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## **Effects of landscape configuration and composition on phylogenetic diversity of trees in a highly fragmented tropical forest**

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## Summary

1. Fragmentation of tropical forests is a major driver of the global extinction crisis. A key question is understanding how fragmentation impacts phylogenetic diversity, which summarises the total evolutionary history shared across species within a community. Conserving phylogenetic diversity decreases the potential of losing unique ecological and phenotypic traits, and plays important roles in maintaining ecosystem function and stability.
2. Our study was conducted in landscapes within the highly fragmented Brazilian Atlantic forest. We sampled living trees with DBH  $\geq 4.8$  cm in 0.1 ha plots within 28 fragment interiors and twelve fragment edges to evaluate the impacts of landscape configuration, composition and patch size, as well as edge effects, on phylogenetic diversity indices (PD, a measure of phylogenetic richness; MPD, phylogenetic distance between individuals in a community in deep evolutionary time; and MNTD, phylogenetic distance between each individual and its nearest phylogenetic neighbour).
3. We found that PD and MPD were correlated with species richness, while MNTD was not. Best models suggest that MPD was positively related to edge density and negatively related to the number of forest patches, but that there was no effect of landscape configuration and composition metrics on PD or MNTD, or on standardized values of phylogenetic structure (sesPD, sesMPD, sesMNTD), which control for species richness. Considering all selected models for phylogenetic diversity and structure, edge density and number of forest patches were most frequently selected.
4. With increasing patch size, we found lower PD in interiors but no change at edges, and lower sesMNTD regardless of habitat type. Additionally, PD and sesMNTD were higher in interiors than at edges.
5. *Synthesis.* Changes in MPD and sesMNTD suggest that extirpation of species at edges or in highly fragmented landscapes increases the dominance of species within a subset of clades (phylogenetic clustering), likely those adapted to disturbance. Smaller patch sizes are phylogenetically diverse and overdispersed, probably due to an invasion of edge-adapted species. Conservation must

enhance patch area and connectivity via forest restoration; pivotally, even small forest patches are important reservoirs of phylogenetic diversity in the highly threatened Brazilian Atlantic forest.

**Key-words:** Habitat fragmentation, habitat loss, landscape structure, phylogenetic structure, edge effect, Brazilian Atlantic Forest

**Tweetable Abstract:** Tree evolutionary history is best saved in unfragmented landscapes in the threatened Brazilian Atlantic forest

## Introduction

Human modification of tropical landscapes is one of the greatest threats to global biodiversity (Lewis, Edwards & Galbraith 2015). Over 150 Mha of tropical forest was converted to farmland between 1980 and 2012 (Gibbs *et al.* 2010; Hansen *et al.* 2013), driving a dramatic loss of species in cleared areas (Gibson *et al.* 2011). What remains is a landscape dominated by fragmentation processes, with 25% of remaining rainforest in the Amazon and Congo Basins and 91% in the Brazilian Atlantic forest within 1 km of an edge (Haddad *et al.* 2015). Remaining tropical forests are thus increasingly isolated, persist in increasingly smaller and more irregular patches, and have greater edge effects (Fahrig 2003; Laurance *et al.* 2006; Arroyo-Rodríguez *et al.* 2013).

Fragmentation drives both shifts in forest structure and biodiversity. There is an increase in the abundance of trees with low wood density (Laurance *et al.* 2006) that drive a decay in functional diversity in just three decades since isolation (Benchimol & Peres 2015), while edge effects that penetrate into the forest, from wind to woody vines, increase tree mortality (Laurance *et al.* 2002). Fragments thus have reduced carbon stocks compared to contiguous forest (Putz *et al.* 2014), particularly at fragment edges (Magnago *et al.* 2015a; Haddad *et al.* 2015). In turn, fragmentation drives the loss of species richness and changes in species composition when compared to contiguous

habitat (Laurance *et al.* 2006, 2007; Arroyo-Rodríguez *et al.* 2013; Magnago *et al.* 2014), in smaller versus larger fragments (Laurance *et al.* 2011), at edges versus interiors (Magnago *et al.* 2014), and in more isolated patches (Fahrig 2003; Magnago *et al.* 2015b). These changes are typified by the replacement of rare interior forest species with edge-tolerant generalist species (Arroyo-Rodríguez *et al.* 2013; Carrara *et al.* 2015) and exotic species (Turner 1996).

While much of the knowledge of the effects of fragmentation on biodiversity is based on species richness, abundance, and composition, it is also important to understand the impacts of fragmentation on phylogenetic diversity—the total evolutionary history shared across all species within a community (Arroyo-Rodríguez *et al.* 2012; Cisneros, Fagan & Willig 2015a; Frishkoff *et al.* 2014). Incorporating measures of evolutionary distinctiveness into conservation planning can help us to preserve as much of the tree of life as possible (Mace, Gittleman & Purvis 2003; Redding & Mooers 2006), while conserving phylogenetic diversity decreases the chance of losing unique phenotypic and ecological traits (Jetz *et al.* 2014), and provides benefits for ecosystem function and stability (Dinnage *et al.* 2012; Cadotte 2013).

