat amount - can produces high diversity in landscape-level scale (Fahrig 2017; Fahring *et al.* 2019). The positive responses may be explained by increased functional connectivity, increased habitat diversity, positive edge effects, stability of interactions like predator–prey, reduced competition both intra and interspecific, spreading of risk, and landscape complementation (see Fahrig 2017 for a full discussion about these factors). Arroyo-Rodríguez *et al.* (2013) found lower beta diversity under patches in landscapes with high levels of fragmentation and higher beta diversity between patches of the highest fragmented landscape concluding that homogenization/differentiation processes regard landscape configuration patterns and spatial-scale. Therefore, contrasting anthropogenic landscapes and undisturbed landscape with environmental heterogeneity of habitats, here expressed as vegetation types, can bring further empirical evidence for the discussion about this paradox of species turnover.

In this sense, the present work aimed to evaluate the beta diversity patterns of fragmented and conserved landscapes with vegetation types as a proxy for habitat heterogeneity. We tested two alternative hypotheses: 1) floristic homogenization at patch-level scale and 2) floristic differentiation at landscape-level scale. We predict higher beta diversity in conserved landscapes than fragmented one, since at patch-level scale fragmentation effects produce negative responses by reducing habitat heterogeneity and homogenizing habitats due habitat losses. We predict higher beta diversity across fragmented landscapes in comparison to conserved/fragmented landscapes, since at landscape-level scale, fragmentation effects produce positive responses by the low or lack of landscape connectivity changing successional trajectories, ecological processes and life-history traits.

Material and Methods

Description of study area

The study area is located in the state of Minas Gerais, in the region of the Espinhaço mountain range, which is located in the North-South axis of the Brazilian states of Minas Gerais and Bahia, and which encompasses three phytogeographic domains: Atlantic Forest, Brazilian savanna (Cerrado) and Caatinga. The first two of these are recognized as global hotspots for biodiversity conservation due to the high number of endemic species, and the high levels of habitat destruction they are subject (Myers *et al.* 2000; MMA 2003; Domingues *et al.* 2012). These areas also shelter about 10% of the botanical diversity of the country, containing many species of highly restricted distribution and low abundance (Rapini *et al.* 2008). Mining is the current most important industrial activity at Espinhaço, indeed, it is the largest area in the world for mine exploration, and one of the most economically important in Brazil due to the presence of metal-rich soils. The region is also important due to essential ecosystem services, mainly the water supply to both local and regional human populations. This function, together with the area's high biodiversity and soil diversity, has led to Espinhaço being designated as a biosphere reserve by UNESCO (Domingues *et al.* 2012).

In this study, three landscapes in the region were sampled: a protected landscape of Parque Estadual da Serra do Rola-Moça (PESRM, latitude -20.02678°, longitude -44.00089°) in the municipalities of Belo Horizonte, Brumadinho, Ibirité and Nova Lima; and two fragmented landscapes in the municipalities Sabará (latitude -19.86203°, longitude -43.80123°) and Brumadinho (latitude of -20.16016°, longitude -44.14894°) (Fig. 1). The climate in the region is classified as a Koppen Cwb with hot and rainy summers and dry winters, mean annual precipitation of 1463.7 mm, and mean monthly temperature of 21.1° C (INMET 2015).

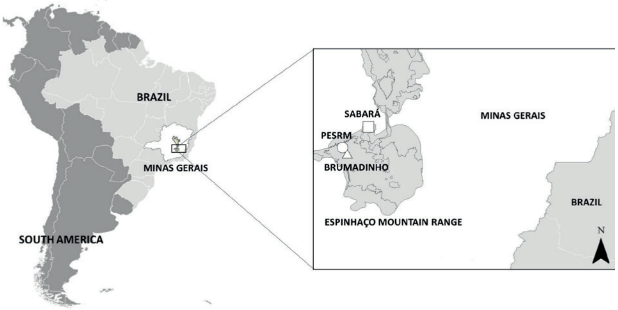

Figure 1. Map of municipalities and localities where sampling was conducted over Espinhaço Range. PESRM represents the protected landscapes and Sabará and Brumadinho fragmented landscapes.

