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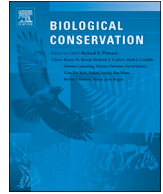
Indirect effects of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species

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A R T I C L E I N F O

A B S T R A C T

Recent studies suggest that habitat amount is the main determinant of species richness, whereas habitat fragmentation has weak and mostly positive effects. Here, we challenge these ideas using a multi-taxa database including 2230 estimates of forest-dependent species richness from 1097 sampling sites across the Brazilian Atlantic Forest biodiversity hotspot. We used a structural equation modeling approach, accounting not only for direct effects of habitat loss, but also for its indirect effects (via habitat fragmentation), on the richness of forest-dependent species. We reveal that in addition to the effects of habitat loss, habitat fragmentation has negative impacts on animal species richness at intermediate (30–60%) levels of habitat amount, and on richness of plants at high (> 60%) levels of habitat amount, both of which are mediated by edge effects. Based on these results, we argue that dismissing habitat fragmentation as a powerful force driving species extinction in tropical forest landscapes is premature and unsafe.

1. Introduction

Habitat loss is the main cause of ongoing worldwide biodiversity loss (Maxwell et al., 2016), yet the effects of habitat fragmentation (i.e., the breaking apart of habitat leading to changes in its spatial configuration) on biodiversity are still a source of intense debate (Miller-Rushing et al., 2019). While some studies challenge the assumption of negative impacts of habitat fragmentation on biodiversity (Fahrig, 2013, 2017, 2019; Fahrig et al., 2019), others argue that habitat fragmentation is relevant for local species extinction (Hanski, 2015; Fletcher Jr. et al., 2018). However, despite the relevance of the subject for predicting and managing ecological patterns and processes in fragmented landscapes (Ewers and Didham, 2006; Fletcher Jr. et al., 2018), standardized, large scale, cross-taxa analyses of the effects of habitat fragmentation are still lacking.

In a seminal review, Fahrig (2003) called attention to the fact that habitat loss and habitat fragmentation are two different processes, suggesting that habitat loss has a greater negative effect on biodiversity than habitat fragmentation. This idea was later conceptualized with the "Habitat Amount Hypothesis" (HAH, Fahrig, 2013), which postulates that the amount of habitat in a landscape is the main determinant of species richness, irrespective of habitat configuration or fragmentation. Among the many studies attempting to isolate the "independent" effects of habitat loss and fragmentation (i.e., fragmentation per se), several confirmed that habitat loss has stronger negative effects on biodiversity than fragmentation per se (e.g., Trzcinski et al., 1999; Cushman and McGarigal, 2003; Ferraz et al., 2007; Uezu and Metzger, 2011; De Camargo et al., 2018). However, numerous studies likewise found strong negative impacts of habitat fragmentation per se on biodiversity, regardless of whether fragmentation was measured as the number of patches (e.g., Robertson et al., 2013; Cooper and Walters, 2002), edge density (e.g., Cushman and McGarigal, 2003; Peak and Thompson, 2013), or mean patch size (e.g., Grossman et al., 2008). Similarly, the HAH (Fahrig, 2013) has been both supported (Melo et al., 2017; Rabelo et al., 2017; Seibold et al., 2017; Vieira et al., 2018) and refuted (Haddad et al., 2017; Lindgren and Cousins, 2017; Torrenta and Villard, 2017). Moreover, a recent review extended previous ideas to propose that effects of habitat fragmentation per se on biodiversity are not only weak but mostly positive (Fahrig, 2017). Nevertheless, both the approach used (i.e., count of positive/negative responses) and the conclusions reached in this review have been questioned (Fletcher Jr. et al., 2018).

