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Drivers of vertebrate pollination network patterns in the Neotropics: from historical biogeography to contemporary anthropogenic impacts

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Drivers of vertebrate pollination network patterns in the Neotropics: from historical biogeography to contemporary anthropogenic impacts

Resumo

As interações entre plantas e polinizadores vertebrados, como beija-flores e morcegos, são fundamentais para a manutenção da biodiversidade e dos serviços ecossistêmicos nas florestas tropicais. No entanto, os fatores que moldam a estrutura e a composição dessas redes de interações ainda estão sendo investigados, especialmente sob uma perspectiva integrativa que considere tanto processos históricos quanto contemporâneos. Nesta tese, investigamos como a história biogeográfica Neotropical e as mudanças recentes nas paisagens, particularmente a perda de habitat e a fragmentação florestal, influenciam redes de interações entre plantas e polinizadores vertebrados. A partir de um banco de dados composto por 67 redes de interações planta-polinizador, abrangendo 12 países e envolvendo 740 espécies de plantas e 179 espécies de polinizadores (principalmente beija-flores e morcegos), nós exploramos como padrões biogeográficos e mudanças antrópicas moldam essas redes. No primeiro capítulo, mostramos que a configuração atual das redes é fortemente influenciada por eventos biogeográficos, como o soerguimento dos Andes, a formação de ilhas e conexões históricas, além do conservadorismo de nicho. Esses processos históricos explicam padrões de composição e de similaridade nas interações ao longo das regiões neotropicais. No segundo capítulo, avaliamos os efeitos das mudanças contemporâneas nas paisagens tropicais. Os resultados mostram que a perda de habitat é o principal fator que promove mudanças estruturais nas redes e o turnover de espécies e interações. Por outro lado, a fragmentação *per se* (ou seja, independente da perda de habitat) não influenciou significativamente a estrutura das redes. De forma geral, os resultados indicam que as redes de interações entre plantas e polinizadores vertebrados das florestas Neotrópicais são moldadas por um balanço entre legados históricos e pressões contemporâneas. Este trabalho reforça a importância de considerar tanto os processos biogeográficos quanto as dinâmicas atuais da paisagem para compreender e conservar redes de interações ecológicas em ambientes tropicais.

Palavras-chave: interações, paisagem, nicho, beija-flor, morcego

Abstract

Interactions between plants and vertebrate pollinators, such as hummingbirds and bats, are fundamental for the maintenance of biodiversity and ecosystem services in tropical forests. Despite this, the factors that shape the structure and composition of these networks are still being studied, especially considering an integrative perspective that considers both historical and contemporary processes. In this thesis, we investigated how biogeographic history in the Neotropics and recent landscape changes, particularly habitat loss and forest fragmentation, influence interaction networks between plants and vertebrate pollinators. Using a database comprising of 67 plant-pollinator interaction networks, covering 12 countries and involving 740 plant species and 179 pollinator species (mainly hummingbirds and bats), we explored how biogeographic patterns and anthropogenic changes shape these networks. In the first chapter, we show that the current configuration of the networks is strongly influenced by biogeographic events, such as the uplift of the Andes, the formation of islands and historical connections, as well as niche conservatism. These historical processes explain patterns of species composition and interaction similarity across the Neotropical regions. In the second chapter, we evaluated the effects of contemporary changes in tropical landscapes. The results show that habitat loss is the main factor driving structural changes in the networks and turnover of species and interactions. On the other hand, fragmentation per se (measured by the spatial configuration of forest fragments) did not show a significant effect on network structure. Overall, the results indicate that interaction networks between plants and vertebrate pollinators in Neotropical forests are shaped by a balance between historical legacies and contemporary pressures. This work reinforces the importance of considering both biogeographic processes and current landscape dynamics to understand and conserve ecological interaction networks in tropical environments.

keywords: interaction, landscape, niche, hummingbird, bat.

Sumário

INTRODUÇÃO GERAL [1]

Você já parou para pensar que boa parte das frutas que chegam até nós, assim como muitos frutos de espécies de plantas nas florestas, só existem porque foram visitadas por um polinizador? Essa tarefa pode ser realizada por invertebrados, especialmente insetos como abelhas, borboletas, mariposas e moscas. Ou por vertebrados, como aves e mamíferos. No caso das florestas tropicais, esse trabalho não é realizado só por insetos: beija-flores, morcegos e até alguns mamíferos não voadores são responsáveis por transportar pólen de uma flor para outra, garantindo que essas plantas consigam se reproduzir e manter suas populações ao longo do tempo. Para se ter uma ideia da importância desse serviço, cerca de 90% das plantas com flores das florestas tropicais dependem de algum polinizador para completar seu ciclo de vida (Ollerton et al. 2011). E o mais fascinante é que muitos desses animais são capazes de percorrer longas distâncias, levando entre áreas bem distantes. Isso ajuda a conectar populações de plantas que, muitas vezes, estão separadas por quilômetros (Heithaus et al., 1975; Wolowski et al., 2013). Esse serviço invisível mantém a diversidade genética das espécies (Duminil et al., 2007), fortalece os ecossistemas e, além disso, sustenta boa parte da biodiversidade que faz das florestas tropicais alguns dos ambientes mais ricos do planeta.