PESRM is a transitional area between the Brazilian savanna and Atlantic Forest Domain (Ab'Saber 1997), comprising savanna below 1000m ASL (Vincent & Meguro 2008; Santos *et al.* 2011; Versieux *et al.* 2011), and rupestrian (quartzitic) grasslands and ironstones (ferruginous grasslands – bounded iron formations) above 1000 m (Conceição & Pirani 2005; Jacobi *et al.* 2007; Jacobi & Carmo 2008; Rapini *et al.* 2008; Vincent & Meguro 2008; Carmo & Jacobi 2013; Skirycz *et al.* 2014; Silveira *et al* 2016). The area also contains riparian (Londe *et al.* 2015) and seasonal semideciduous forests (Santos *et al.* 2011). Sites sampled in Brumadinho and Sabará represent landscapes strongly modified by mining. There are no ecotones in Brumadinho in the sampling area once it is an extremely fragmented landscape surrounded by pasture and areas of mining exploration. In Sabará, besides mining areas, the sampled sites included the encroaching *Eucalyptus* spp. plantations (Tab. 1).

Vegetation Sampling

Sampling was conducted in non-contiguous 115 permanent plots of 20 x 20 m (400 m^2). Inside each landscape, we identified the local environmental variation in the different vegetation types by coordinates and preview knowledge by Vale's technical team in the field . Since we defined the vegetation types to be sampled in each one, we distributed randomly the plots in the landscapes focusing to sample this environmental heterogeneity within and between each vegetation type , also considering microenvironmental conditions in each one. This environmental heterogeneity includes the edge and interior of the vegetation types, irregular terrain mainly in Brazilian savanna, ironstone and forest slopes and gaps by tree mortality covering as best as possible the diversity from each patch. Distribution of plots within each landscape was different, due to differing vegetation composition (Tab. 1). In the two fragmented landscapes, some vegetation types were absent and hence could not be sampled. Vegetation types are described in Tab. 2.

Due to these sampling differences a rarefaction curve was used to demonstrate the sufficiency of sample sizes (supplementary materials, Fig. S1). In all the landscapes, measured species richness could have been increased by greater sampling effort. Although sampling was lowest at PESRM, it had the highest floristic diversity (Fig. S1). The criteria for inclusion, of tree individuals, was the circumference at breast height (CBH) larger than or equal to 15.7 cm.

Data analyses

Beta diversity inside each landscape

To test the homogenization hypothesis, we calculated the beta diversity among vegetation types within the same landscape (PERMS, Brumadinho and Sabará) through separate matrices of presence and absence of species in each one. We used the beta-partitioning approach proposed by Baselga (2010), in which the dissimilarity between sample units is divided into two components, one associated with species substitution (turnover-βsim) and another associated with situations in which a unit is a floristic subset of another and there is no actual differentiation (Nestedness - βsne). This approach disentangles floristic patterns in antithetic processes underlying beta diversity, replacement or losses of species, and also corrects possible

Table 1. Distribution of plots in the sampled landscapes in the Espinhaço Range. Floristic relationships and similarities between vegetation types are presented in the supplementary material, Figure S3.

Landscape	Vegetation types	Landscape characterization	All plots/plots per vegetation type (20 x 20 m)	Total richness
PESRM	- Semi-deciduous seasonal forest; - Ironstone; - Brazilian savannah; - Ecotone forest/ironstone and - Ecotone forest/Brazilian savannah.	Intact landscape without anthropogenic disturbance or destruction	25/5	186
Brumadinho	- Semi-deciduous seasonal forest; - Ironstone; - Brazilian savannah and - Anthropogenic vegetation called 'anthropogenic pastures' – open area of secondary succession after disturbance.	Landscape fragmented by mining, with consequent absence of ecotones and presence of grass	40/10	131
Sabará	- Semi-deciduous seasonal forest; - Ironstone; - Brazilian savannah; - Ecotone and - Anthropogenic vegetation called 'anthropogenic pastures' – open area of secondary succession after disturbance.	Landscape fragmented by mining, presence of ecotones with *Eucalyptus* spp. plantation, presence of grass	50/10	146

Table 2. Characterization of vegetation types sampled at all landscapes surveyed.