Reviewing the literature, we identified only six studies on trees and one study on bats that used phylogenetic metrics to evaluate the effects of forest fragmentation (Table S1), and we discovered that there is no consensus in the range of fragmentation metrics and phylogenetic diversity indices used. Of these studies, two showed that forest fragments have lower phylogenetic diversity than contiguous landscapes (Santos *et al.* 2014; Munguía-Rosas *et al.* 2014). Four investigated the effect of fragment area and/or amount of forest cover on phylogenetic diversity and phylogenetic structure with conflicting findings: With declining fragment size or percentage forest, bats in Caribbean lowlands, Costa Rica, lost phylogenetic diversity (Cisneros, Fagan & Willig 2015a), trees in the Brazilian Atlantic both lost (Andrade *et al.* 2015) and retained (Santos *et al.* 2010) phylogenetic diversity, and trees in Los Tuxtlas, Mexico, retained phylogenetic diversity (Arroyo-Rodríguez *et al.* 2012). Finally, two studies investigated the impact of edges on tree phylogenetic diversity, one revealing reductions at fragment

edges (Santos *et al.* 2010), the other no difference between edge and interior (Benitez-Malvido *et al.* 2014).

Beyond the impacts of fragment area and edge effects, the degree of isolation from other fragments and fragment shape are also likely to determine impacts on phylogenetic diversity. This is because the retention of species in fragments can be influenced by the level of isolation (Boscolo & Metzger 2011; Magnago *et al.* 2015b) and the shape of fragments (Hill & Curran 2003). However, we identified just one study that investigated the impacts of isolation and fragment shape (Cisneros, Fagan & Willig 2015a). Cisneros, Fagan & Willig (2015a) found that the phylogenetic diversity of bats increased as proximity between forest patches and shape irregularity of patches decreased. Thus a key question still remains, which is how the phylogenetic diversity of communities is affected by fragment isolation and shape.

Here we focus on trees species of the imperiled Brazilian Atlantic Forest. Trees are the best-known group for understanding fragmentation effects on phylogenetic diversity (Table S1) and they are also important for habitat structure (Boscolo & Metzger 2011; Magnago *et al.* 2014), carbon storage (Nascimento & Laurance 2004; Laurance *et al.* 2006; Magnago *et al.* 2015b), and represent a significant part of the species diversity in the tropics (Banks-Leite *et al.* 2014). Previous studies allow us to create two hypotheses about expected changes in the phylogenetic diversity of tree communities that are under the effects of fragmentation, including high irregularity of shape, isolation and edge effects:

- (i) Considering previous studies that support the hypothesis of low phylogenetic conservatism in functional traits vulnerable to fragmentation processes (Santos *et al.* 2010; Arroyo-Rodríguez *et al.* 2012), we hypothesized that in recently fragmented landscapes, such as those used in this study (i.e., <100 years), metrics of landscape configuration, composition and habitat loss (i.e., fragment size) would have driven species losses randomly or uniformly throughout the phylogenetic tree rather than losses of entire lineages of trees, and;

- (ii) Given the severe effects of abiotic filters commonly cited for edge habitat (Laurance *et al.* 2002; Magnago *et al.* 2015a), which commonly lead to tree species loss and altered species composition (Laurance *et al.* 2002; 2006), we hypothesized that a significant proportion of lineages of tree species may also be lost in fragment edge relative to interior habitat.

## Materials and methods

### *Study sites*

Our 220 km long study area was based in Espírito Santo (19°3'48.02" S and 39°58'58.52" W) northwards to southern Bahia (17°43'29.30" S and 39°44'26.60" W), east Brazil (Fig. 1 and see Table S2 for details). Remaining forests in the region are highly fragmented, situated in a landscape matrix of cattle pastures, and plantations of *Eucalyptus* spp., sugar cane, coffee, and papaya (Rolim *et al.* 2005). These forest areas are included in the Atlantic Forest domain (IBGE 1987; also termed Tableland forest, Rizzini 1979), typified by large flat areas rising slowly from 20 to 200 m a.s.l., and according to the Brazilian vegetation classification are Lowland Rain Forest (IBGE 1987). The prevailing climate is wet tropical (Köppen climate classification), with low rainfall from April to September followed by high precipitation from October to March, and with minimal variation in climate across sampling sites: precipitation ranges from 1,228 mm yr<sup>-1</sup> in Espírito Santo (Peixoto & Gentry 1990) to ~1,403 mm yr<sup>-1</sup> in Bahia (Gouvêa 1969), with similar average temperatures in the dry season (Espírito Santo ~15.6°C; Bahia ~14°C) and the wet season (Espírito Santo ~27.4°C; Bahia ~23°C).

Historically, the studied landscape remained well preserved until the 1950's. Thereafter, Espírito Santo and Bahia experienced rampant clearcut logging and charcoal production, followed by agriculture (Garay & Rizzini 2004). The main deforestation period in our study area was thus between 1950s and early 1970s (Simonelli 2007), with conversion of forests primarily to sugar cane and cattle pastures. Because our fragments were 40 to 60 years old when sampled, extinction debts of some long-lived tree species are likely still to be paid. However, trees species

composition in the interior of smaller fragment alters rapidly (most within the first 10 years since isolation) to reflect a more disturbed community (Laurance *et al.* 2002; Laurance *et al.* 2006), indicating that our time since isolation is sufficient to detect many important impacts of fragmentation.

