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Habitat loss, not fragmentation per se, drives structural changes and species turnover in plant–vertebrate pollinator networks☆

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ABSTRACT

When natural areas are converted for human use, resulting changes in the landscape often lead to habitat loss and fragmentation, which can disrupt key ecological interactions such as pollination by animals. In this study, we investigated the independent effects of habitat loss and fragmentation on the structure and composition of plant-vertebrate pollinator interaction networks, focusing on interactions mediated by birds and bats in the Neotropical region. We assessed how landscape structure influences network properties, including plant and pollinator richness, number of interactions, connectance, nestedness and modularity. We also evaluated the potential of indirect effects to propagate through the network (i.e. species changes driven by cascading interactions across the network), the occurrence of extinction cascades (sequential species losses triggered by the disappearance of key mutualistic partners), and interaction dissimilarity across landscapes. Our results show that habitat loss (i.e. reduced forest cover) is associated with lower plant and pollinator richness, fewer interactions, reduced nestedness, increased connectance and vulnerability to cascading effects. Species turnover emerged as the main driver of interaction dissimilarity between contrasting landscapes (e.g., sites with high vs. low forest cover), whereas in more similar landscapes, where species pools overlap, rewiring of interactions played a larger role. In contrast, fragmentation per se (i.e. independent of habitat amount) had no significant effect on any of the network metrics analyzed. These findings suggest that habitat loss and changes in species composition, rather than fragmentation per se, shapes the structure and dynamics of plant-vertebrate pollinator networks in distinct landscapes.

1. Introduction

The Anthropocene is a period characterized by human activities reaching a scale large enough to modify the Earth's system and functioning (Malhi et al., 2014; Zalasiewicz et al., 2024). One of the major causes of these changes is the human-based modifications in tropical forests, specifically through land use (Malhi et al., 2014). Land use promotes changes in the landscape structure, i.e., the spatial arrangement, composition, and configuration of different elements or features within a landscape, leading to the rupture of previously suitable habitats for maintaining biodiversity (Fahrig, 2003; Geist and Lambin, 2002). The disruption of once-continuous habitats (fragmentation) and the reduction of forested areas (habitat loss) have historically been driven by land conversion for agro-pastoral activities (Malhi et al., 2014), and urban development (Santos et al., 2022). As a result, many biomes worldwide are now highly fragmented and deforested (Riva et al., 2024; Vancine et al., 2024). This widespread transformation has prompted decades of research focused on understanding the impacts of habitat loss and fragmentation on biodiversity (Fahrig, 2003; Geist and Lambin, 2002; Matuoka et al., 2020; Morante-Filho et al., 2021; Rios et al., 2021; Rocha-Santos et al., 2020).

Decades of empirical research have shown that habitat loss is a major driver of biodiversity decline, whereas the evidence for negative effects of fragmentation per se (i.e., the spatial breakup of continuous habitat into smaller and more isolated patches, independent of habitat loss) remains limited (Fahrig, 2003; Martínez-Ruiz et al., 2025; Watling et al.,

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2020). This conceptual distinction is crucial: while habitat loss refers to a reduction in the total amount of habitat, fragmentation per se refers specifically to changes in the spatial configuration of the remaining habitat, particularly an increase in the number of patches or their isolation, without necessarily changing the total area (Fahrig et al., 2019). Importantly, fragmentation is a landscape-scale process, whereas most studies still rely on patch-scale metrics (Fahrig, 2017; Riva et al., 2025) which are inherently confounded with habitat amount and therefore fail to assess the independent effects of fragmentation (Fahrig, 2017). We are currently in a position to move beyond and disentangle the effects of habitat amount and fragmentation per se to comprehend human consequences on ecosystem assembly and functioning (Vélez et al., 2025).

While it is well established that taxonomic diversity responds strongly to landscape changes such as habitat loss, growing evidence suggests that these changes also disrupt key ecological processes, including pollination (Carlos et al., 2025; Ferreira et al., 2020; Soares et al., 2021). Pollination is an essential ecological interaction sustaining tropical forest ecosystems, where over 90 % of flowering plants rely on pollinators to achieve sexual reproduction (Ollerton et al., 2011; Tong et al., 2023). However, human activities are increasingly threatening pollination dynamics (Rodger et al., 2021). Although the impacts are well-documented for invertebrate pollinators (Ferreira et al., 2020; Newton et al., 2018), and for vertebrates at local scales (Bernard and Fenton, 2003; Carlos et al., 2025; Farneda et al., 2015; Hadley et al., 2018, 2014; Hadley and Betts, 2009; Leimberger et al., 2022; Teixido et al., 2022; Volpe et al., 2016; Quesada et al., 2003), the consequences for vertebrate-mediated pollination at macroecological scales remains an open question. In the Neotropical forests, hummingbirds (Trochilidae) and bats (Phyllostomidae) play a crucial role in pollination dynamics, serving as primary pollinators for sixty-five and sixty-seven families of angiosperms, respectively, placing them as keystone species for ecosystem functioning (Fleming et al., 2009). Their interactions shape not only reproductive success at the species level, but also the structure and functioning of entire communities, particularly in ecosystems where insect pollinators are scarce or seasonally variable (Dellinger et al., 2023). Despite increasing knowledge about the effects of habitat loss on pollinator diversity and pollination services, we still know little about how fragmentation per se affects these ecological interactions, particularly at broad spatial scales (Hadley and Betts, 2012).

The effects of landscape changes on species interactions at the community level can be effectively studied using a network approach (Ferreira et al., 2020; Keyes et al., 2021; Carranza-Quiceno et al., 2024; Vélez et al., 2025). In mutualistic networks, environmental disturbances such as habitat loss can reduce species richness and/or reshape interactions, often leading to structural shifts in network structure (Bonfim et al., 2023; Ferreira et al., 2020; Menezes Pinto et al., 2021). Changes in species composition may reorganize ecological interactions, increasing the dissimilarity among networks (Poisot et al., 2015). As a consequence, changes in network structure and composition may affect the stability and resilience of mutualistic systems (Bascompte et al., 2003; Bonfim et al., 2023; Souza et al., 2018). The shifts in composition and the way species interact can be assessed by the beta-diversity of interactions, capturing the variation in interaction patterns across different locations (Carstensen et al., 2014; Poisot et al., 2015, 2012). Lastly, given the interdependence of species within mutualistic networks, disturbances in landscapes, like deforestation, can propagate through the network, leading to cascading effects (Dáttilo et al., 2016; Fricke et al., 2018). These cascading effects, in turn, propagate through indirect interactions, where species indirectly influence other species (Pires et al., 2020). For instance, plants sharing common pollinators are indirectly connected through this pollinator, meaning that a change in one plant may cascade to another plant through the pollinator (Bergamo et al., 2017; Bergamo et al., 2021). Indirect pathways can alter the whole network's ecological and evolutionary dynamics (Carvalheiro et al., 2014; Guimarães et al., 2017; Maia and Guimarães Jr, 2024). Among these indirect interactions, one fundamental problem is the emergence of coextinction cascades (Pires et al., 2020).