Conflicting results regarding the effects of habitat fragmentation may arise from the lack of consideration of the interdependence between habitat loss and fragmentation processes, habitat loss is the primary process causing habitat fragmentation in real landscapes. Therefore, trying to determine "independent" effects of habitat loss and fragmentation has been considered conceptually flawed, as they are hierarchically linked (Didham et al., 2012; Ruffell et al., 2016; Fletcher Jr. et al., 2018; Morante-Filho et al., 2018). This critique implies that the common statistical approach of controlling the variance explained by habitat amount and then attributing the remaining variance to
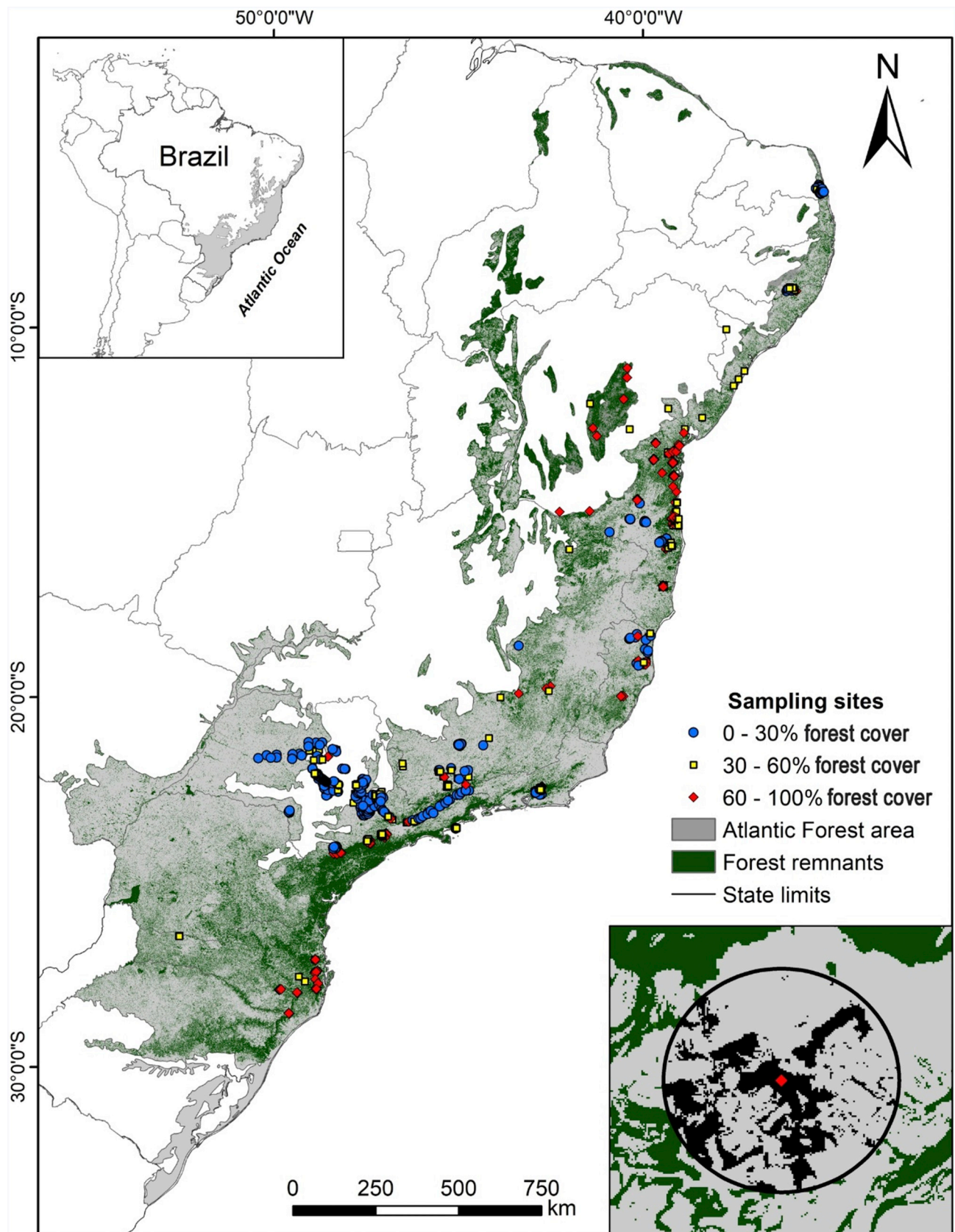
Fig. 1. Spatial distribution of 1097 sampling sites in the Atlantic Forest. The shaded area represents the original extension of the Atlantic Forest, while current forest fragments are shown in green. Lines are state limits. Symbols are sampling sites with < 30% (blue circles), 30–60% (yellow squares), or > 60% (red diamonds) of forest cover in the surrounding landscape (circular buffer area with 2 km radius). The detail in the lower right is an example of the landscape surrounding a sampling site, forest remnants included in the calculation of forest cover shown in black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

habitat fragmentation (which was adopted in 72% of the studies included in Fahrig, 2017) might be inappropriate to unravel the relative importance and the direction of effects of habitat loss and fragmentation on biodiversity (Didham and Ewers, 2012; Ruffell et al., 2016).

Another common simplification is the assumption that the effects of habitat loss and fragmentation on biodiversity are linear along the entire gradient of habitat amount (Villard and Metzger, 2014). However, relationships between habitat amount and fragmentation metrics are known to be nonlinear. For example, at low overall levels of landscape-wide habitat amount (e.g., < 30%), number of patches as well as edge density increase with increasing landscape-wide habitat amount, while both metrics decrease with increasing habitat amount at high levels of landscape-wide habitat amount (e.g., > 60%, Fahrig, 2003; Villard and Metzger, 2014). Therefore, changes in the direction as well as in the strength of biodiversity response to habitat loss and fragmentation along the gradient of habitat amount could simply result from this nonlinear relationship between metrics.

Indeed, evidence exists that effects of patch size and isolation vary along the gradient of habitat amount and should be especially strong at either low (< 30%, Andrén, 1994) or intermediate levels of habitat amount (~30%, Pardini et al., 2010, Villard and Metzger, 2014). Below ~30% of habitat amount, unproportioned biodiversity loss is supposed to be caused by an exponential increase of inter-fragment distances (Andrén, 1994; Fahrig, 2003), which is supported by a variety of studies on species richness (e.g., Andrén, 1994; Pardini et al., 2010), community dissimilarity (e.g., Banks-Leite et al., 2014; Püttker et al., 2015), and population parameters (e.g., Püttker et al., 2011, 2013). Between 20% and 50% of habitat amount, habitat fragmentation effects on species richness are assumed to be more likely due to the greater potential variability in habitat configuration compared to landscapes with either high or low amount of habitat (Villard and Metzger, 2014). Finally, above a certain level of habitat amount (~60%), habitat loss and fragmentation effects are no longer expected, given the low variability in landscape configuration (Villard and Metzger, 2014) and high percolation of landscapes (Stauffer and Aharony, 1992), resulting in well-connected habitat patches forming a continuous cluster (Gardner et al., 1987; With and Crist, 1995).