#### *Data collection*

Fieldwork was conducted between January 2008 and July 2014 in 27 forest fragments that ranged in area from 13 to 23,480 ha (see Table S2). Within each fragment, we sampled one randomly placed transect except for the second largest fragment of 17,716 ha in which we sampled two transects separated by 4 km, positioned  $\geq 200$  m from the forest edge (28 transects in total; see Fig. 1 and Table S2). Additionally, within 11 of these fragments again spanning 13 to 23,480 ha, we sampled one transect again, two transects separated by 4 km were sampled in the 17,716 ha fragment, each positioned  $\sim 5$  m from the forest edge and each running perpendicular to the paired interior plot sampled within the same fragment (see Magnago *et al.* 2014 and Table S2). We thus have a dataset of 28 interior transects and 12 edge transects (i.e., paired with 12 of the 28 interior transects). Each transect consisted of ten  $10 \times 10$  m plots (0.1 ha in total) spaced at 20 m intervals. Thus our sample comprises 280 plots (2.8 ha) in fragment interiors and 120 plots (1.2 ha) in fragment edges. We only sampled primary forests, with no evidence of recent logging, although we cannot rule out the occurrence of limited logging several decades ago.

Within each plot, we sampled all individuals living and rooted within our plots with diameter at breast height (DBH; 1.30 meters above ground height)  $\geq 4.8$  cm. Individuals that were not identified at the site were collected and classified into morphospecies, subsequently identified by morphological comparison in the Herbarium of Vale (CVRD) or botanical experts for their families. The botanical material collected in reproductive stage was deposited in the Herbarium of the Federal University of Viçosa, Minas Gerais (VIC) and CVRD.

## Data analysis

### *Landscape metrics*

Our landscape design followed the “patch-landscape” approach of McGarigal & Cushman (2002). In this design, all response variables (phylogenetic metrics) were measured for each transect within each forest patch, while the landscape configuration and composition metrics (explanatory variables; see below) were measured in a circular buffer of 2 km around each transect. This buffer size is large enough to include the wide variation of the explanatory variables (see Table S3), as well as being at a scale that comprises structural variation of trees (Rocha-Santos *et al.* 2016), variation in alpha- and beta-diversity of generalist and specialist bird species (Carrara *et al.* 2015), and variation in diversity, abundance and uniformity of bats (Arroyo-Rodríguez *et al.* 2016).

In each buffer, we measured three metrics of landscape configuration, which describe geometric arrangement, isolation and position of fragment or matrix elements and which exhibit a wide variation in our landscapes (see Table S3): (1) landscape shape index – measures the degree of shape complexity of all fragments belonging to the same class (forest) across a landscape. For a given landscape, a low number means that fragments within a landscape are on average more regularly shaped and thus have less edge effects; (2) mean forest nearest neighbour – gives the average value of the forest nearest neighbour metric when considering all forest fragments within each buffer; and (3) edge density – measures the length (m) of all forest edges divided by the total area (ha) of the landscape (thus measured in m/ha). For a given landscape, a low number indicates lower edge effects within the landscape.

Additionally we measured two metrics of landscape composition, which describe the quality or quantity of fragment or matrix elements that compose the landscape and which exhibit a wide variation in our landscapes (see Table S3): (4) forest cover – measures the percentage of the landscape covered by forest, with a high number reflecting largest remaining forest cover; and (5) number of forest patches – measures

the number of fragments within each landscape, thus indicating the degree of forest fragmentation.

We identified the configuration and composition metrics of landscapes using the vegetation map of the Brazilian Atlantic forest (reference year 2005; [www.sosma.org.br](http://www.sosma.org.br) and [www.inpe.br](http://www.inpe.br)), developed by SOS Mata Atlântica/INPE (2015). This dataset depicts the spatial distribution of the main forest formations within this biome (see also Supplementary Methods, Text S1), and has been used to describe landscape structure via forest loss and fragmentation (Ribeiro *et al.* 2009) and to generate estimates of carbon loss due to habitat fragmentation (Pütz *et al.* 2014). However, omission and commission errors were detected after comparison with available very-high optical spatial resolution satellite data from 2012 (World Imagery 2015). These errors were then manually corrected to obtain the most accurate spatial delineation of the forest fragments within each circular buffer of 2 km. After correction, within each buffer we divided our landscape into forest (i.e. only Tableland forest) and non-forest (i.e. all other types of non-natural areas [matrix]). All forest fragments and non-forest matrix areas were then converted to raster format using the same spatial resolution (30 meters) used to generate the vegetation map of this biome with ArcGis (v 10.1).

Posteriorly, we used the files generated in ArcGis to calculate configuration and composition metrics in FRAGSTATS (v 4.2; McGarigal & Ane 2012) using 2 km of source radius and the eight-cell neighbourhood rule. Among the wide range of metrics for landscape study offered in FRAGSTATS, many are comparative and difficult to use for biological interpretation (McGarigal & Ane 2012). In this sense, our selected metrics of fragmentation, habitat loss and edge are more directly related to our hypotheses and to the literature on landscape ecology (see Boscolo & Metzger 2011; Carrara *et al.* 2015; Cisneros, Fagan & Willig 2015a; Cisneros, Fagan & Willig 2015b; Rocha-Santos *et al.* 2016).