Esses encontros entre plantas e polinizadores não acontecem de forma isolada na natureza. Eles fazem parte de complexas redes de interação, onde cada espécie ocupa um papel, seja como quem oferece alimento (como néctar e pólen), seja como quem transporta esse pólen (Bascompte and Jordano, 2014). E entender como essas redes se formam, se mantêm ou se transformam é essencial para o manejo do ambiente, bem como para conservar a biodiversidade de maneira efetiva (Keyes et al., 2021). O que nós vemos hoje nas florestas, ou seja, se uma espécie de polinizador visita determinada planta com características específicas e quais espécies estão ali, não é fruto apenas do que acontece agora. É também resultado de uma história que começou há milhões de anos, como o movimento dos continentes, o surgimento de cadeias de montanhas como os Andes, e a formação de conexões entre ilhas e continentes (Barreto et al., 2023; Dellinger et al., 2024). Tudo isso deixou marcas profundas na diversidade e nas relações entre plantas e animais (Vollstädt et al., 2025).

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[1] Optei por escrever a introdução geral em uma linguagem próxima da comunicação científica, por ver nesse espaço a chance de dialogar com um público mais amplo, sem abrir mão do rigor conceitual.

Mas não é só o passado que conta. A forma como transformamos as paisagens hoje também tem um impacto enorme sobre as espécies e as interações que elas mantêm na natureza. Isso significa que fatores como urbanização, o desmatamento e a fragmentação das florestas podem redefinir quem consegue sobreviver em determinado ambiente e, consequentemente, quem interage com quem (Bonfim et al., 2023; Maruyama et al., 2024). E, embora algumas consequências pareçam óbvias, a verdade é que ainda não sabemos muito sobre como essas transformações afetam as redes de interações ecológicas, como a polinização. Estamos vivenciando um cenário de transformações ambientais intensas e aceleradas, muitas vezes imprevisíveis. Nesse contexto, nem sempre sabemos como interações mutualísticas — como aquelas entre plantas e seus polinizadores — respondem a pressões como o desmatamento e a fragmentação. Apesar da existência de estudos importantes sobre o tema (Bomfim et al., 2018; Bonfim et al., 2023; Ferreira et al., 2020; Librán-Embid et al., 2021; Soares et al., 2021), muitas questões permanecem em aberto. E tem um detalhe que nem sempre é tão óbvio, mas que importa bastante para entender esse quebra-cabeça: a fragmentação da paisagem não é a mesma coisa que simplesmente ter mais ou menos floresta (Fahrig, 2003). Uma região pode até manter uma boa quantidade de mata, mas se essa vegetação estiver muito dividida em pequenos pedaços isolados, isso levanta uma pergunta importante — como será que isso influencia a vida das espécies e as interações que elas mantêm entre si? Até aqui, a ciência ainda tinha poucas respostas sobre como exatamente a fragmentação, independentemente da quantidade de floresta que sobra, afeta as interações (Cazetta and Fahrig, 2022) e processos como a polinização (Hadley and Betts, 2012).

Foi a partir de todas essas reflexões que esta tese nasceu. A ideia foi entender como as redes de interações entre plantas e polinizadores vertebrados como beija-flores e morcegos são moldadas tanto pelo que aconteceu há milhões de anos, quanto pelo que está acontecendo nas paisagens hoje. Afinal, até que ponto o passado determina as interações? E quanto disso é afetado pelas mudanças que fazemos no presente? Para responder essas perguntas, construímos um banco de dados reunindo informações já publicadas sobre interações entre plantas e polinizadores ao longo de quase 40 anos. Isso resultou em um conjunto de 67 redes de interação entre plantas e polinizadores vertebrados, distribuídas por 12 países do Neotrópico: Brasil (32 redes), Equador (9), Colômbia (7), Costa Rica (5), México (3), Bolívia (2), Cuba (2), Porto Rico (2), Dominica (2), Granada (1), Jamaica (1) e Peru (1). No total, essas redes incluem 740 espécies de plantas, pertencentes a 76 famílias botânicas, e 180 espécies de polinizadores vertebrados, como beija-flores, morcegos e algumas aves passeriformes. A partir desse banco de dados, dividimos o nosso trabalho em dois capítulos. No primeiro capítulo, olhamos para o passado: investigando como a história biogeográfica, os movimentos dos continentes, o surgimento dos Andes, a formação de ilhas, ajudou a moldar as redes de interação que estruturaram a polinização nas florestas Neotropicais. Isso resultou no capítulo intitulado "*Biogeography of Vertebrate Pollination on the Neotropics*". No segundo capítulo, voltamos o olhar para o presente: analisando como as mudanças na paisagem, especificamente a perda de habitat e a fragmentação, afetam as interações entre plantas e polinizadores, o que resultou no manuscrito "*Habitat loss, not fragmentation per se, drives structural changes and species turnover in plant–vertebrate pollinator networks*". Ao compreender como o passado e o presente se combinam para moldar as interações entre plantas e polinizadores, também entendemos melhor como conservar esses sistemas.