In this study, we investigated how habitat loss and forest fragmentation per se affect the structure and vulnerability of plant-vertebrate pollination networks mediated by birds and bats in the Neotropical region (Fig. 1a). Specifically, our objectives were to investigate the independent effects of forest loss and fragmentation on (i) the structural properties of the networks (plant and pollinator richness, number of interactions, connectance, nestedness and modularity), (ii) the potential propagation of indirect effects within the networks, (iii) network vulnerability to extinction cascades, and (iv) the dissimilarity in species interactions. We hypothesize that fragmentation per se has limited effects on plant–vertebrate pollinator networks, whereas forest loss plays a more critical role in shaping network structure and vulnerability. This hypothesis is supported by previous studies showing that (habitat amount is more important in sustaining biodiversity than the spatial arrangement of forest patches - Fahrig, 2013; Rios et al., 2021; Watling et al., 2020).

Accordingly, we expect that (i) networks in landscapes with lower forest cover would support fewer plant and pollinator species, fewer interactions, and reduced nestedness due to the loss of specialist species, which are often more sensitive to disturbances (Aizen et al., 2012). In addition, changes in species composition and limited resources may lead to more compartmentalized networks, increasing modularity. These changes can result in structurally simplified networks dominated by generalists and highly connected species (Fig. 1b). Additionally, we expected that (ii) indirect effects would play a reduced role in such landscapes, as less rich and less nested networks are likely to exhibit fewer pathways connecting species (Guimarães et al., 2017). Regarding extinction cascades, we predicted that (iii) reduced forest cover would lead to greater vulnerability to secondary extinctions, as networks in degraded landscapes become structurally weakened due to the loss of pollinators (Bernard and Fenton, 2003; Heer et al., 2015; Lindberg and Olesen, 2001; Tinoco et al., 2017). Finally, we hypothesized that (iv) in similar landscapes (regarding forest cover), interaction dissimilarity will be better explained by the rewiring of interactions. In these landscapes, species may persist across sites but interact differently — with a higher likelihood of co-occurrence, leading to low species turnover and high interaction rewiring. Conversely, in dissimilar landscapes, we expect low species co-occurrence, resulting in minimal interaction rewiring but high species turnover. This pattern would reflect strong environmental filtering promoting species replacement across contrasting landscapes (White et al., 2022) (Fig. 1c). While we anticipated limited influence of fragmentation per se (patch density) on network structure and vulnerability, we formally tested its independent contribution in all analyses, recognizing that in some ecological contexts, habitat fragmentation may play a meaningful role.

2. Methods

2.1. Vertebrate pollination interaction dataset

We gathered a dataset on neotropical pollination interactions, including only flying anthophilous vertebrates - birds and bats -, using four available databases: Web of Life (Fortuna et al., 2014), Interactions Web (http://www.ecologia.ib.usp.br/iwdb), Atlantic pollination (Iamara-nogueira et al., 2022), and Neobat interactions (Florez-Montero et al., 2022). We also searched in the DRYAD (https://datadryad.org/), Scopus, and Web of Science repositories using the following terms: "*plant-pollinator network*" OR "*pollination network*" OR "*floral visitation network*" OR ("*mutualistic interaction network*" AND *pollinator*) AND "*tropical*". We only include empirical studies conducted in neotropical forests that focused on the community level. The networks included legitimate pollination interactions, but floral visits may also be included in some cases. We opted for this approach because (1) information on the reproductive consequences of visiting events is often absent; (2) the