### *Phylogeny construction*

For the preparation of our phylogenetic tree, we constructed a list of all our family/genus/species according to APG III (2009). In the program Phylocom version 4.2 (Webb *et al.* 2008), we then used the PHYLOMATIC function to return the phylogenetic hypothesis for the relationship between our 72 families, 273 genera and 604 species sampled in 6,802 tree individuals, using the new modified megatree R20120829mod.new for vascular plants from Gastauer & Meira-Neto (in press). In our phylogenetic hypothesis, more than two species per family or more than two genera of an unresolved family in R20120829mod.new were inserted as polytomies. Finally, to estimate the lengths of branches in millions of years for our ultrametric phylogenetic tree, we used the file "ages\_exp", (Gastauer & Meira-Neto, in press) and the BLADJ algorithm in Phylocom program version 4.2 (Webb *et al.* 2008, see Fig. S1).

### *Phylogenetic diversity metrics*

From our phylogenetic hypothesis, we calculated metrics that evaluate the evolutionary history present in our landscapes (Faith 1992; Webb *et al.* 2000; Webb *et al.* 2002): (i) phylogenetic diversity (PD); (ii) mean pairwise distance (MPD); (iii) mean nearest taxon distance (MNTD); (iv) standardized phylogenetic diversity (sesPD); (v) standardized mean pairwise distance (sesMPD); and (vi) standardized mean nearest taxon distance (sesMNTD). The standardized metrics are equivalent to PD, MPD and MNTD, but are standardized for species richness (Swenson 2014; Coronado *et al.* 2015; see also Supplementary Methods, Text S2). PD is calculated based on the presence and absence of species, and measures the sum of evolutionary history in a community; MPD is weighted by abundance and measures the average phylogenetic distance between all combinations of pairs of individuals (including conspecifics); and MNTD is weighted by abundance and measures average phylogenetic distance between an individual and the most closely related non-conspecific individual. Using Pearson correlations, we checked if all of our phylogenetic metrics are free from significant effects of species richness.

For the standardized effect size (ses) calculations, our tree was compared with 10,000 null model randomizations using the algorithm "phylogeny pool". Posteriorly, we extracted the centile of each observed community PD, MPD and MNTD value from the null distribution as a probabilistic indicator of deviance from a null expectation (Frishkoff *et al.* 2015; Edwards *et al.* 2015). The applied null model randomizes the identity of species occurring in each sample, but maintains constant species richness and abundance within each transect. This approach assumes, therefore, that all species are equally likely to occur in any fragment the landscape (Arroyo-Rodríguez *et al.* 2012). We calculated these six metrics using "picante" package (Kembel *et al.* 2010) in R, version 3.2.1 (R Development Core Team. 2015).

### *Statistical analyses*

We analysed the effects of landscape configuration and composition on each phylogenetic metric using Generalized Linear Models (GLM), with Gaussian error and an identity link (normality was tested and confirmed by the Shapiro Wilk test), as implemented in the 'glm' function from *stats* package. Thus our GLM related each metric of phylogenetic diversity (PD, MPD and MNTD) and phylogenetic structure (sesPD, sesMPD and sesMNTD), as response variables, with all metrics of landscape configuration and composition (Cisneros, Fagan & Willig 2015a; Cisneros, Fagan & Willig 2015b), as explanatory (predictor) variables. However, multicollinearity between predictor variables was confirmed by Spearman correlation analysis (see table S4), and any pair of explanatory variables that have a high correlation ( $r \geq 0,6$ ) were included in separate models and subjected to selection of the best model (Magrath, Santamaría & Larrinaga 2012). The Akaike Information Criterion of Second Order (AICc indicated for small sample sizes), with  $\Delta AICc \leq 2$ , was used to select our best models (Burnham *et al.* 2011), although we also consider all selected models.

Additionally, we investigated the impacts of fragment area and edge effects on metrics of phylogenetic diversity, phylogenetic structure and species richness. We considered two predictor variables: (i) fragment size in log scale and (ii) habitat type with two levels (edge and interior). We also consider the possible interactions between these two predictor variables (see Magnago *et al.* 2014 for details). These analyzes

were conducted using Generalized Linear Mixed Model (GLMM), with site as a random variable (Bolker *et al.* 2009). The GLMM was built using the function “lmer” in the package *lme4*, with Gaussian error and an identity link. After creating each model, we applied the “dredge” function in the package MuMIn and our best model was considered the one with value of  $\Delta AICc=0$ . All statistical analyses were performed in R, version 3.2.1 (R Development Core Team. 2015). Data can be found in Matos *et al.* (2016).

## Results

We recorded 6,802 Individuals of 604 tree species, spanning 273 genera and 72 families according to the classification of the Angiosperm Phylogeny Group's III (2009) across our 28 interior transects and twelve edge transects. Average and standard deviation of species richness for interior transects was  $75.10 \pm 12.6$  (range: 52 to 94 species) and  $80.75 \pm 11.42$  (range: 62 to 101 species) for edge transects.