Vegetation type	Description
Semideciduous seasonal forest	Composed mainly by trees, this forest environment is characterized by the loss of 30 to 60 % of its leaves in the dry season, conditioned by the double climatic seasonality (Veloso *et al*. 1991; Oliveira-Filho 2009).
Ironstone	It is included in the definition of rupestrian grassland *sensu latu* (Silveira *et al.* 2015). Occurs on ferruginous fields, mostly above 1000 m altitude (Vincent & Meguro 2008). It contains a high richness of herbaceous species and high endemism on the layer of compacted ironstone; the occurrence of trees and shrubs is restricted to depressions, where the soil layer is deeper (Fernandes 2016).
Brazilian savannah	Characterized by low-altitude, fertile soils with high aluminum content. The vegetation comprises trees and shrubs, with dense understory and soil covered by grasses (Schaefer *et al*. 2016). Plant diversity is mediated by the presence of quartzitic outcrops, fire (Fernandes 2016), depth of the water table and by soil characteristics (Ribeiro & Walter 2008).
Ecotone	"...a transition between two or more vegetation type; it is a junction zone or tension belt which may have considerable linear extent but is narrower than the adjoining community areas themselves." (Odum 1953). Additionally, ecotones from PESRM have demonstrated be floristically and phylogenetically distinct vegetation type with own particularities (Souza *et al*. 2020).
Anthropogenic vegetation: 'anthropogenic pastures'	Open area of secondary succession after disturbance covered by grasses.

distortions due to richness differences (Baselga 2010). We used the *betapair* function in the *betapart* package (Baselga & Orme 2012) in R (R Development Core Team 2013), with *Sorensen* as the index of dissimilarity between units. A non-parametric similarity analysis (ANOSIM) was conducted to statistically compare the landscapes to verify that the observed beta diversity distributions did not occur by chance (999 permutations). The *metaMDS* function in the R package *vegan* was used to build a non-metric multidimensional scaling (NMDS) from βsim data of each landscape to explore the turnover of floristic composition in a multivariate space. To run NMDS and ANOSIM analysis, we used βsim (derived from *Sorensen*) and *Sorensen* respectively as the indexes of dissimilarity, metrics appropriate to presence-absence data.

Beta diversity between landscapes and vegetation types

To address the differentiation hypothesis, three presence/absence matrices were created for the calculation of beta diversity: one matrix with fragmented landscapes (Sabará and Brumadinho, the matrix BS) and two with the combination of protected landscape (PESRM) and each one of the fragmented landscapes (matrices RB and RS). Subsequently, presence/absence matrices were created using data on the relationships among each vegetation type: for example, for forest vegetation type, one matrix with the forests of two fragmented landscapes (matrix BSf) and two matrices with the protected forest and one fragmented forest of each landscape (matrices RBf and RSf). The procedure was repeated for each of the other vegetation types (ironstone, Brazilian savanna and ecotone). For ecotones, calculations were made using matrices for three ecotones in two landscapes, due to the absence of vegetation type ecotones in Brumadinho and the presence of two ecotones in PERSM. There were two ecotones at PESRM (forest/Brazilian savanna and forest/ironstone) and one in Sabará (forest/Brazilian savanna). For the ironstone, there were only two plots with one species in Brumadinho due to the lack of tree individuals. PESRM had the largest number of vegetation types (five), as expected from a protected landscape, Sabará had four and Brumadinho three. The area "anthropogenic pastures" was removed from analysis due to the lack of tree individuals, which were only found in Sabará and Brumadinho in regions of extreme mining exploration and initial successional stage represented by *Solanum lycocarpum* A.St.-Hil (Brumadinho) and *Mimosa scabrella* Benth. (Sabará).

From the matrices we then calculate beta diversity following the afore-mentioned procedure, using beta diversity partitioning in βsim and βsne, together with analysis of similarity (ANOSIM). The rarefaction curve was made using the package *INEXT* (Hsieh *et al.* 2015).

Results

Beta Diversity in each landscape

Overall, we analyzed three landscapes and 12 vegetation types, which comprised 321 species and 2763 tree individuals. The PESRM is the most species-rich landscape with 186 species (supplementary material, Fig. S2, Tab. 1). According to NMDS, the three landscapes have high species turnover (Fig. 2). Despite the mining activities, the vegetation types demonstrated distinct floristic composition in the fragmented landscapes, except for ironstone vegetation type in Brumadinho, which did not form a distinct floristic group due to the low sample size of tree species, probably due to the environment degradation. In the protected landscape (PESRM) ecotones appear to form distinct floristic characters, which were not seen in the other landscapes (Fig. 2). Brazilian savanna also showed high dissimilarity, but only in this landscape (Fig. 2).