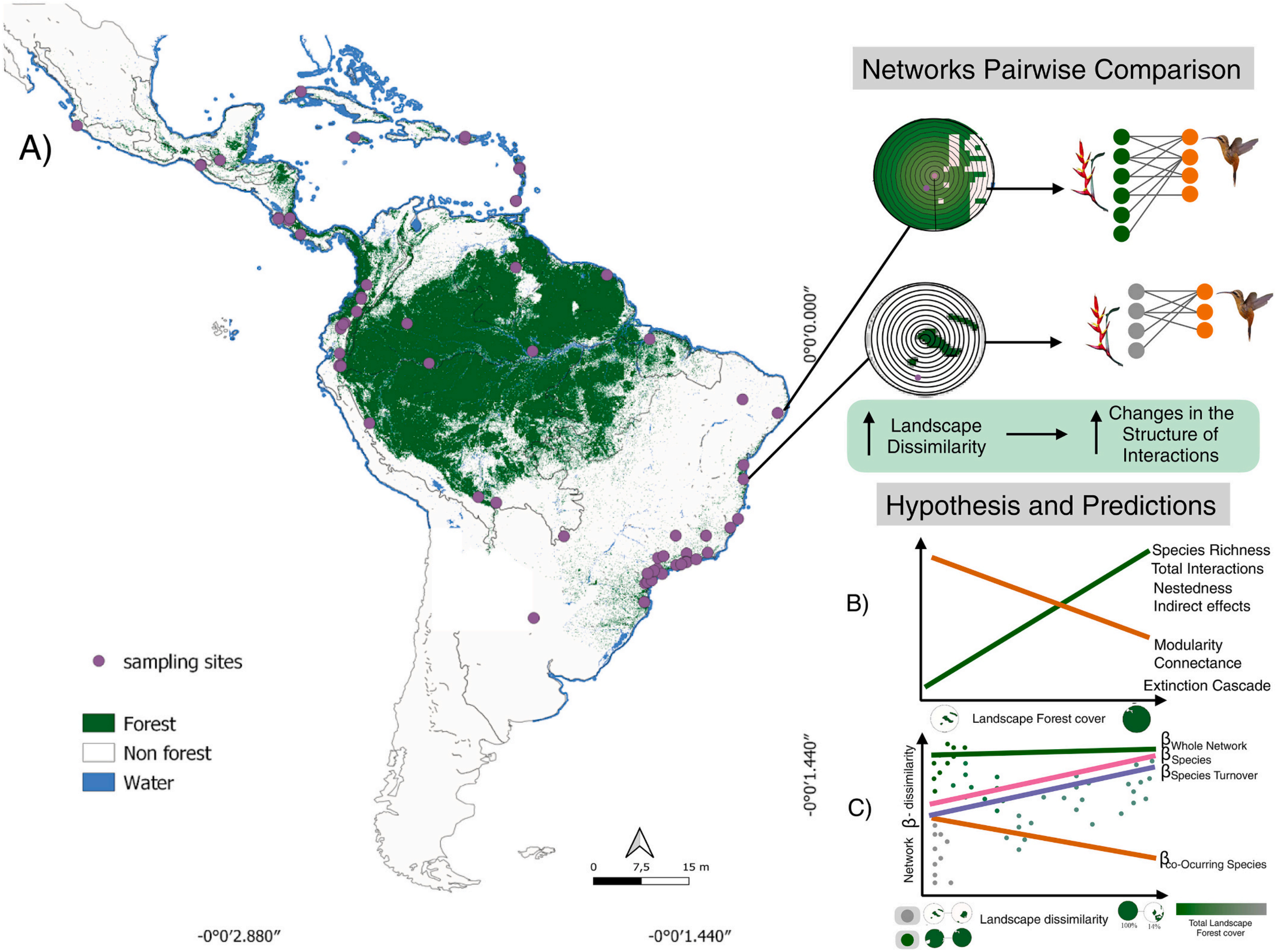

Fig. 1. Predicted effects of forest cover and landscape dissimilarity on network structure and interaction beta-diversity on plant-vertebrate networks. (A) Study Area – Map of Neotropical Humid Forests. The map illustrates the forest cover in the Neotropical region, with purple dots marking the locations of the 67 interaction networks sampled. To the right, a zoomed-in view highlights the buffers used for landscape analyses, with 12 buffers ranging from 250 to 3000 m around the network locations. With the buffer representation, we provide an example of a plant-pollinator interaction network, where vertebrate pollinators are depicted in orange and flowering plants in light green (for high forested landscapes) and gray (for low forested landscapes). B) Conceptual relationships between forest cover and network metrics. As forest cover increases, species richness, number of interactions, nestedness, and indirect pathways are expected to increase (green line), while modularity, connectance, and extinction cascade likelihood tend to decrease (orange line). C) Expected linear relationship between landscape dissimilarity and the components of interaction beta-diversity. Greater dissimilarity between landscapes leads to increased beta-diversity of interactions driven by species turnover (βst) and decrease of interaction dissimilarity explain by species co-occurrence and consequently interaction rewiring (βos). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

role of a given animal can vary in space and time, shifting from pollinators to non-pollinating floral visitors (Thompson, 2005); (3) pollinators and non-pollinating floral visitors affect the ecology and evolution of plant-pollination systems. Therefore, we treated all such interactions as pollination in a broad sense.

We extracted the geographic coordinates of the sites where each study was conducted and the networks resulting from sampling interactions. In our study, we analyzed 67 plant-vertebrate pollinator networks (Fig. 1a), each originating from a different sampling site within moist tropical forest fragments. These networks were compiled from 47 separate studies, conducted between 1979 and 2019. The networks were obtained by the authors using different sampling methods, including focal observation (most frequent), transect, camera traps, and pollen collection using capture methods such as mist nets or a combination of these methods (described in Table S1). In this context, each sampling site or coordinate corresponds to a unique forest fragment where the studies were conducted, and each site provided one network used in our analysis. We tested whether any sampling method was associated with our response variables and found no and found no significant relationship (Kruskal-Wallis test: $p = 0.7$ for both forest cover and patch density), suggesting that while different methods may introduce some noise, they do not systematically bias our results and instead highlight their robustness even in heterogeneous datasets.

2.2. Landscape metrics

To understand the effects of habitat loss and fragmentation per se on network predictors, we used two landscape metrics: i) the percentage of forest cover; and ii) patch density (number of patches per unit area) (Horning, 2008). Both metrics are commonly used to characterize landscape structure in ecological studies (Bonfim et al., 2023; Lausch et al., 2015; Morante-Filho et al., 2018). Notably, when considered independently from forest cover, patch density is an indicator of fragmentation per se. Using the geographic coordinates provided by each study, we first collected spatial data, specifically, mappings of forest cover within the Neotropical region (Fig. 1a). We collected these mappings through the dataset developed by the European Commission that mapped the forest cover change in tropical moist forests (TMF) using a 41-year time series, between 1990 and 2022 (Vancutsem et al., 2021). This dataset includes all forests in the humid tropics, comprising rainforest and the tropical moist deciduous forest. We chose the 'annual change collection' because it provides detailed information on different types of forests and deforested areas, based on Landsat satellite images. This product offers a spatial resolution of 0.09 ha (each pixel represents a 30 by 30-m area), making it especially useful for calculating landscape metrics. Thus, we extracted maps for each sampling site, corresponding to the year of sampling or the closest available year when an exact match was not possible. All raster files were classified into two categories: forest and non-forest. Finally, we calculated the percentage of forest cover and patch density within circular buffers ranging from 250 to 3000-m, at 250-m intervals, around each sampling site to evaluate the scale of effect (Jackson and Fahrig, 2015; Miguet et al., 2015). The scale of effect refers to the spatial extent at which landscape metrics best predict each network descriptor (Dáttilo et al., 2023). Because we lack prior knowledge of the spatial scale at which landscape variables affect network predictors, we used a multi-scale analysis to determine the spatial extent with the greatest explanatory power. The buffer size range (250 to 3000-m radius) was based on previous studies on movement ecology and landscape use by nectarivorous birds and bats (Aguiar et al., 2014; Bernard and Fenton, 2003; Hadley et al., 2018; Hadley and Betts, 2009; Loayza and Loiselle, 2008; Volpe et al., 2016). Landscape metrics were calculated in R (version 4.3.2) using the *landscapemetrics* package (Hesselbarth et al., 2019).