### Species richness and phylogenetic metrics

We found that PD (Pearson:  $r = 0.95$ ,  $P = 0.0001$ ) and MPD (Pearson:  $r = 0.48$ ,  $P = 0.001$ ) were strongly correlated with species richness, whereas MNTD was not correlated with species richness (Pearson:  $r = -0.27$ ,  $P = 0.091$ ). After the calculation of standardized effect sizes, we found no significant correlation between species richness and sesPD (Pearson:  $r = -0.006$ ,  $P = 0.970$ ), sesMPD (Pearson:  $r = -0.05$ ,  $P = 0.732$ ), and sesMNTD (Pearson:  $r = 0.11$ ,  $P = 0.501$ ). Thus the standardized values reduced to a minimum the effects of species richness.

### Impacts of landscape configuration and composition on phylogenetic diversity

#### *Phylogenetic diversity*

Our best models ( $\Delta AICc=0$ ) indicated that the configuration and composition of landscapes did not change PD or MNTD (the average number of years between each species of its closest relative in a community) (Table 1). However, according to our best model ( $\Delta AICc=0$ ; Table 1), the average number of years of evolutionary history that separates species in a community (MPD) was best explained by edge density and the

number of forest patches in the landscape. We found that increasing edge density led to a positive increase in MPD (GLM:  $t = 2.305$ ,  $P = 0.029$ , Fig. 2a), while increasing number of forest patches decreased MPD (GLM:  $t = -0.9352$ ,  $P = 0.040$ , Fig. 2b).

Considering the four models ( $\Delta AICc < 2$ ) for PD, edge density and forest cover were present in two models (Table 1). For MPD, two models were selected with values  $\Delta AICc < 2$ , and edge density and number of forest patches were present in the same model (Table 1). For MNTD, there were two models with values  $\Delta AICc < 2$ , and edge density was in one model (Table 1). Finally, considering all 40 selected models, edge density and number of forest patches (both seventeen times) were the most frequently selected variables, followed by mean forest nearest neighbor (thirteen times), forest cover (twelve times) and landscape shape index (five times) (Table S5).

#### *Phylogenetic structure*

For phylogenetic structure (sesPD, sesMPD and sesMNTD), our best models ( $\Delta AICc = 0$ ) were null models (Table 1). Considering the two models with values  $\Delta AICc < 2$  selected for sesPD, mean forest nearest neighbor was present in one model (Table 1). For sesMPD, five models were selected with values  $\Delta AICc < 2$  (Table 1), with edge density (three times) the most frequently selected variable, followed by number of forest patches (two times), landscape shape index and forest cover (both one time). For sesMNTD, we had two models with values  $\Delta AICc < 2$ , with edge density occurred in one model (Table 1). Finally, considering all 41 selected models, edge density and number of forest patches (both eighteen times) were the most frequently selected variables, with mean forest nearest neighbor (fourteen times), forest cover (eleven times) and landscape shape index (five times) (Table S6).

### **Impacts of fragment size and edge-effects on phylogenetic diversity**

#### *Phylogenetic diversity*

Considering our best model ( $\Delta AICc = 0$ , Table 2), phylogenetic diversity (PD) was significantly affected by the interaction between fragment size and fragment interior versus edge (GLMM:  $t = -3.470$ ,  $P = 0.004$ , Fig. 3a): with increasing fragment size, we

found a significant reduction of PD in interiors ( $F = 6.685$ ,  $P < 0.027$ , Fig. 3a), but no significant change of PD at edges ( $F = 2.530$ ,  $P = 0.142$ , Fig. 3a). PD was significantly greater in fragment interiors than fragment edges (GLMM:  $t = 3.773$ ,  $P = 0.002$ , Fig. 3b). Our best model ( $\Delta AICc=0$ ) of the effect of forest patch size and habitat on MPD was the null model (Table 2). For MNTD, our best model ( $\Delta AICc=0$ ) was composed of forest patch size and edge-interior habitats. However, there was only marginal evidence that forest patch size (GLMM:  $t = -1.941$ ,  $P = 0.064$ ) or edge-interior habitat (GLMM:  $t = 1.944$ ,  $P = 0.063$ ) altered MNTD.

Considering the three models with values  $\Delta AICc < 2$  selected for PD, edge-interior habitat was present in two models and forest patch size in one (Table 2). Two models were selected for MPD with values  $\Delta AICc < 2$ , with habitat type present in one model (Table 2). For MNTD, we found four models with values  $\Delta AICc < 2$ , with forest patch size and type of habitat present in two models (Table 2). Lastly, considering all thirteen selected models for the three responses variables of phylogenetic diversity (Table S7), forest patch size (seven times) was the most frequently selected variable, with habitat (six times) also frequently selected.