Here, we test for the strength and direction of the effects of habitat amount and fragmentation on biodiversity by confronting a structural equation model embodying these hierarchical and nonlinear relationships with a comprehensive, multi-taxa database including 2230 estimates of forest-dependent species richness, obtained at 1097 different sampling sites throughout the Atlantic Forest, a top-ranked biodiversity hotspot (Mittermeier et al., 2004; Laurance, 2009). We quantify the direction and magnitude of (1) direct and indirect effects of habitat amount and (2) direct effects of habitat fragmentation on forest-dependent species richness over the entire gradient of habitat amount as well as separately for landscapes with low (< 30%), intermediate (30–60%) and high (> 60%) levels of habitat amount. We test for two different drivers of fragmentation effects on richness by comparing the two most commonly used metrics of habitat fragmentation (number of patches and edge density), each of which is linked to different ecological processes (McGarigal et al., 2012; Wang et al., 2014). We expect to find negative effects of habitat fragmentation on biodiversity, especially within landscapes with low and/or intermediate levels of habitat amount (Andrén, 1994; Fahrig, 2003; Villard and Metzger, 2014).

2. Methods

2.1. Data compilation

2.1.1. Compilation of species richness estimates
Since 2016 the "Synthesis in Atlantic Forest Ecology and Sustainability Group" (SES-MA in Portuguese acronym) has been building a network of researchers to compile primary and high-quality empirical datasets for biodiversity obtained within the Brazilian

Atlantic Forest. All datasets included in our database were carefully selected to meet two main criteria, which allowed a robust assessment of habitat amount and fragmentation effects on biodiversity. First, each dataset included at least eight forest sampling sites for the same taxonomic group in the same study area, sampled at the same time period using standardized methods, therefore resulting in directly comparable estimates of species richness among sites (e.g., Vieira et al., 2018). Second, each dataset contained samples taken at forest sites within fragmented landscapes, i.e., datasets collected exclusively in large stretches of continuous forests were not included, as habitat amount and configuration vary little in those. No limitations were established regarding the taxonomic group studied, which led to a unique, broad cross-taxa database, including vertebrates (amphibians, reptiles, birds, non-volant mammals, and bats), invertebrates (spiders, harvestman, beetles, butterflies, termites, bees, ants, and other insects), and plants (bryophytes, pteridophytes and higher plants, Table A1 in supplementary material). Datasets of different taxonomic groups sampled in the same area were considered as separate datasets in the analyses, due to differences in sampling methods.

We used species richness as surrogate for biodiversity, because it is a simple and synthetic measure that has been used in several studies to infer ecological processes in fragmented landscapes (e.g., Haddad et al., 2017; Melo et al., 2017; Vieira et al., 2018), facilitating comparisons of our results with the literature. However, we restricted the analyses to forest-dependent species only, as our definition of habitat applies to forest formations (see below), making inferences on effects of habitat fragmentation conditional on the group of species dependent on this type of habitat (Fahrig, 2013). Thus, unlike overall species richness, which may obscure ecological patterns by combining generalist and specialist species (e.g., Banks-Leite et al. 2012, Morante-Filho et al., 2016), forest-dependent species richness combines species richness and composition into a single metric, focusing on the species of higher conservation concern, and which should be more strongly affected by forest loss and fragmentation (Pardini et al., 2010; Betts et al., 2014; Almeida-Gomes et al., 2016). Decisions regarding the classification of species as forest-dependent were made a priori by the primary researchers responsible for each dataset, thus using the best biological knowledge available for each taxonomic group.

Our database thus contains a total of 59 datasets, which include 2230 estimates of species richness collected at 1097 sampling sites that were widely distributed across the Atlantic Forest (Fig. 1). Additional to the analyses including overall forest-dependent species richness, we analyzed the data separately for the groups of flora and fauna in order to reveal potential differences in responses among groups of species. We did not include analyses of more specific subsamples (e.g., vertebrates, invertebrates) because we were interested in the overall biodiversity response to habitat loss and fragmentation. Furthermore, a more specific subsampling would cause data deficiency for some groups (e.g., invertebrates).

2.1.2. Extraction of landscape metrics
In order to evaluate the effects of habitat loss and fragmentation, we adopted the concept of a local landscape provided by Fahrig (2013), i.e. a circular landscape centered on each sampling site. For all sampling sites, we defined local landscapes of varying extents in order to be able to define the scale of effect (see Data analyses and Text A1). We calculated three landscape metrics at each sampling site and each extent of the landscape: 1) percentage of forest cover (hereafter, forest cover), 2) number of patches, and 3) edge density, calculated as the total length of forest edge divided by landscape size. We relied on the number of patches, because, as pointed out by Fahrig (2019), this metric is directly linked to the definition of habitat fragmentation (i.e., habitat is more fragmented if broken into a larger number of patches). However, habitat fragmentation effects can also be due to edge effects (i.e., increase in fragmentation leads to more edges), which can be estimated via edge density (McGarigal et al., 2012; Wang et al., 2014; Fahrig, 2017).

Number of patches and edge density are also the most commonly used metrics to quantify habitat fragmentation (Fahrig, 2017). Moreover, they are simple and interpretable, and are clearly linked to distinct ecological processes associated with habitat fragmentation, either the subdivision of habitat (McGarigal et al., 2012) or edge effects. In contrast, patch isolation metrics are associated with the amount of habitat surrounding patches (Fahrig, 2013) and thus have not been used to assess habitat fragmentation at the landscape level (see studies in Fahrig, 2017). We did not consider other variables that could potentially affect forest-dependent species richness, as our focus was on quantifying the magnitude and direction of habitat loss and fragmentation effects, rather than on explaining all sources of variability of forest-dependent species richness. However, our analysis controlled for potential variation in relevant variables across datasets, such as forest age or time since fragmentation, as we used mixed-effects modeling (see Data analysis).