2.3. Network descriptors

For each sampling site, we built a matrix **A** in which columns represent plant species, rows represent vertebrate pollinators, in which the element $a_{ij} = 1$ indicates the presence of an interaction between the plant i and the pollinator species j, and $a_{ij} = 0$ otherwise. Using these matrices **A** for each site, we characterized the plant- vertebrate pollinator networks with the following metrics: number of interactions, number of plant species (plant richness), number of pollinator species (pollinator richness), connectance, which is the proportion of interactions observed among all the possible interactions in each site (Dunne et al., 2002; P. Jordano, 1987), nestedness and modularity. The nestedness estimates the average overlap between the assemblage of the interaction partners of specialist and generalist species. Nestedness was estimated by the NODF index (Almeida-Neto et al., 2008), ranging from 0 (no nestedness) to 100 (perfectly nestedness) (Almeida-Neto et al., 2008). Modularity describes the formation of cohesive sub-groups of species within the network that interact strongly among themselves (Bascompte and Jordano, 2013), forming groups. We used the Barber's Q metric to estimate modularity in networks with two sets of interacting elements, such as plants and pollinators (i.e., bipartite graphs). The values of Q typically range from 0 (no significant levels of modularity) to 1 (strong modularity), and were estimated using the Beckett algorithm (Beckett, 2016). We calculated nestedness and connectance through the function *networklevel* and modularity using *computeModules*. Both functions are part of the *bipartite* package (Dormann et al., 2009).

We employed a null model approach to evaluate whether the observed values of nestedness and modularity significantly deviate from those expected under random network assembly. The null model generated random networks that preserved key features of the observed network, such as the number of species and interactions, while reshuffling connections to remove any underlying non-random structure. We applied the Patefield algorithm, which randomizes the distribution of links between species while keeping the number of links per species constant (Dormann et al., 2009). We generated 1000 null model networks for each site and subsequently computed the Z-scores for nestedness and modularity based on the observed values relative to the corresponding values derived from the random networks: $Z - \frac{X-\mu}{\sigma}$, where X is the observed metric value (nestedness or modularity); $\mu =$ average value of the metric obtained through the 1000 null model networks; and $\sigma =$ standard deviation of the ensemble of null model networks.

We investigated the potential impact of landscape changes on indirect effects and extinction cascades using the approach introduced by Guimarães et al. (2017) for coevolutionary dynamics and adapted to coextinction cascades by Pires et al. (2020). Indirect pathways represent the effects induced by species that are not directly connected as interacting partners. To compute the potential for indirect effects in plant-networks, we used **A** to populate a square matrix **B** in which all species (plants and pollinators) are depicted in both rows and columns in such a way that both row i and column i depict the same species i. The matrices **A** and **B** contain the same information, but **B** allows to compute the matrix operations that are needed to estimate the potential for indirect effects in a network. To do so, we standardized each row of **B** to sum one, leading to the matrix **B**′. We then computed a total effects matrix $\mathbf{T} = (\mathbf{I}\text{- R}\mathbf{B'})^{-1}$, in which **I** is the identity matrix with the same dimensions of **B**′ and R is the dependence between interacting species. In our study, R was kept constant for all species in the network, with a value of 0.95 chosen to enhance the visualization of indirect effects in the network (Bonfim et al., 2023; Pires et al., 2020). The matrix **T** summarizes the potential of direct and indirect effects of propagating in the network under the assumption that the effects die off along the pathway length. From the total effects matrix **T**, we computed the overall potential of indirect effects of a given network using the following equation:

$$U = \sum_i^N \sum_j^N t_{ij} \left(1 - b_{ij}\right) / \sum_i^N \sum_j^N t_{ij}$$

Here, t_{ij} is derived from the total effects matrix (**T**) and represents the potential that a species in column j affects a species in row i. The (1 - b_{ij}) is used to remove the effects between direct interactions. In addition, matrix **T** also allows us to assess the influence of species present in the network in propagating both total effects (T_{out}) and indirect effects for each species (*for details see* Pires et al., 2020). Therefore, we obtained the influence of a species on the other species in the network through paths of varying lengths (both direct and indirect paths, T_{out}), as well as the extent of the indirect effects that the species propagates in the network.

Finally, to assess the effects of the landscape on extinction cascades, we simulate the extinction of vertebrate species using the T_{out} values. We utilized the method developed by Vieira and Almeida-Neto in 2015, adapted by Pires et al. in 2020, to determine the average size of the extinction cascade within each network. We standardize T_{out} values to range from 0 to 1 (with higher values associated with a greater spread of links in networks, that is, greater influence), we targeted species with values closest to 1 for extinction. In cases where more than one species presented a T_{out} value of 1, we randomly selected one of them for extinction. Our simulations specifically focused on the extinction of animal species, as our primary goal was to calculate extinction cascades. Therefore, it was unnecessary to target species from both trophic levels, aligning with our previous objective. To quantify the extinction cascade, we counted the species that became extinct following the extinction simulation and expressed this as a percentage of the total number of species in the network.

2.4. Beta diversity of interactions

To assess the effect of landscape structure on dissimilarity of interactions, we calculated the beta-diversity of interactions, i.e., the dissimilarity between each pair of interaction networks. Following Poisot et al., 2012, we decomposed the dissimilarity into four components: (i) β_s, the dissimilarity in species composition between communities, considering each network as a local community; (ii) β_{wn}, the overall dissimilarity between networks, which is further partitioned into

(iii) β_{os}, the dissimilarity of interactions among species shared between networks (i.e. rewiring), and (iv) β_{st}, the dissimilarity due to species turnover among networks. These metrics build on classical dissimilarity indices such as Whittaker's (1960), but are adapted to account for species interactions rather than only species composition (see Novotny, 2009 and Poisot et al., 2012 for details). This decomposition allows us to identify the extent of dissimilarity between networks and also understand the source of this variation, whether it results from species turnover or from changes in the interactions among shared species (Poisot et al., 2012). Finally, we also partitioned the turnover component β_{ST} to assess whether species turnover is driven by pollinator turnover, plant turnover, or combined turnover of both groups, following Novotny, 2009. We also assessed the relative importance of each of these components to the total interaction dissimilarity, identifying which group contributed most strongly to network variation. We calculated interaction beta diversity using the *betalink* function (Poisot et al., 2012), applying a correction to avoid underestimating the β_{ST} component (Fründ, 2021).