#### *Phylogenetic structure*

We found no significant interaction effects between fragment size and interior versus edge location for any of the phylogenetic diversity metrics standardized for species richness (Table 2). According to our best model ( $\Delta AICc=0$ ), sesMNTD was affected by fragment size and edge-interior: increasing forest patch size led to a significant reduction of sesMNTD (GLMM:  $t = -2.903$ ,  $P = 0.007$ , Fig. 3c), while sesMNTD was significantly greater in fragment interiors than edges (GLMM:  $t = 3.154$ ,  $P = 0.004$ , Fig. 3d). Our best model ( $\Delta AICc=0$ ) indicated that forest patch size and edge-interior habitat do not significantly alter sesPD (Table 2). For sesMPD, our best model ( $\Delta AICc=0$ , Table 2) included habitat type, but this was marginally non-significant (GLMM:  $t = 1.905$ ,  $P = 0.081$ ). In terms models selected with value  $\Delta AICc < 2$  (Table 2), the only model selected for sesPD was the null model (Table 2), two models were selected for sesMPD and habitat type occurred in one model (Table 2), and for

sesMNTD, a single model contained forest patch size and edge-interior habitat (Table 2). Lastly, considering all twelve selected models (Table S8), habitat type (seven times) was the most frequently selected variable, followed by forest patch size (five times).

## Discussion

Forest fragmentation is a major driver of the global extinction crisis (Haddad *et al.* 2015; Lewis, Edwards & Galbraith 2015). A key question is how the degree of isolation and shape of landscapes impacts phylogenetic diversity. Saving phylogenetic diversity prevents the loss of evolutionarily unique species (Purvis *et al.* 2000; Vamosi & Wilson 2008), conserves as much of the tree of life as possible (Mace, Gittleman & Purvis 2003; Redding & Mooers 2006) and underpins the retention of key ecosystem services and functions (Cadotte, Cardinale & Oakley 2008; Cadotte 2013). Here, we found that with increasing edge density, there was an increase in the average phylogenetic distance between all combinations of pairs of individuals (MPD), whereas with increased numbers of forest patches in the landscape (i.e., more landscape fragmentation), MPD was reduced. However, we did not find impacts of landscape configuration (i.e., shape, isolation and edge density) and composition (i.e., forest cover and number of forest patches) characteristics on standardized values for species richness (sesPD, sesMPD and sesMNTD, phylogenetic structure), suggesting that highly fragmented landscapes are still able to retain important phylogenetic diversity (also see Arroyo-Rodríguez *et al.* 2012).

### Impacts of landscape configuration and composition on phylogenetic diversity

Our results show that edge density and number of forest patches most frequently affect the phylogenetic diversity and structure of remaining tree assemblages, and thus that these metrics are most relevant in understanding the effects of deforestation and habitat fragmentation on phylogenetic diversity. However, best models suggest that only mean pairwise distance (MPD) was affected significantly and thus that edge density and number of forest patch effects were caused by differences in species richness (Coronado *et al.* 2015; Prescott *et al.* 2016). Considering the negative effects of edge

on species richness (Magnago *et al.* 2014), the increase of MPD in landscapes with high edge density was unexpected. One possibility is that edge density is directly related to the complexity in fragment shape (McGarigal, Cushman & Ene 2012; Carrara *et al.* 2015), which increases the interchange of individuals of species from less compact fragments (Ewers & Didham, 2006), leading to changes in species composition (Hill & Curran 2003). However, a study investigating the effect of shape irregularity in fragmented landscapes on the phylogenetic diversity of bats in Costa Rica (Cisneros, Fagan & Willig 2015a) demonstrated a reduction of PD with increased irregularity of fragments (i.e., higher edge effect), suggesting that so far there is no consensus on the effect of complexity in fragment shape on phylogenetic diversity.

In terms of the effect of landscape composition, we found that increasing the number of forest patches (i.e., more fragmentation) led to a reduction of MPD. This reinforces evidence that increasing landscape fragmentation in tropical forests promotes negative effects on the phylogenetic diversity of tree species (Munguía-Rosas *et al.* 2014), as well as negative effects on tree species richness via reduced fragment size (Laurance *et al.* 2011) and tree functional diversity via size and edge effects (Magnago *et al.* 2014).

We found no effect of landscape metrics of configuration and composition on the phylogenetic diversity metrics corrected for species richness (sesPD, sesMPD and sesMNTD). This suggests that any loss of trees in recently fragmented tropical forest landscapes (i.e., <100 years) occurs randomly or uniformly across the phylogenetic tree, supporting our hypothesis that losses are not clustered within specific lineages (Santos *et al.* 2010; Arroyo-Rodrigues *et al.* 2012). However, in the Yucatan Peninsula, Mexico, much older fragmentation (~1,700 years) has reduced phylogenetic diversity (Munguía-Rosas *et al.* 2014), suggesting that our findings should be interpreted with caution when considering very long-term conservation value and further studies should focus on different taxonomic groups and the phylogenetic signal of functional traits vulnerable to fragmentation processes in trees (Cisneros, Fagan & Willig 2015a).