Landscape metrics were measured based on an intermediate-resolution (30 m) map of the Atlantic Forest provided by MapBiomas (http://mapbiomas.org, collection 2.3). The definition of habitat was based on categories 3, 4, and 5, which correspond to native forest formation (including dense, open and mixed ombrophilous forest, semideciduous and deciduous seasonal forest, and pioneer formation, corresponding to 99.9% of forest area), and mangroves (corresponding to 0.1% of the forest area). All other land-use categories were classified as matrix. We relied on the map of 2011 because most studies collected data in that year (median year of sampling = 2011, 1st quantile = 2009, 3rd quantile = 2012, Fig. A1 in supplementary material). As between 1985 and 2017 the Brazilian Atlantic Forest lost < 2% of forest cover (http://mapbiomas.org), and additionally, most studies were conducted in 2011 ± 4 years (Fig. A1) no important effect of land cover change is expected between 2011 and other years. All metrics were measured using ArcGIS 10.6 (ESRI, 2018) and FRAGSTATS v4.2.1 (McGarigal et al., 2012).

2.2. Data analysis

We first transformed all variables to facilitate comparability of results (see details in Text A1, Fig. A2 in supplementary material). Second, we used model selection to define the size (extent) of the landscape to measure landscape metrics, because the extent to which landscape metrics best predict forest-dependent species richness (i.e., the "scale of effect", Jackson and Fahrig, 2015) was unknown a priori. Depending on the database (all, flora or fauna) and habitat fragmentation metric, a radius of 2 km or 1.8 km was selected for the analyses as the scale of effect (Tables A2, A3). We then defined the most likely (if any) spatial autocorrelation function to control for spatial correlation among sampling sites within the same study area/dataset (Table A2, Text A1, Fig. A2b). To check for possible pseudo-replication caused by large overlap among neighboring landscapes, we calculated the distances between all pairs of sampling sites within each dataset. We observed that only 4.2% of these distances were below 2 km, and 91% of all landscape-pairs showed no overlap at all. Additionally, close pairs of sampling sites (i.e. with low distances between them) were highly spread across the different datasets (Fig. A3). We therefore considered that pseudo-replication was low and negligible.

To assess the direct and indirect (via habitat fragmentation) effects of habitat loss, our general structural equation model was formulated as a combination of two coupled Linear Mixed Effects Models (LMMs): one for predicting species richness and one for predicting habitat fragmentation (Fig. A2c). LMMs predicting species richness included forest cover, one of the two habitat fragmentation metrics, and sampling effort as fixed explanatory factors. Both forest cover and the habitat fragmentation metric were also considered as random slopes to account for potential differences in direction and magnitude of effects on forest-dependent richness across datasets. Because number of patches and edge density were correlated (r_s = 0.28, df = 2228, P < 0.0001),

increasing the variance of estimates (Zuur et al., 2009; Ruffell et al., 2016), we considered habitat fragmentation metrics separately in different analyses. By including both forest cover and the fragmentation metric in the models, we were able to estimate the independent effect of each variable while controlling for the other one (Smith et al., 2009). Indeed, multiple regression to control for habitat amount when estimating fragmentation effects is the most commonly applied method in studies investigating independent effects of both variables (see Fahrig, 2017), and proved to be the statistical method providing most reliable estimates when compared to other methods (Smith et al., 2009).

LMMs predicting habitat fragmentation included forest cover as both fixed factor and random slope for the same reason stated above. In addition, all LMMs (both explaining richness and habitat fragmentation) included the dataset ID (1 to 59) as a random intercept to account for dependence within datasets related to spatial proximity, applied field methods, surveyed taxonomic group, landscape or forest history, among others. For each of the three different databases (overall richness of forest-dependent species, richness of forest-dependent plants [flora], and richness of forest-dependent animals [fauna]), we ran eight structural equation models, which differed in the habitat fragmentation metric included (four including number of patches and four including edge density), and in the gradient of forest cover under consideration (0–100, < 30, 30–60, > 60%).

We first applied the structural equation model to the database spanning the entire gradient of habitat amount (0–100%). We then analyzed the data within three different levels of habitat amount (< 30%, 30–60%, and > 60%) to test whether the magnitude and/or direction of the effects of habitat loss and fragmentation vary across levels of habitat amount (Andrén, 1994; Fahrig, 2003; Villard and Metzger, 2014). Databases for different levels of habitat amount were built by retaining only sampling sites that fulfilled the respective condition defined by the interval of habitat amount at the predefined spatial extent of the landscape. Subsequently, we filtered the data excluding datasets with less than five remaining sampling sites to preserve a minimum statistical power. This resulted in varying numbers of sampling sites and datasets included across the 24 different databases (i.e., combinations of species group, levels of habitat amount and habitat fragmentation measures, Table A2).

Importantly, of all 24 analyses, the quadratic term linking forest cover and the fragmentation metric (number of patches or edge density) was only included in the six models applied to the entire gradient of habitat amount. This term was dropped in analyses related to different levels of habitat amount (< 30%, 30–60%, and > 60%), as the relations between forest cover and habitat fragmentation metrics approached linearity (Fig. A4).