According to ANOSIM, βsim was highly significant in Brumadinho (R > 0.3; p < 0.001), Sabará (R = 0.25; p = 0.004) and PESRM (R = 0.3; p = 0.011) (Fig. 3). Only Brumadinho presented significant differences in βsne (R > 0.3; p < 0.001) (PESRM: R = -0.22; p = 0.96; Sabará: R = -0.06; p = 0.84) (Fig. 3).

Beta diversity between landscapes and vegetation types

Turnover was high for the three comparisons: BS, RB and RS. βsim was significant in BS (R = 0.09; p = 0.02), RB (R = 0.07; p = 0.049) and RS (R = 0.12; p = 0.004) (Fig. 4), but βsne did not differ significantly among these areas: BS (R = -0.02; p = 0.76), RB (R = -0.02; p = 0.69) and RS (R = -0.04; p = 0.9) (Fig. 4). For forest, ironstone, Brazilian savannah and ecotone vegetation types, βsim and βsne largely followed the same pattern of significance, though with some notable differences. In fragmented forests (BSf) βsne presented value next to significance (R = 0.2; p = 0.064) (Fig. S4) and βsim differences were not significant between protected and fragmented forests from Sabará (RSf) (R = -0.2; p = 0.9) (Fig. S5). βsne was significant for comparisons between the two ecotones from PESRM (RR) (R = 0.4; p = 0.5) (Fig. S4). In the comparison between the two fragmented ironstones (BScg), βsim was not significant (R = 0.32; p = 0.12) (Fig. S5). For Brazilian savanna the βsim value for protected and fragmented sites from Sabará (RScru) was not significant (R = 0.21; p = 0.1) (Fig. S5).

Discussion

Both within and between landscapes, differentiation processes seem to play a crucial role in beta diversity in our studied sites. The conserved landscape indeed presents the