## Impacts of fragment size and edge-effects on phylogenetic diversity

PD was lower in the interior of larger fragments (Fig. 3a), a result that is driven by species richness (no effect on sesPD; Table 2). One explanation of high PD values inside small fragments is that there is a spill-over of individuals of species from the fragment edges (Hill & Curran 2003) and non-forest matrix (Cook *et al.* 2002; Cisneros, Fagan & Willig 2015a) into the interior of small fragments. This suggests that small fragments still have high phylogenetic diversity of trees and thus high conservation value (Arroyo-Rodríguez *et al.* 2009; Magnago *et al.* 2014). In addition, we found lower PD at edges than interiors (Fig. 3b; Santos *et al.* 2010, but see Benítez-Malvido *et al.* 2014). In our fragments, edge effects change microclimatic conditions (Magnago *et al.* 2015a), reduce species richness (see also Laurance *et al.* 2006) and alter functionality (Magnago *et al.* 2014). Thus, while reductions in species richness in part explain the loss of PD, changes in PD are also likely underpinned by other environmental and ecological factors.

The lack of significant effects of fragment size or edge effects on the average number of years of evolutionary history separating individuals of species in a community (MPD) and its respective standardized value (sesMPD) suggests that the changes in the species composition and species richness in our fragments (see Magnago *et al.* 2014) may have resulted from replacing species randomly or uniformly throughout the phylogenetic tree, but not altering entire clades. Also, this result supports the hypothesis of low phylogenetic conservatism in functional traits vulnerable to fragmentation processes in landscapes with a recent history of fragmentation (i.e., <100 years) (see also Santos *et al.* 2010; Arroyo-Rodríguez *et al.* 2012).

The standardized value of phylogenetic distance between each individual and its nearest phylogenetic neighbour (sesMNTD), increased with decreasing fragment size, regardless of the habitat type (edge vs. interior). A possible explanation is that smaller fragments and edges have strong change in species composition and abundances (see Magnago *et al.* 2014), making the remaining species community more likely to have

evolved from lineages at more terminal parts of the phylogenetic tree (i.e., intra-family or intra-genera levels).

Lastly, we found less sesMNTD and thus phylogenetic clustering at edges than interiors (Fig. 3d). Because edge effects reduce species richness, community dissimilarity (Laurance *et al.* 2006) and important functional groups (Lopes *et al.* 2009; Magnago *et al.* 2014), the next individual sampled is likely a close relative of at least one kind of individual already sampled (Vamosi *et al.* 2009). However, recent work in the Brazilian Atlantic forest (Santos *et al.* 2010) and Mexican dry forest (Benítez-Malvido *et al.* 2014) found no impact of edge effects on the phylogenetic structure of trees, suggesting that they were predominantly assembled by stochastic processes (Hubbell 2001). However, these results should be interpreted with caution, since other fragmented tropical regions showed a random pattern in the phylogenetic structure of trees following fragmentation and habitat loss effects (Santos *et al.* 2010; Arroyo-Rodríguez *et al.* 2012). Thus, so far, phylogenetic changes in tree species due to fragmentation do not show a consistent pattern across tropical forests.

### **Conclusions and conservation implications**

Impacts of anthropogenic-induced landscape changes are usually made measuring losses of the taxonomic dimension of biodiversity (i.e., species richness and species diversity; Fahrig 2003; Metzger 2000; Girão *et al.* 2007). To reach a more comprehensive framework for the conservation of biodiversity and resulting ecosystems services, it is critical to understand anthropogenic impacts at the functional and evolutionary levels (Santos *et al.* 2010; Arroyo-Rodríguez *et al.* 2012; Magnago *et al.* 2014; Cisneros, Fagan & Willig 2015a). Our results show that changes in phylogenetic diversity caused by landscape configuration and composition were, at some level, promoted by changes in species richness, since (i) observed changes in phylogenetic diversity were for MPD, which was significantly correlated with species richness, and (ii) standardised values of sesPD, sesMPD, and sesMNTD did not respond to any of the landscapes configuration and composition metrics. This supports the low conservatism

hypothesis of functional traits vulnerable to fragmentation processes (Santos *et al.* 2010; Arroyo-Rodríguez *et al.* 2012) and indicates that in recently fragmented landscapes, tree extirpation and compositional changes occurs randomly or evenly, and does not eliminate entire lineages (i.e., major phylogenetic clustering).

From a conservation perspective there are both negatives and positives of our results. On the negative side, edges retain lower MPD than interiors, while interior plots embedded within a highly fragmented matrix have lower MPD, indicating more phylogenetic clustering. This suggests that extirpation of species in edge habitats or in highly fragmented landscapes results in increasing dominance of species within a subset of clades, likely those adapted to disturbance (Magnago *et al.* 2014). To reverse such trends, it would be vital for conservation to extend forest cover via forest restoration to enhance patch area and connectivity in the highly threatened Brazilian Atlantic forest (Banks-Leite *et al.* 2014).

On the positive side, however, we found that interiors of smaller fragments are phylogenetically diverse and phylogenetically overdispersed in relation to larger fragments, which tend to be more phylogenetically clustered. Thus high phylogenetic diversity values are not always linked to high integrity of fragments, although this will likely reflect the invasion of species from the edge or matrix habitats into small fragment interiors. Pivotaly, therefore, even small forest patches in highly fragmented landscapes could be a major reservoir of phylogenetic diversity, and could represent important sources of seeds of evolutionarily distinct species for reforestation and restoration projects, as well as stepping-stones for dispersal between larger, viable patches.