The global fit of each structural equation model was evaluated with Fisher's C statistic, which is adequate for mixed-effect models (Shipley, 2000, 2009). The coefficients of each path model were then extracted to estimate path coefficients, which indicated the direct and indirect effects of forest cover and each habitat fragmentation metric on species richness. To calculate the indirect effect of forest cover on species richness, we multiplied the path coefficient linking forest cover to the fragmentation metric, and the path coefficient linking habitat fragmentation to species richness (Grace, 2006). Total effects of forest cover were calculated by summing the direct and indirect effects. Total and indirect effects were calculated when analyzing databases within the three levels of habitat amount (< 30, 30–60, or > 60%), but not for the analyses based on the entire gradient of habitat amount (0–100%) given the strongly non-linear relationship between forest cover and each fragmentation metric (Fig. A4). All analyses were conducted in R-environment, ver. 2.15.0 (R Core Team, 2016).

3. Results

Overall, structural equation models fitted the data considerably well (of 24 analyses, all but three Fisher's $P \geq 0.1$, Figs. 2, 3, A5, A6). When

relying on the databases spanning the entire gradient of habitat amount (0–100%), estimates of the direct effects of both forest cover and habitat fragmentation on species richness were similar among models including different habitat fragmentation metrics, regardless of the species group considered (Figs. 2, A5). However, when different levels of habitat amount were considered (< 30, 30–60 and > 60%), these effects varied across levels, habitat fragmentation metrics, and groups of species (Figs. 3, A6).

3.1. Entire gradient of habitat amount

Considering the entire gradient of habitat amount, the direct effect of forest cover was the main determinant of species richness, with a positive and significant coefficient, regardless the habitat fragmentation metric or species group included (Figs. 2, A5). Conversely, both number of patches and edge density had a non-significant effect on species richness. Expectedly, the relationship between forest cover and either number of patches or edge density was bell-shaped as indicated by the significantly negative coefficients linking the quadratic function of forest cover to each variable (Figs. 2, A5).

3.2. Different levels of habitat amount

When considering number of patches as habitat fragmentation metric, forest cover proved to have a significantly positive effect on species richness only in landscapes with < 30% forest cover (Figs. 3a, A6.1a). Number of patches did not have a significant effect on richness in any of the three levels of habitat amount, regardless of the species group included (Figs. 3a–c, A6.1a–c, A6.2a–c), although plant species richness showed a strong trend to be negatively affected at highly forested landscapes (Fig. A6.1c). However, the effect of forest cover on number of patches was strong at all three levels of total habitat amount but varied in direction in accordance with the bell-shaped relationship between these variables (Fig. A3): positive in landscapes with low habitat amount (< 30%, Figs. 3a, A6.1a, A6.2a), but negative in landscapes with intermediate (30–60%, Figs. 3b, A6.1b, A6.2b) and high

(> 60%, Fig. 3c, A6.1c, A6.2b) habitat amount. The indirect effect of forest cover on richness via number of patches was comparatively small and mostly positive.

Considering edge density as the habitat fragmentation metric and flora and fauna combined, forest cover had a significantly positive direct effect on overall species richness in landscapes with both low and intermediate habitat amount (Fig. 3d, e) but was unimportant in landscapes with high habitat amount (Fig. 3f). Separate analyses of flora and fauna revealed that the positive effect of forest cover at landscapes with low habitat amount was driven by plant species richness (Fig. A6.1d), while its positive effect at intermediately forested landscapes was driven by animal species richness (Fig. A6.2e). Edge density had a negative effect on overall species richness, particularly in landscapes with intermediate habitat amount, but also in landscapes with high habitat amount (Fig. 3e, f). In fact, the effect of edge density on overall species richness in these landscapes was stronger than the effect of forest cover. Again, separate analyses showed distinct responses of flora and fauna: the relationship of edge density and plant species richness was significantly negative at high forested landscapes exclusively (Fig. A6.1f), while edge density had a negative effect on animal species richness only at intermediately forested landscapes (Fig. A6.2e). The effect of forest cover on edge density was strong and variable among levels of habitat amount regardless of the species group considered, in accordance with the bell-shaped relationship between these variables: while it was significantly positive considering both low and intermediate levels of habitat amount (Figs. 3d-e, A6.1d,e, A6.2d,e), it was significantly negative in landscapes with high habitat amount (Figs. 3f, A6.1f, A6.2f). The indirect effects of forest cover on richness via edge density were negative at low and intermediate habitat amount, but positive at high habitat amount.