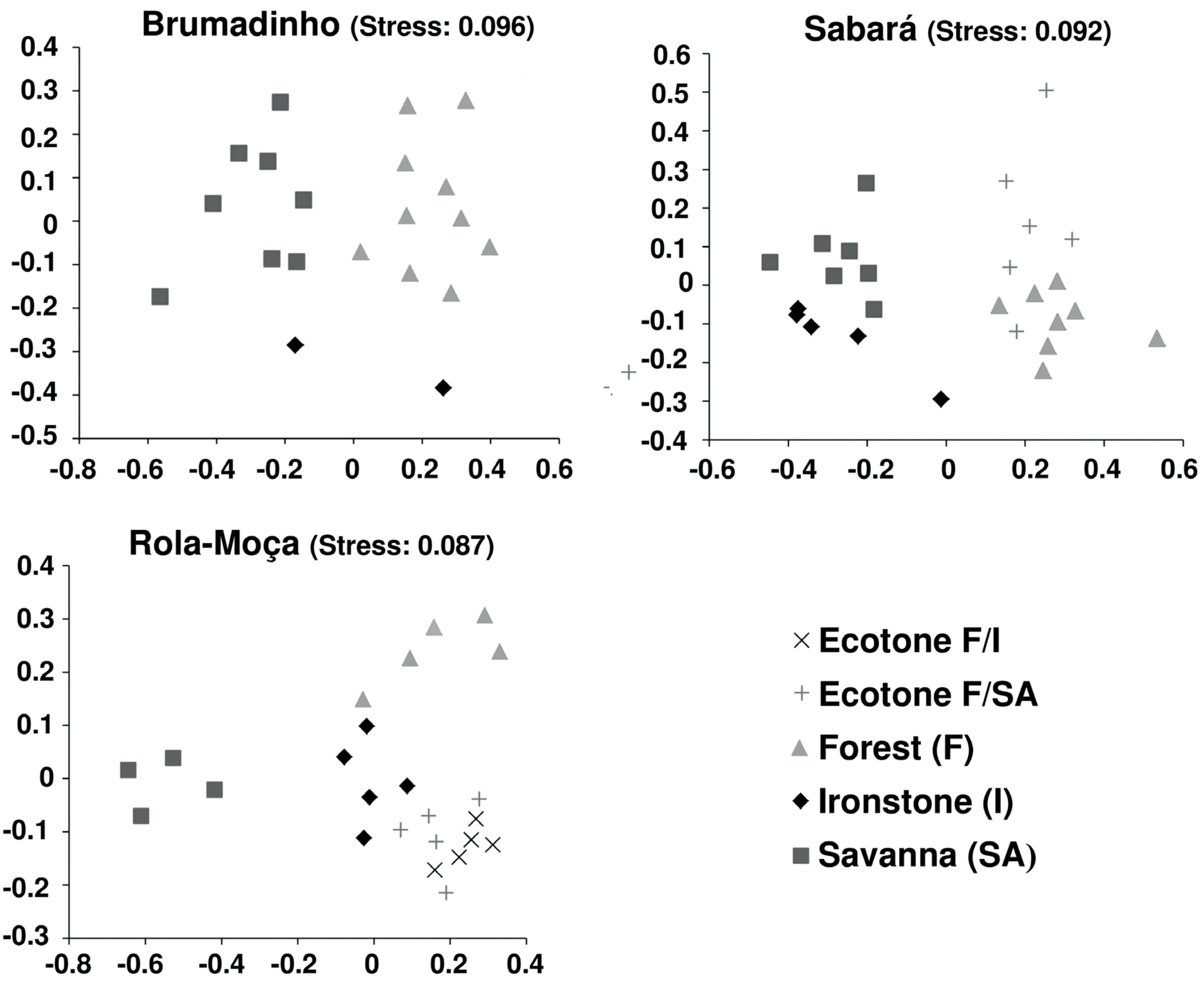

Figure 2. Non-metric multidimensional scaling of the three landscapes with a total of five vegetation types, three in Brumadinho, four in Sabará and five at PESRM. The distance among plots indicates the similarity among them regarding the beta diversity.

greatest alpha and gamma diversity, but did not differ from the two fragmented landscapes in species turnover. Overall, landscapes showed high species turnover, and comparisons among fragmented and protected landscapes and vegetation types showed significant differences, with some exceptions (Figs. 3, 4, S4, S5). We expected that habitat heterogeneity loss and floristic homogenization would play a crucial role in the floristic composition of fragmented landscapes. In fact, it was possible to notice that habitats or vegetation types with lower richness due to local disturbance conditions showed high beta diversity. The most contrasting pattern observed was the increase of beta diversity in fragmented landscapes due to mining activities, which may be considered a large-scale and infrequent disturbance (Turner *et al*. 1998; Araújo *et al*. 2016). Existing models for this disturbance predict that the greater the intensity, the lower amounts of botanical remnants (resprouts), and the greater the size, the greater the distance required for propagules of neighbor areas to reach an area by dispersal, thus affecting the floristic composition (Turner *et al*. 1998; Araújo *et al*. 2016).

Beta Diversity in each landscape

NMDS data of the three landscapes (Fig. 2) showed that the closer the plots, the lower the beta diversity. Despite the distinctions between vegetation types and the high turnover of species in each landscape, the dissimilarity among plots is higher in fragmented landscapes than at PESRM. Thus, the fragmentation effects along space and time in plant communities can lead to differences in the floristic composition (Arroyo-Rodríguez *et al*. 2013; Collins *et al*. 2016). Such patterns are different because the larger the disturbance regime, the more processes are involved in the species distribution. According to our predictions, it is expected that protected areas contain higher beta diversity than fragmented ones. However, we found higher species turnover in fragmented landscapes, but this is not necessarily an indication of ecosystem health. In our "control" landscape (PESRM) the vegetation types share a greater number of species, except Brazilian savanna that presents peculiar characteristics. At the landscape scale, this floristic similarity among areas may be caused mainly by the existence of ecotones, transitional areas that connect them, thereby promoting species flow (Socolar *et al.* 2016) (Fig. 5). Thus, the sharing of species through ecotones may limit beta diversity. In the heavily disturbed areas, however, the greater the extent of disturbance, the less likely that propagules will be able to colonize distant patches, and the more intense the disturbance, the fewer sources of propagules remain (Turner *et al.* 1998; Araujo *et al.* 2016). The combined result is that these isolated patches become distinct through greatly reduced opportunities for migration and immigration, effectively becoming islands of habitat in a barren landscape (Laurance *et al.* 2007).