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### Data Accessibility

Fragment x species abundance matrices, and GLM and GLMM input files: DRYAD entry doi:10.5061/dryad.fq988

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#### **Supplementary Materials:**

Text S1 – Supplementary methods: *Landscape structure*

Text S2 - Supplementary methods: *Standardized values*

Table S1 – Studies investigating fragmentation impacts on phylogenetic diversity and structure

Table S2 – Fragment details

Table S3 – Values of landscape configuration and composition metrics in study fragments

Table S4 – Correlations between landscape variables

Table S5 – Results of information-theoretic-based model selection for the impacts of landscape configuration and composition metrics on the phylogenetic diversity

Table S6 - Results of information-theoretic-based model selection for the impacts of landscape configuration and composition metrics on the phylogenetic structure

Table S7 – Results of generalized linear mixed models for fragment size and habitat impacts on phylogenetic diversity

Table S8 – Results of generalized linear mixed models for fragment size and habitat impacts on phylogenetic structure

Figure S1 – Phylogenetic tree of tree species sampled

Supplemental references

## Tables

Table 1 - Results of information-theoretic-based model selection for the impacts of landscape configuration and composition metrics on the phylogenetic diversity and phylogenetic structure. We present only the models with values of  $\Delta AICc < 2$ . PD = Phylogenetic diversity (millions of years); sesPD = Standardized value of phylogenetic diversity (PD); MPD = Mean phylogenetic distance (millions of years); sesMPD = Standardized value of MPD; MNTD = Mean nearest taxon phylogenetic distance (millions of years); and sesMNTD = Standardized value of MNTD. AICc = Akaike information criterion for small samples;  $\Delta AICc$  = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes).

Response variable	Model variables	AICc	$\Delta AICc$	AICcWt
PD	Null model	436.92	0	0.21
	Edge density+Forest cover	437.20	0.28	0.18
	Forest cover	438.19	1.26	0.11
	Edge density	438.35	1.42	0.10
sesPD	Null model	8.98	0	0.30
	Mean forest nearest neighbour	10.85	1.87	0.12
MPD	Edge density+Number of forest patches	192.71	0	0.25
	Null model	193.59	0.87	0.16
sesMPD	Null model	6.69	0	0.21
	Landscape shape index	7.27	0.58	0.15
	Edge density+Forest cover+Number of forest patches	7.66	0.97	0.13
	Edge density+Number of forest patches	8.19	1.50	0.10
	Edge density	8.45	1.76	0.09
MNTD	Null model	196.57	0	0.29
	Edge density	198.50	1.93	0.11
sesMNTD	Null model	11.96	0.00	0.29
	Edge density	13.73	1.77	0.12

Table 2 - Results of information-theoretic-based model selection for the impacts of fragment size and fragment location (edge vs. interior). We present only the models with values of  $\Delta AICc < 2$ . PD = Phylogenetic diversity (millions of years); sesPD = Standardized value of phylogenetic diversity (PD); MPD = Mean phylogenetic distance (millions of years); sesMPD = Standardized value of MPD; MNTD = Mean nearest taxon phylogenetic distance (millions of years); and sesMNTD = Standardized value of MNTD. AICc = Akaike information criterion for small samples;  $\Delta AICc$  = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). Habitats = edge vs. interior.

Response variable	Model variables	AICc	$\Delta AICc$	AICcWt
PD	Forest patch size+Habitats+Forest patch size:Habitats	362.90	0	0.39
	Null model	363.20	0.28	0.34
	Habitats	364.90	1.94	0.15
sesPD	Null model	14.50	0	0.66
MPD	Null model	164.40	0	0.54
	Habitats	165.90	1.46	0.26
sesMPD	Habitats	-5.10	0	0.43
	Null model	-4.90	0.26	0.38
MNTD	Forest patch size+Habitats	171.10	0	0.28
	Habitats	171.40	0.27	0.25
	Forest patch size	171.50	0.28	0.25
	Null model	171.60	0.43	0.23
sesMNTD	Forest patch size+Habitats	3.70	0	0.81

**Figures (high resolution files attached separately)**

Fig. 1 - Study area and forest fragments sampled in the Brazilian Atlantic Forest. Size of each fragment and their coordinates can be seen in Table S2.

Fig. 2 - Effect of edge density (a) and number of forest patches (b) on the average number of years of evolutionary history separating species in a community (mean phylogenetic distance-MPD), analyzed in 28 transects sampled in the Brazilian Atlantic forest. Values were obtained after the summation of the raw residuals with the expected values for variable (y), assuming average value for the variable (partial residuals plots).

Fig. 3 - Relationship between fragment area and location (i.e., edge vs. interior) with phylogenetic diversity and structure, sampled in 24 transects of the Atlantic forest. (a) The effect of the interaction between fragment size and habitat type (interior: continuous line vs edge: dashed line) on phylogenetic diversity PD, partial residuals plots; (b) the effect of habitat on PD; (c) the effect of fragment size on standardized mean nearest taxon distance (sesMNTD), partial residuals plots; and (d) the effect of habitat type on standardized mean nearest taxon distance (sesMNTD). Circles (a) and (c) represent values obtained after summation of raw residuals with the expected values for each variable, assuming average values for other covariates; errors bars represent standard errors.