4. Discussion

Our results reinforce the notion that habitat loss has strong negative impacts on species richness of forest-dependent species (Fahrig, 2003; Fahrig, 2013). However, they do not support the claim that the effects
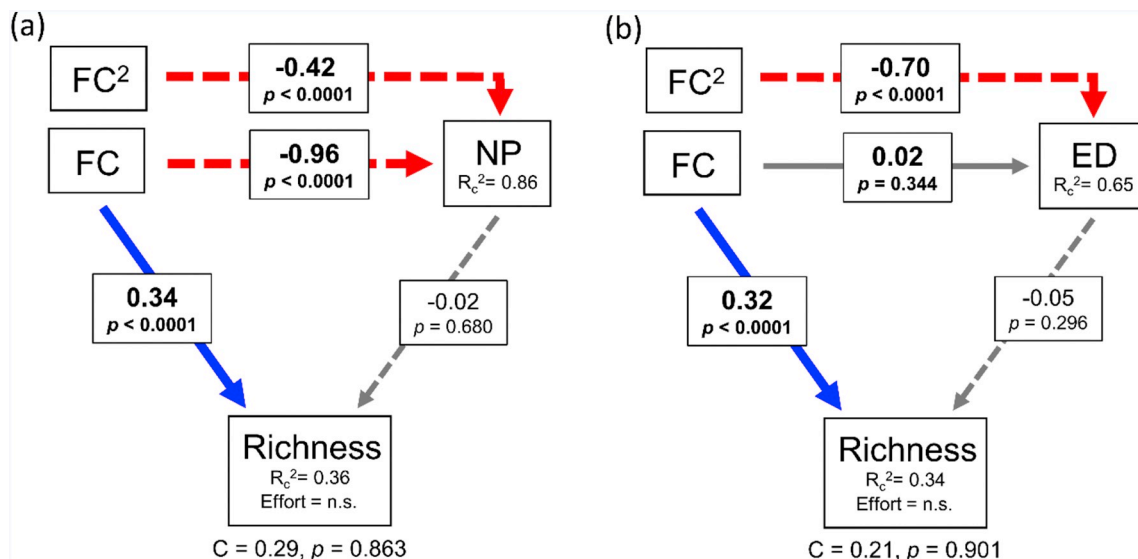
Fig. 2. Path diagram representing the path model investigating the effects of habitat amount, measured as forest cover (FC and FC as a quadratic function), and (a) number of patches (NP) or (b) edge density (ED) on overall species richness (Richness), considering vertebrates (amphibians, reptiles, birds, non-volant mammals, and bats), invertebrates (spiders, harvestman, beetles, butterflies, termites, bees, ants, and other insects), and plants (bryophytes, pteridophytes and higher plants). Arrows represent unidirectional relationships among variables. Colored arrows are either positive (blue) or negative (red) significant relationships ($p < 0.05$), grey lines are non-significant paths. Solid arrows depict positive influences, while dashed arrows represent negative relations. Standardized path coefficients are given in associated boxes together with corresponding p-values. Conditional R_c^2 for component models are given in boxes of response variables. The variable 'Effort' has been omitted for clarity, the corresponding standardized path coefficient is given instead in the box of the response (n.s. = not significant). The overall fit of the model to the data measured by Fisher's C is given below along with the corresponding p-value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
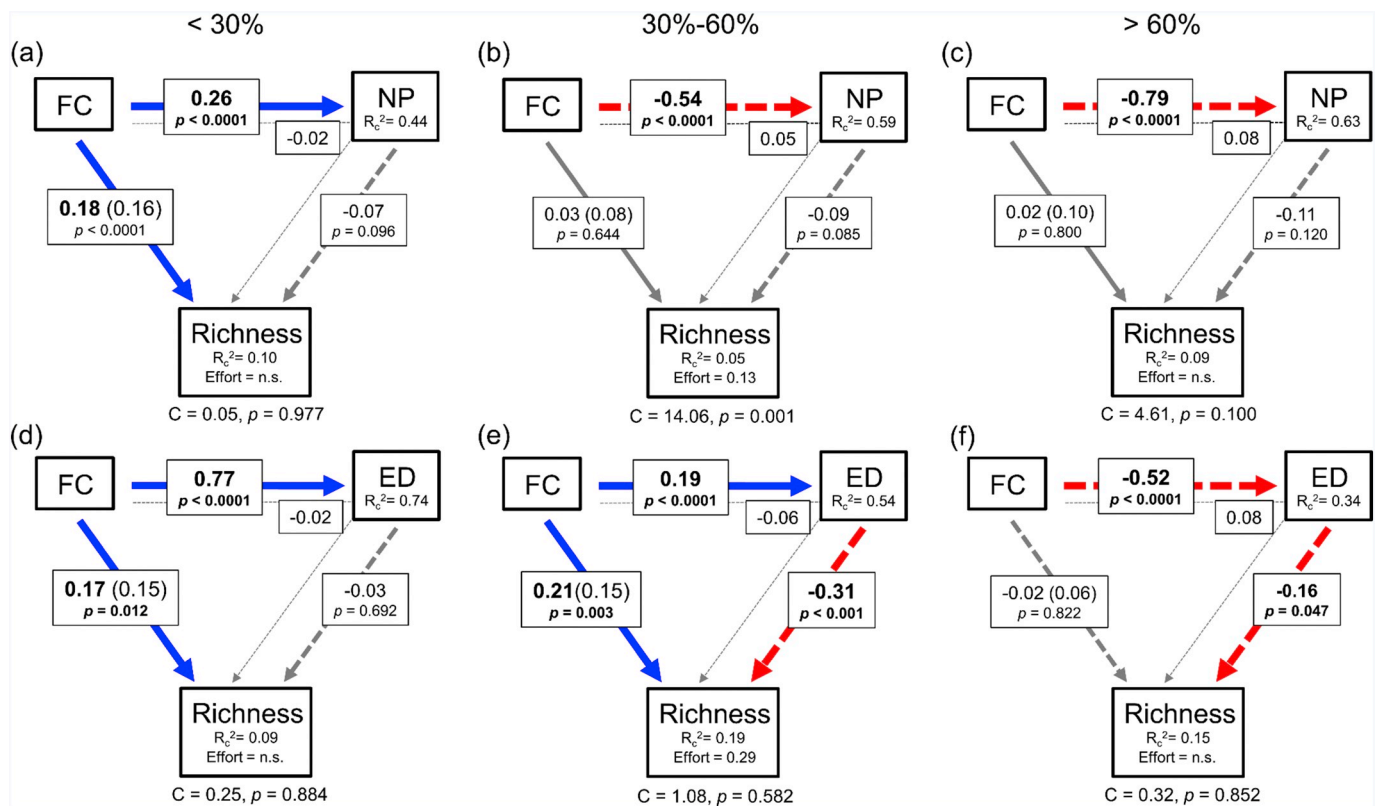
Fig. 3. Path diagram representing the structural equation model investigating the effects of habitat amount, measured as forest cover (FC), and number of patches (NP) or edge density (ED), on overall species richness (Richness) at landscapes with (a) and (d) low (< 30%), (b) and (e) intermediate (30–60%), and (c) and (f) high (> 60%) habitat amount. Arrows represent unidirectional relationships among variables. Colored arrows are either positive (blue) or negative (red) significant direct relationships ($p < 0.05$), grey lines are non-significant paths. Solid arrows depict positive influences, while dashed arrows represent negative relations. The dotted arrows represent indirect effects of FC on richness. Standardized coefficients are given in associated boxes together with corresponding *p*-values. The box quantifying the effect of FC on richness shows the direct and the total effect after considering the indirect effect via fragmentation metric (value in parenthesis). Conditional R_c^2 for component models are given in boxes of response variables. The variable 'Effort' has been omitted for clarity, instead the corresponding standardized path coefficient is given in the box of the response (n.s. = not significant). The overall fit of the model to the data measured by Fisher's C is given below together with the corresponding p-value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of habitat fragmentation are predominantly positive (Fahrig, 2017, 2019). Negative habitat fragmentation effects were evident not only in landscapes with intermediate habitat amount but unexpectedly also in landscapes with high habitat amount. Thus, our findings do not support the hypothesis that habitat fragmentation effects are stronger in landscapes with low levels of habitat amount (< 30%, Andrén, 1994), but support the idea of stronger habitat fragmentation effects at intermediately forested landscapes (Pardini et al., 2010; Villard and Metzger, 2014). In addition, our analyses indicate that the ecological processes underlying habitat fragmentation effects are associated with edge-induced effects. Given that these results are based on a comprehensive database including a large number of species with very distinct life-history-traits across a large spatial extent, they provide robust evidence that (1) habitat loss has both direct and indirect effects on species richness, and (2) habitat fragmentation effects are negative and associated with the creation of edges, and can be as strong or even stronger than the direct effects of habitat loss in landscapes with intermediate and high amounts of habitat.