2.5. Data analysis

To evaluate the effects of habitat loss and fragmentation per se on plant-vertebrate pollination networks, we fitted linear models using forest cover and patch density as predictors of distinct network descriptors. Given that habitat amount can strongly influence fragmentation metrics, we assessed fragmentation effects by including both predictors simultaneously. In contrast, we evaluated the isolated effects of habitat loss by fitting models with forest cover alone. To assess whether and how vertebrate-mediated pollination networks are influenced by habitat loss, we employed linear models with different distributions, tailored to the nature of the response variable (see details in the supplementary material) and the explanatory variable - forest cover, considering the scale of effect (see topic 2.2 of methods). Thus, we fitted linear models for each network metric (number of interactions, plant and pollinator richness, connectance, nestedness, modularity, proportion of indirect effects, and average size of the extinction cascade, the latter weighted by network size). To control for effects of sampling effort on the descriptors, we calculated sampling intensity, and included it as a covariate in the statistical models (Emer et al., 2020). The sampling intensity of each network was estimated as $\frac{\sqrt{N}}{\sqrt{S}}$, where N is the number of interactions in the network, and S is the size of the network, that is, the sum of the number of plant species and the number of animal species in a network (Emer et al., 2020; Schleuning et al., 2012). Since environmental variables can represent a source of variation at broad spatial scales, we extracted three bioclimatic variables—average annual temperature (°C), average annual precipitation (mm), and topography represented from the digital elevation model (DEM). These data were obtained at a resolution of 30 arc *sec* from WorldClim v.2.0 (Fick and Hijmans, 2017) and STRM (https://srtm.csi.cgiar.org/). Using Pearson's correlation test, we evaluated the existence of collinearity between predictor variables and covariates (Zuur et al., 2010). Temperature was significantly correlated with altitude ($r = -0.82$) and precipitation ($r = 0.40$) (Fig. S2). Therefore, only uncorrelated covariates, that is, altitude, precipitation, and sampling intensity were used in further analysis. These covariates were subjected to model selection using the stepwise method, choosing the simplest and most parsimonious model using ΔAICc $\leq$2. Our goal was not to evaluate their effects but to control them, thus, we do not discuss their results.

Next, to assess the effect of fragmentation per se we followed the statistical protocol proposed by Watling et al. (2020). We first determined the appropriate scale of effect for patch density and then conducted model selection by comparing three competing models: (1) a model including forest cover, (2) a model including both forest cover and patch density, and (3) a null (intercept-only) model, also choosing the simplest and most parsimonious model using ΔAICc $\leq$2. If fragmentation had an independent effect, the model including both forest cover and patch density should provide a better fit than the model including only forest cover. We additionally examined potential spatial autocorrelation using Moran's I statistic, and we did not detect spatial correlation structure in our models after accounting for the geographic coordinates of each study ($p > 0.05$ for all models, see Supplementary materials). Finally, we present the coefficients of each predictor and the variance explained by the linear model with best fit (R^2). We obtained the adjusted R^2 for linear models with negative binomial and beta distributions by using the *piecewiseSEM* package (Lefcheck, 2016).

To evaluate the relationship between network dissimilarity and landscapes, we developed a landscape dissimilarity index: $LD = \frac{Fc_{max} - Fc_{min}}{Fc_{max}}$, where LD is the landscape dissimilarity index, Fc_{max} is the maximum forest cover value between the landscape pairs and Fc_{min} is the minimum forest cover value between the landscape pairs. The resulting index provides a standardized measure of forest cover dissimilarity between landscapes, ranging from 0 to 1. Pairs of landscapes with similarly low forest cover are positioned on the left side of the x-axis, whereas pairs with extreme differences (e.g., low forest cover vs. high forest cover) are located on the far-right end of the x-axis (Fig. 1c). This approach allowed us to effectively capture and compare varying levels of landscape dissimilarity in relation to network dissimilarity.

For each interaction dissimilarity component (β_s, β_{wn}, β_{os}, and β_{st}), we fitted five statistical models to explore different potential responses to landscape heterogeneity. These models included: (1) a simple generalized linear model (GLM); (2) a quadratic model to capture potential non-linear relationships; (3) a linear mixed-effects model (GLMM) with random intercepts for Neotropical sub-regions (Andes, Caribbean, lowland South America and North & Central America), accounting for potential regional variation; (4) a quadratic GLMM also with Neotropical subregions as random effect, and (5) a generalized additive model (GAM) aimed at identifying unexpected patterns or complex associations. All models were fitted using a binomial distribution for the response variable, with landscape dissimilarity as the predictor variable. The most parsimonious model for each index was selected considering ΔAICc $\leq$2 as the best fit (Table S2).

3. Results

We obtained 67 plant-vertebrate pollinator networks, distributed in twelve neotropical countries – Brazil (32), Ecuador (9), Colombia (7), Costa Rica (5), Mexico (3), Bolivia (2), Cuba (2), Puerto Rico (2), Dominica (2), Grenada (1), Jamaica (1), Peru (1). The networks included 179 species of vertebrates, of which 135 species belong to the family Trochilidae, 19 belong to other groups of birds (such as Thraupidae, Icteridae, Cotingidae, and Picidae), and 25 species of bats belonging to the Phyllostomidae family. We recorded 740 plant species across 76 botanical families. The most frequent vertebrate species were *Thalurania glaucopis* and *Phaetornis ruber*, found in 30 % ($n = 20$) and 18 % ($n = 12$) networks, respectively. Among plants, *Nidularium innocentii* (Bromeliaceae) was the most frequent species, occurring in 16 % ($n = 11$) networks. In general, species richness within the networks ranged from 4 to 84 species (including both plants and pollinators). The number of plant species varied between 2 and 64, while the number of pollinator species ranged from 2 to 23. The networks were immersed in a landscape context ranging from 8 % to 100 % of forest cover and from 1 to 239 forest fragments (considering the maximum analyzed spatial scale of 3000 m).

All response variables were better explained by models including forest cover alone (Table S3). The scale of effect varied among the response variables, but we found the 3000 m radius to be the best scale for most models about forest cover (Table 1). Regarding network structure, we found the forest cover to be significantly associated with the plant and pollinator richness, the number of interactions, connectance, and nestedness, but not with modularity (Fig. 2F).

Table 1

Results of linear regression models testing the influence of forest cover (FC) on plant-vertebrate pollinator networks. The scale represents the scale of effect, that is, the spatial extent where the independent variable was measured with the best response to the dependent variable. R^2 represents an estimate of how much the best model explains the variation. Finally, the symbol "+" indicates that the variable presented below is covariant to explain the changes in the corresponding network predictor.