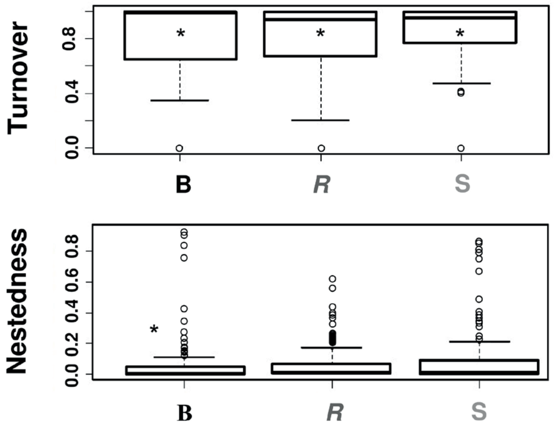

Figure 3. Boxplot of beta diversity (turnover and nestedness) in the three studied landscapes. B = Brumadinho; S = Sabará; *R* = PESRM. Asterisks represent significance in the analysis of similarity (ANOSIM). Each box encompasses the 25th to 75th percentiles; the median is indicated by the horizontal line within the box and the other horizontal lines outside the box indicate the 10th and 90th percentiles.

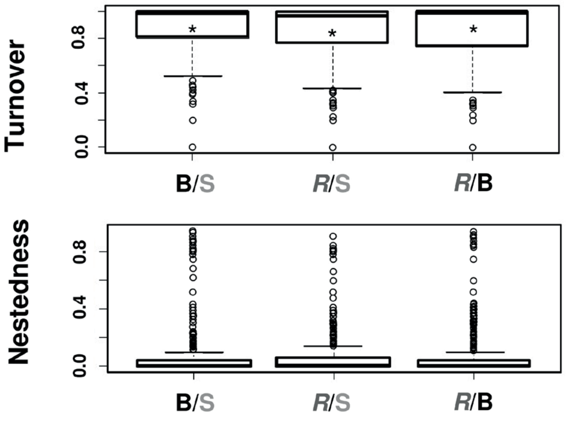

Figure 4. Boxplot of the beta diversity components (turnover and nestedness) in the three relationships: B/S = fragmented landscapes (Brumadinho and Sabará); *R/S* = protected x fragmented landscape (PESRM and Sabará); *R/B* = protected x fragmented landscape (PESRM and Brumadinho). B = Brumadinho; S = Sabará; *R* = PESRM. Asterisks represent significance in the analysis of similarity (ANOSIM). Each box encompasses the 25th to 75th percentiles; the median is indicated by the horizontal line within the box and the other horizontal lines outside the box indicate the 10th and 90th percentiles.

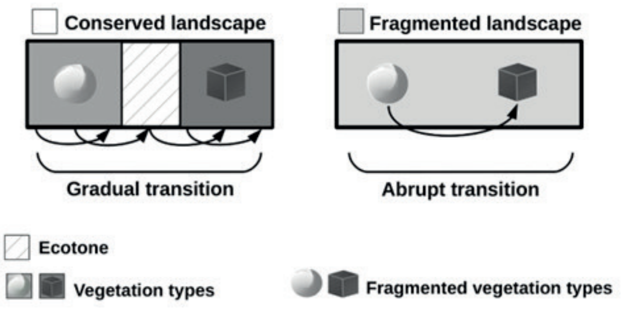

Figure 5. A conceptual framework showing consequences of reducing habitats using ecotone vegetation as an example . Abrupt transitions increase distance from propagules from species due habitat loss. While gradual transition allows higher species flow, abrupt transition enhances beta diversity leading to a potential differentiation process.

High beta diversity in the landscapes could be explained by many vegetation types sampled, but it is important to highlight that fragmented landscapes showed less vegetation types (reduced landscape habitats), but expressive beta diversity. The floristic similarity of ironstone and Brazilian savanna in Sabará represents an example of the settlement of species non-natural to the respective habitats due to the human disturbance that altered edaphic conditions. Ironstone and Brazilian savanna from PESRM shared only one species, *Myrcia guianensis* (Aubl.) DC. Ironstone and Brazilian savanna from Sabará shared six species: *Byrsonima verbascifoilia* (L.) DC., *Dalbergia miscolobium* Benth., *Eremanthus glomerulatus* Less., *Handroanthus ochraceus* (Cham.) Mattos, *Kielmeyera coriacea* Mart. & Zucc. and *Vochysia thyrsoidea* Pohl. The reduction of habitats in anthropogenic landscapes, like ecotones in Brumadinho, the absence or disrupting of edaphic-plant associations and even the presence of anthropogenic areas, like the here called "anthropogenic pastures", may have influenced positively the result of beta diversity in these landscapes.