In general, our results confirm that habitat loss is an important predictor of species richness, in agreement with the habitat amount hypothesis (HAH, Fahrig, 2013). However, they highlight the variability in the strength of direct effects of habitat loss depending on the overall habitat amount at the landscape, as well as the species group considered. Significant direct effects of forest cover were only present at low and intermediate levels of habitat amount. Indeed, we expected no strong direct effects of forest cover in landscapes with high habitat amount, given the overall high habitat availability for species

(Crouzeilles et al., 2014) and the high connectivity and percolation of habitat (Gardner et al., 1987; With and Crist, 1995). This variability in the strength of habitat loss effects is not predicted by the HAH, which is a much simpler model considering a single direct path linking habitat amount and species richness. As HAH does not account for the interdependence of habitat amount and fragmentation, it assumes that effects on biodiversity across all levels of habitat amount are due to direct effects of habitat loss. As such, the HAH appears to be oversimplified.

More importantly, our findings contrast those of Fahrig (2017) and provide evidence that habitat fragmentation effects can be strong and negative. This discrepancy is likely due to a combination of factors. First, the way studies were classified into levels of overall habitat amount in the review of Fahrig (2017, by using the median habitat amount) does not necessarily mean that only landscapes with low, intermediate or high habitat amounts were considered within each level. Second, Fahrig (2017) considered the effects on particular groups of species by testing for any particular group at a time (for instance, considering separately specialist/threatened species, and tropical species), while we simultaneously considered a combination of conditions that are common in other ecosystems (i.e., forest-dependent species of several different taxa across a large tropical domain). Third, Fahrig (2017) considered different types of response variables, probably obscuring effects on richness. Finally, Fahrig (2017) counted significant effects of habitat fragmentation across heterogeneous studies while we reanalyzed data standardizing statistical procedures, making results comparable across original datasets. Our study thus provides strong empirical support for negative habitat fragmentation effects on the

richness of tropical forest-dependent species, which are modulated by the total amount of habitat in the landscape (Villard and Metzger, 2014). Our results thereby indicate that it is premature to dismiss the negative effects of habitat fragmentation altogether as a "zombie idea" (Fahrig, 2017), that is, a notion that persists despite repeated evidence to the contrary (Fletcher Jr. et al., 2018).