Network metric	Best model	distribution	scale (m)	β	SE	t/z value	R^2
Plant richness	FC + sampling intensity	Negative binomial	3000	0.008 2.276	0.003 0.400	2.871 5.686	**0.54**
Pollinator richness	FC + Sampling intensity +precipitation	Negative binomial	3000	0.006 1.478 −0.000	0.002 0.363 0.000	2.170 4.069 −1.732	**0.38**
Number of interactions	FC + Sampling intensity	Gaussian (log transformed)	3000	0.006 3.822	0.002 0.356	2.437 10.716	**0.64**
Connectance	FC + sampling intensity	Gaussian (log transformed)	3000	−0.005 −0.731	0.002 0.336	−2.008 −2.176	**0.11**
Z-NODF	FC + sampling intensity	Gaussian	3000	0.000 0.073	0.000 0.014	1.916 4.960	**0.29**
Z- modularity	FC + sampling intensity	Gaussian	2750	−7.841e-05 −4.222e-02	5.157e-05 7.049e-03	−1.520 −5.990	**0.37**
Proportion of indirect effects	sampling intensity	Beta	3000	1.239	0.2894	4.282	0.11
Mean cascade size	~FC+ sampling intensity	Gaussian (log transformed)	3000	−0.008 −2.822	0.003 0.457	−2.507 −6.165	0.40

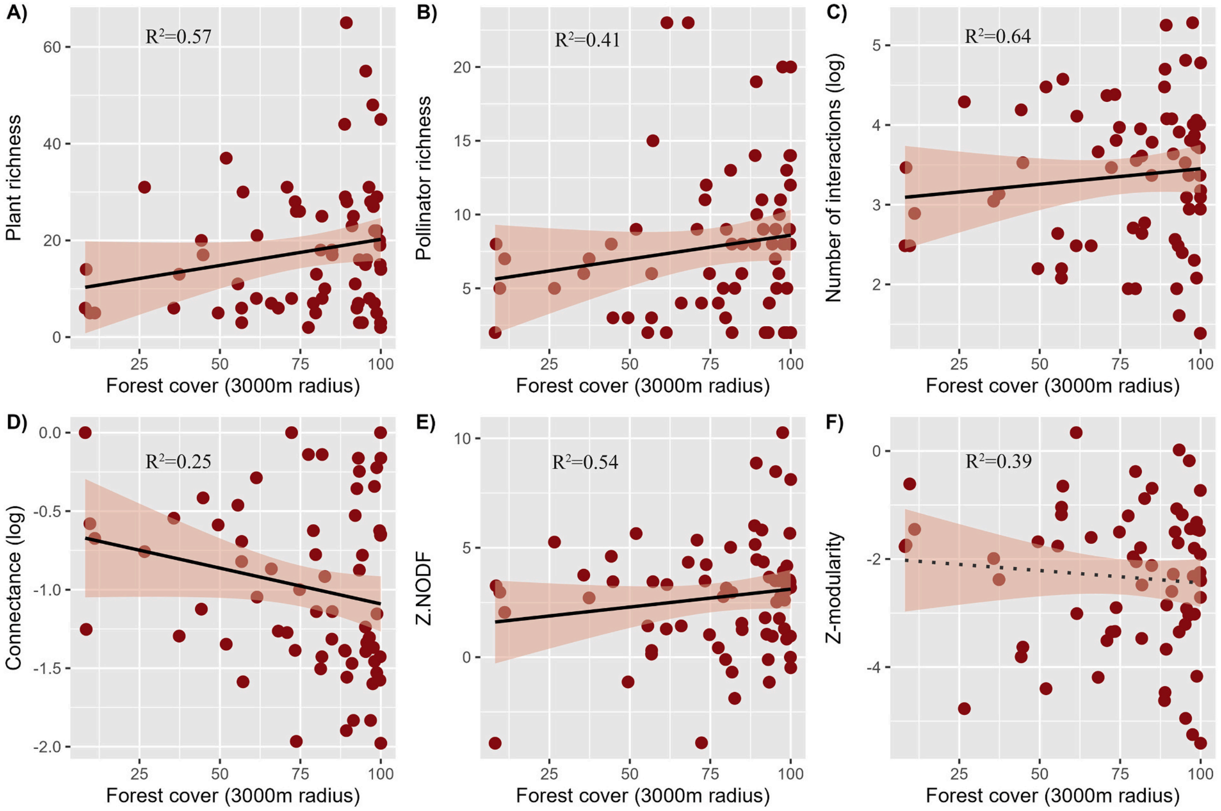

Fig. 2. Effects of landscape changes on structure of Neotropical plant-vertebrate pollinator networks. The effects of forest cover (the opposite of habitat loss) are shown in A) Plant richness; B) Pollinator richness C) Number of interactions; D) Connectance, E) Nestedness (*Z*-NODF) and F) Modularity. R^2 represents an estimate of how much the adjusted model explains the variation. The dashed line indicates no significant relationship.

Additionally, we found a positive association among the number of interactions and the plant/pollinator richness (Fig. 2A-C; Table 1), while connectance exhibited a negative relationship (Fig. 2D; Table 1). The percentage of forest cover was positively related to nestedness. Finally, for modularity, we do not find any significant relationship (Fig. 2E-F; Table 1).

We did not find any relation among the proportion of indirect effects on networks and the evaluated landscape metrics (Fig. 3A; Table 1). In contrast, cascading effects, measured by average cascade size, we found a negative relationship with forest cover (Fig. 2B). Our results, obtained for networks comprising bats and birds (67 networks), remained consistent when analyzing only hummingbird networks, except for nestedness, where we did not find significant relationship, and indirect effects, which showed a positive relationship with forest cover (Fig. S3-S4). Although no significant relationship was found between forest cover and the proportion of indirect effects when considering all 67 networks, a closer inspection revealed that this result is influenced by three small bat-pollination networks, which contain fewer nodes and