The substitution of species was the predominant pattern of floristic change for the landscapes from PESRM and Sabará, while in Brumadinho the beta diversity by nestedness was significant (Fig. 3). To explain these patterns, it is necessary to know the effects of anthropogenic disturbance, in this case, mining activities on the floristic composition and species diversity. Spatial sorting of species or an environmental constraint (*e.g.*, anthropogenic disturbance) in regional scale in a mesoregion like Espinhaço Range with high gamma diversity may explain the replacement of species in these landscapes, even in the fragmented ones (Qian *et al.* 2003; 2005). On the other hand, nestedness in Brumadinho was significant suggesting an ordinate loss of species (Almeida-Neto 2008; Baselga 2010). Indeed, Brumadinho's landscape showed the lowest values of species diversity and number of vegetation types besides less exclusively species suggesting that mining activities were more intense in this region compared to Sabará landscape, for example. Thus, mining disturbance played a crucial role in beta diversity patterns and Brumadinho seems to be a subset of the biota at richer mesoregion studied. In addition, species nesting in Brumadinho is caused by landscape fragmentation due to mining activities and loss of vegetation types like the ecotone, which is present in Sabará. This result reinforces the importance of habitat loss as one of the main causes of fragmentation and consequently ecosystems and species biodiversity losses.

Beta diversity between landscape and vegetation types

The Southern region of Espinhaço Range lies in an ecotone area between Brazilian savanna and Atlantic Forest phytogeographic domains (Ab'Saber 1997), and the diversity of geological, topographic and climatic conditions (Mello-Barreto 1942) make this mesoregion highly heterogeneous. Due to the high gamma diversity, a consequence of this set of features, the mesoregion has high beta diversity both between fragmented landscapes (B/S) and between fragmented and protected landscapes (R/S and R/B) (Fig. 4).

Decomposing the landscape and relating beta diversity to vegetation types led to different responses with no significance, both in fragmented and protected forest and Brazilian savanna, as well as in the ironstone from fragmented landscapes. Habitat loss may act as an ecological filter and decrease (Puttker *et al.* 2014) or increase beta diversity (Arroyo-Rodríguez *et al.* 2013). As already demonstrated for some areas and landscapes, this increase of beta diversity occurs if habitat losses represent limitations to the dispersion pattern (Hubbell 2001; Myers *et al.* 2016), which depends on the predominant functional groups, the distance between botanical remnants and the type of matrix that connect them (Machado *et al.* 2016). The geographic distance (~ 20 km between protect and fragmented landscapes and 40 km between both fragmented landscapes) and the values of beta diversity increasing turnover of species in fragmented vegetation types point to a floristic differentiation process in the overall gamma diversity in the mesoregion of the Espinhaço Range, but a temporal monitoring is necessary to attribute these patterns to divergence in composition in this degraded landscape.

Although ecotones are characterized as transitional areas (Gosz 1993; Risser 1995), their floristic composition was distinct from the vegetation types connected by them (results; Souza *et al.* 2020). This result highlights the importance and singularity of these ecotone regions, which have been known as distinct vegetation units (Kark & Van Rensburg 2006). Such heterogeneity may be comprehended through the observation of different ecotone scales present in the area, among biomes and among communities (Souza *et al.* 2020). Therefore, it is a unique region strongly threatened and poorly protected, since the richness present in the non-protected areas is not completely included in PESRM. The importance of Espinhaço Range and ecosystem services provided are relevant and natural resources need to be preserved.

Concluding remarks

Many studies showed the positive effects of habitat fragmentation (Fahrig 2017 and studies there in; Fahrig *et al.* 2019) in beta diversity in fragmented landscape, considering the importance of small fragmented patches to conservation. Here, we demonstrated the role of differentiation processes in landscape-level scale, but in a different way from other studies, since we showed that conserved landscapes harbor more species richness and habitat types (*e.g.*, vegetation types) than fragmented landscapes, even with similar patterns of beta diversity. Also, it is necessary to take into account the βsne contribution to high beta diversity patterns in fragmented landscapes that represents the ordinate loss of species, not the replacement of species, like in Brumadinho landscape.

Fragmentation effects can promote misleading interpretation and high beta diversity patterns as we demonstrated here. The vegetation types diverged in composition both within and between landscapes. It is therefore paramount that researchers pay attention to the ecosystem functions associated with diversity patterns, especially in the context of biodiversity conservation. Long-term study of these landscapes will bring further data to disentangle homogenization-differentiation processes. Finally, we also suggest that ecotones should be considered when defining priority areas for conservation, and as their resources are used, they need to be recovered, as well as the other vegetation types.

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