Based on theory and previous evidence, we expected to find negative effects of habitat fragmentation either at landscapes with intermediate habitat amounts, where the potential for variation in habitat configuration is greatest (Villard and Metzger, 2014), or at landscapes with low habitat amount, due to the exponential increase in the distance between habitat patches (Andrén, 1994). Given that we found effects of habitat fragmentation on animal species richness (and no effect on plants) at landscapes with intermediate habitat amount, our results suggest that distance among habitat patches is not the main factor modulating habitat fragmentation effects (Andrén, 1994; Pardini et al., 2010). Surprisingly, but congruent with the notion that inter-fragment distance is not the main factor increasing the relevance of habitat fragmentation effects, we found negative effects of fragmentation on plant species richness at landscapes with high habitat amount, indicating that landscape configuration effects – particularly edge effects – are relevant not only at intermediate but also highly forested landscapes.

Because we did not include a comprehensive number of habitat fragmentation metrics, general inferences must be made with caution. However, habitat fragmentation effects were observed mainly when considering edge density (rather than number of patches). Thus, our findings indicate that the ecological processes underlying the negative effects of habitat fragmentation on the richness of forest-dependent species are edge-induced. It is well-known that proximity to edges, especially in tropical forests, induces a series of abiotic and biotic changes in habitat quality, which in turn can influence species occurrence (Murcia, 1995; Laurance et al., 2002; Ewers and Didham, 2006; Ewers and Banks-Leite, 2013). Our results show that these negative edge effects are not limited to landscapes with intermediate levels of habitat amount where habitat configuration can vary the most (Villard and Metzger, 2014), but are also relevant in highly forested landscapes, especially for plants. This is consistent with the mounting evidence of the crucial importance of edge effects for species distributions in anthropogenic landscapes (e.g., Fletcher, 2005; Banks-Leite et al., 2010; Didham and Ewers, 2012; Barlow et al., 2016; Pfeifer et al., 2017). It is also congruent with the knowledge that plants are particularly vulnerable to edge effects, especially in tropical forest where small clearcuts are known to drastically increase tree mortality and change microclimate inducing strong changes in species composition (Laurance et al., 2002, 2006). In contrast, in highly deforested landscapes, all remaining forest is likely to be near edges due to the small size of habitat patches (Ribeiro et al., 2009; Banks-Leite et al., 2011; Haddad et al., 2015), and thus core forest habitat may be rare or non-existent regardless of habitat spatial arrangement. Most edge-avoiding species are likely to be regionally extinct in these landscapes (Bogoni et al., 2017), making edge density, and thus habitat fragmentation, a poor predictor of forest-dependent species richness.

In our structural equation model, we assumed that habitat loss is the leading process causing habitat fragmentation patterns, an approach considered to be more relevant and theoretically sound than traditional approaches that assume independence between the two processes (Giam et al., 2010; Didham et al., 2012; Francoso et al., 2015; Ruffell et al., 2016; Morante-Filho et al., 2018). Our approach allows a more detailed understanding of how the direct, indirect and total effects of habitat loss vary in landscapes with low, intermediate or high habitat amounts, including three main points. First, regardless of the total habitat amount in the landscape, the total effect of forest cover (i.e., the sum of direct and indirect effects via habitat fragmentation) on species richness was almost always positive. This result reinforces that preventing habitat loss must remain a central conservation target (Giam

et al., 2010; Francoso et al., 2015; Morante-Filho et al., 2018). Second, both the total and the direct effects of forest cover were most evident in landscapes with low (flora) and intermediate (fauna) total habitat amount. Thus, biodiversity conservation actions aiming to prevent habitat loss and/or increase habitat amount (e.g., through restoration or regeneration) should be most effective in landscapes with low to intermediate total habitat amount, as previously suggested (e.g., Tambosi et al., 2014). Third, the strongest indirect effect of forest cover occurred in landscapes with high habitat amount, especially considering plant species. Indeed, in such landscapes, indirect effects were even stronger than direct effects, indicating that increasing habitat amount has an overall positive effect on species richness mainly by reducing edge density. Thus, at highly forested landscape, management should focus on reducing edge effects, particularly on plants. Restoring forests adjacent to remnants to increase areas less (or not) affected by edge effects can thus be an effective strategy to prevent forest-dependent species extinctions (Brancalion et al., 2013; Rother et al., 2018).

5. Conclusions

Our findings have important implications for research and conservation in fragmented landscapes. First, while negative effects of habitat fragmentation may occur in many landscapes, our analyses suggest that their detection requires considering the variation of strength and direction of effects along the gradient of habitat amount. Such analyses require large datasets, which fortunately are becoming increasingly available (e.g., Hudson et al., 2014), and the application of hierarchical models. Second, edge effects may be more important than ecological processes associated with the number of patches in landscapes with intermediate to high total habitat amount. Since the magnitude of edge effects depend on the land use next to habitat, our results highlight that – besides increasing habitat amount – reducing total length of edges and/or edge contrast and thereby the extent of edge effects in intermediate to high forested landscapes may be a very effective tool in maximizing species retention (e.g., by managing the matrix and restoring forests adjacent to existing remnants, Antongiovanni and Metzger, 2005, Brancalion et al., 2013, Biz et al., 2017, Boesing et al., 2018, Rother et al., 2018). Third, our results suggest that forest fragmentation should have detectable impacts on species even in highly forested landscapes. If the configuration of forest patches in such landscapes results in high edge density, biological, and especially plant communities, may lose a significant number of species, even at high total levels of habitat amount and connectivity. We therefore reinforce that negative habitat fragmentation effects should not be dismissed as a "zombie idea", as suggested by Fahrig (2017) but contested recently (Fletcher Jr. et al., 2018; Fahrig et al., 2019).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.108368.

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