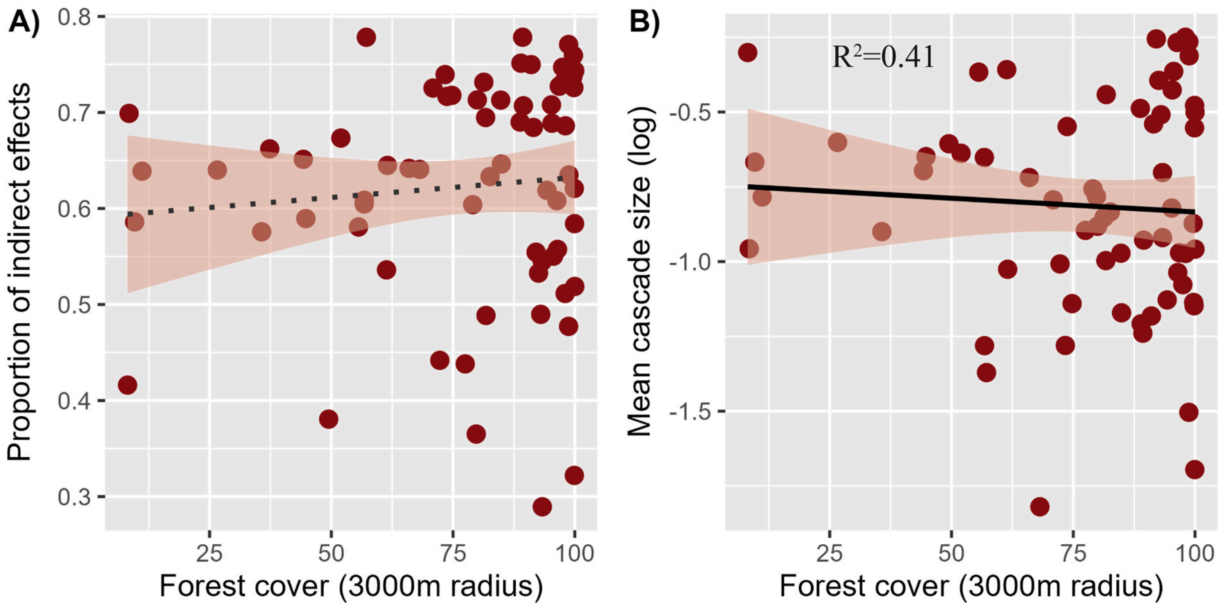

Fig. 3. Effects of landscape changes on the indirect interactions within Neotropical plant–vertebrate pollination networks. The effects of percentage of forest cover are shown in A) Proportion of indirect effects, and B) Mean cascade size in networks. R^2 represents an estimate of how much the adjusted model explains the variation. The dashed line indicates no significant relationship.

interactions. When the analysis is restricted to the 48 hummingbird networks, the relationship between forest cover and the proportion of indirect effects becomes statistically significant (Fig. S4). This suggests that variation in composition across functional groups may influence the overall pattern observed in the full dataset.

Finally, the networks were highly dissimilar from each other independently of landscape dissimilarity gradient, both in terms of species composition (β_s) and interactions (β_{wn}). However, the drivers of this interaction dissimilarity varied according to differences in landscape characteristics. We find a positive linear relationship between landscape dissimilarity caused by species turnover (β_{st}) and a negative relationship with interaction rewiring (β_{os}) (Table 2, Fig. 4A). The partitioning analysis of interaction turnover revealed that the main driver was the simultaneous replacement of both plants and pollinators, which occurred most frequently across sites. This was followed, in importance, by interaction turnover driven primarily by species replacement among plants (Fig. 4B).

4. Discussion

Our findings show that habitat loss, rather than fragmentation per se, is the primary driver of changes in the structure of plant–vertebrate pollinator networks in the Neotropics. Forest loss was associated with declines in plant and pollinator species richness, as well as a reduction in the total number of interactions. These biodiversity losses were accompanied by structural shifts in network organization, including increased connectance, reduced nestedness, and marked species turnover. Moreover, forest loss contributes to larger cascade sizes within the networks, reducing their overall robustness.

Table 2

Results of statistical models evaluating the influence of landscape dissimilarity on plant–pollinator interaction dissimilarity. The best model is the fitted model with the lowest ΔAICc among the five tested (GLM, GLMM, GAM, Quadratic and GLMM with quadratic term).

Best model	β (Estimate)	SE	z value	p-value
$\beta s \sim$ landscape dissimilarity + (1|subregions)	3.305	2.190	1.509	0.131
$\beta wn \sim$ landscape dissimilarity + (1|subregions)	1.362	2.406	0.566	0.571
$\beta os \sim$ landscape dissimilarity + (1|subregions)	**−1.176**	**0.457**	**-2.571**	**0.010**
$\beta st \sim$ landscape dissimilarity	**1.079**	**0.393**	**2.746**	**0.006**

In plant–vertebrate networks, we found that species loss triggers a cascade of structural changes that undermine the network's robustness to further extinctions. In our study, the decrease in plant and pollinator richness led to a decrease in the total number of interactions, which in turn directly impacted network structure, resulting in two main structural patterns: increased connectance and reduced nestedness. This effect is commonly observed in deforested landscapes, where networks become smaller yet more densely connected. Such patterns are well documented in ecological networks, where species-poor communities tend to exhibit proportionally higher connectance (Jordano, 1987). A likely explanation is that the number of potential interactions increases with the product of plants and pollinator richness. Thus, as the network shrinks, the number of observed interactions gets closer to the number of potential interactions among the remaining species (Jordano, 1987). The second effect, reduced nestedness, is a predictable outcome of species loss, given the well-established positive relationship between richness and nestedness in ecological networks (Bastolla et al., 2009). This decline likely results from the loss of specialist species, which often contribute disproportionately to the nested structure by interacting with highly generalist partners (Bomfim et al., 2018).

Nested networks are considered resilient, but they are not immune to structural disturbances from species loss (Thébault and Fontaine, 2010). While superconnected species help maintain network integrity, the loss of specialists—who interact with subsets of generalist partners—can significantly disrupt network structure. Specialist species, which are more vulnerable to environmental change (Aizen et al., 2012; Vidal et al., 2014), play a key role in maintaining network hierarchy and nestedness, and their extinction weakens these structural (Bascompte et al., 2003; Bomfim et al., 2018). Their loss reduces structural coherence, increases the risk of secondary extinctions, and compromises the system's ability to absorb disturbances. Such changes affect a key emergent property: network robustness to species loss (Gaiarsa and Guimarães, 2019). Although mutualistic networks initially buffer species loss through nestedness and interaction redundancy (Memmott et al., 2004), habitat degradation gradually undermines these

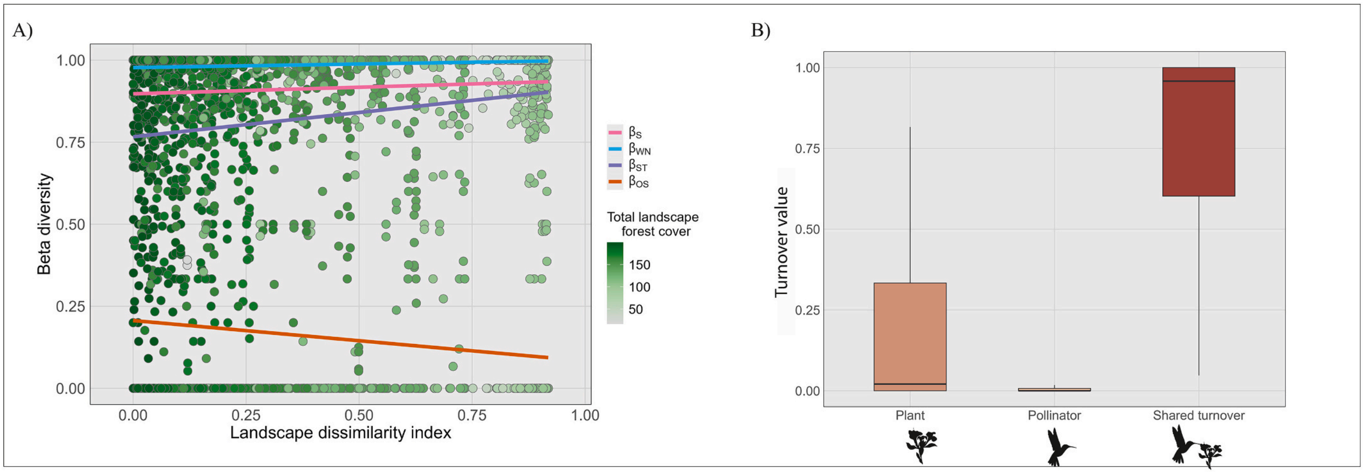

Fig. 4. Beta diversity of plant-pollinator interactions along landscape dissimilarity gradient in the Neotropics. A) Relationship between beta diversity and landscape dissimilarity for the components of network dissimilarity. Each line represents a linear model fitted to a given component: βs - Dissimilarity in the species composition of communities, β_{WN} - overall dissimilarity of interactions, and its components β_{OS}; dissimilarity due only to changes in interactions among shared species: rewiring) and β_{St} (dissimilarity of interactions due to species turnover). The points in the graph are colored according to the total amount of forest between the compared landscapes (sum of forest cover in the two landscapes). Shades of dark green indicate higher forest amount, while gray indicate lower forest amount. B) Partitioning turnover, where β_{St} is further partitioned into components due to the absence of plant, pollinator and absence of both. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mechanisms. Generalists may compensate temporarily for the loss of specialists, but growing dependence on a few highly connected species increases vulnerability to cascading extinctions (see Yeakel et al., 2020 for a similar result for food webs). This progressive breakdown of nestedness and redundancy ultimately threatens the persistence and functioning of the entire ecological community (Kaiser-Bunbury et al., 2017). Our results support this view by showing that forest loss increases the risk of cascade extinction.

We found high species dissimilarity (β_s) and interaction dissimilarity (β_{wn}) across the entire gradient of landscape dissimilarity. This pattern was expected, as interaction dissimilarity often follows the same trend of species dissimilarity within communities (Poisot et al., 2012). In other words, networks are generally dissimilar regardless of landscape dissimilarity, due to habitat heterogeneity and local adaptation. However, the underlying cause of the dissimilarity shifts along the landscape gradient. Although species turnover constitutes the primary component driving interaction dissimilarity throughout the entire gradient of landscape change, differences are observed. At one extreme, in contrasting landscapes (i.e., sites with high vs. low forest cover), interaction dissimilarity is primarily explained by species turnover (β_{st}). When landscape dissimilarity is complete (i.e. near 1), species turnover becomes the dominant driver, explaining nearly 90 % of the observed interaction dissimilarity. Thus, in such landscapes, the species turnover drives differences between networks, as habitat loss likely excludes certain species while favoring others, affecting plant or animal species (Aizen et al., 2012). When partitioning species-driven interaction turnover, we observed that the majority of the turnover was explained by the simultaneous replacement of plants and pollinators across landscapes. This indicates that differences in network structure are largely driven by shifts in the composition of both trophic groups, rather than changes confined to a single group. The joint turnover of plants and pollinators suggests that habitat loss impacts multiple levels of the community simultaneously, leading to reorganization of plant- vertebrate pollinator networks. These findings reinforce the sensitivity of plants and vertebrates to anthropogenic disturbances such as habitat loss (Hadley et al., 2014; Rocha-Santos et al., 2017) and the potential of the loss of species to alter not only components of beta diversity but also the structure of ecological networks (Bonfim et al., 2023; Carstensen et al., 2014; Soares et al., 2021).

In similar landscapes, rewiring of interactions emerges (though less prominent) as an important component of network dissimilarity, likely because the chance of species coexisting in similar landscapes is higher; however, they may not interact in the same way, leading to a rearrangement of interactions (White et al., 2022; Poisot et al., 2015). This suggests that even when the same species persist across sites, variables such as environmental conditions, local trait distributions, local abundances (neutral process) or even species invasion (Davis et al., 2025; Valido et al., 2019) may cause interactions to be reorganized (Carstensen et al., 2014; Poisot et al., 2015; White et al., 2022). The contrasting patterns of β_{st} and β_{os} along the landscape dissimilarity gradient, with β_{st} (species turnover) increasing and β_{os} (interaction rewiring) decreasing as landscape dissimilarity increases, suggest that environmental filtering acts differently on species and interactions (White et al., 2022).

To conclude, our results show that habitat loss is the main factor driving changes in the structure of plant–vertebrate pollinator networks in the Neotropics. In contrast, we did not find consistent or significant effects of fragmentation per se on these interactions. Although fragmentation might influence specific ecological processes, such as the movement of pollinators or edge-related dynamics, its direct contribution to changes in network structure was not supported by our analyses. This pattern is consistent with a growing number of studies across different taxonomic groups that also report weak or inconsistent effects of fragmentation per se (Fahrig, 2017, Galán-Acedo et al., 2019a,b). Our results collectively demonstrate how habitat loss initiates a cascade of changes that alter species composition and interaction patterns, ultimately compromising the resilience and persistence of plant–vertebrate pollination networks. Based on this evidence, we argue that the most effective strategy for conserving vertebrate pollination interactions is to focus on maintaining and restoring forest cover. While small habitat fragments can still play important roles by enhancing connectivity and supporting some ecosystem services, it is the overall amount of forest that best explains the integrity of plant–vertebrate pollinator networks in highly modified landscapes.

CRediT authorship contribution statement

Milena Gama: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Pamela C. Santana:** Writing – review & editing,

Visualization, Formal analysis, Conceptualization. **Paulo R. Guimarães:** Writing – review & editing, Supervision, Conceptualization. **Eliana Cazetta:** Writing – review & editing, Supervision, Methodology, Conceptualization.

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111419.

Data availability

All data used in analyses will be found at https://github.com/ upon acceptance of the study.

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