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Capítulo I

Biogeography of Vertebrate Pollination on the Neotropics

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Abstract

In Neotropical forests, about 90% of plant species depend on pollinators to complete their reproductive cycles, and a considerable portion relies on vertebrate pollinators, such as hummingbirds and bats. These animals are crucial for maintaining gene flow between plant populations, especially due to their ability to travel long distances, directly influencing the genetic structure of plant populations. The geological history of the Neotropics, from the breakup of Gondwana (~100 million years ago) to events like the uplift of the Andes, the Caribbean islands formation and the Panama land bridges, played a key role in species diversification and in shaping plant–pollinator interactions. The independent evolution of nectar-feeding hummingbirds and bats illustrates how these historical processes have influenced ecological interactions. To understand how biogeographic processes shape these interactions, we analyzed an extensive dataset of vertebrate pollination networks spanning approximately four decades of records from Neotropical rainforests. Our goal was to understand how large-scale historical processes influence plant–pollinator interactions. Specifically, we addressed two central questions: (i) how do biogeographic processes affect network structure, species composition, functional traits, and the ecological roles of pollinators across different Neotropical regions? and (ii) are interaction patterns primarily determined by niche conservatism, reflecting evolutionary history, or by niche evolution, driven by local adaptation? Our results show that networks are generally nested, weakly connected, and have low modularity, but exhibit high interaction turnover within and between subregions. The Caribbean and Andes represent contrasting extremes: the Caribbean harbors simpler, less diverse networks, likely shaped by island-related processes such as extinctions and low diversification. In contrast, the Andes host richer, more complex networks, with high species and interaction dissimilarity, reflecting rapid diversification driven by the uplift of the mountain range. Beyond this biogeographic variation, niche conservatism emerges as a key structuring process, indicating that evolutionary history imposes constraints on ecological interactions. These results highlight how evolutionary and biogeographical legacies continue to shape plant–vertebrate pollinator networks across the Neotropics.

Key-words: networks, niche conservatism, beta-diversity, hummingbird, bat.

1. Introduction

Nearly 90% of flowering plant species rely on animal pollination in tropical forests (Ollerton, Winfree & Tarrant, 2011; Tong *et al.*, 2023), within which a subset of these species depends on vertebrates for pollination (Feinsinger & Colwell, 1978; Bawa, 1990). In the neotropics the main vertebrate pollinators are birds and mammals, particularly hummingbirds (Trochilidae) and nectar feeding bats (Phyllostomidae) (Fleming, Geiselman & Kress, 2009) (Figure 1). Hummingbirds visit approximately 95 plant families contributing to the pollination of around 7,000 species (Fleming & Muchhala, 2008; Rodríguez-Flores *et al.*, 2019; Barreto *et al.*, 2023). Meanwhile, bats visit around 67 plant families and are pollinators for approximately 530 plant species (Kunz *et al.*, 2011). Although these species represent a relatively small percentage of the total flora, there is notable diversity in their growth habits, ranging from shrubs to trees (Fleming, 2005). In fact, hummingbird pollination may be associated with the accelerated rate of diversification of certain plant groups, such as Bromeliaceae, Gesneriaceae, and Campanulaceae (Bawa, 1990; Barreto *et al.*, 2023). Therefore, nectar-feeding vertebrates play a crucial role in shaping the Neotropical biota and the ecological and evolutionary dynamics of the region (Fleming & Muchhala, 2008; Dalsgaard *et al.*, 2021).

In general, ecological and evolutionary processes are spatially structured, generating unique interaction and biogeographic patterns of ecological dynamics (Sexton *et al.*, 2009; Cumming *et al.*, 2010). For instance, the geographic overlap between plants and pollinators is essential for the occurrence of the interaction (Duffy & Johnson, 2017; Phillips *et al.*, 2020). Even plants pollinated by generalist species are constrained by the need of their interactors to reproduce and survive (Moeller *et al.*, 2012). Additionally, pollinators are essential for maintaining the gene flow between distant plant populations (Duminil *et al.*, 2007). Vertebrate pollinators, such as bats and non-territorial hummingbirds, are capable of traveling long distances foraging over many kilometers, increasing their role in affecting plant population genetic structure (Heithaus, Fleming & Opler, 1975; Wolowski *et al.*, 2013). A global study revealed that the exclusion of bat and bird pollinators would result in declines of 83% and 46% in fruit and seed production, respectively, for some plant species (Ratto *et al.*, 2018). Therefore, integrating knowledge on biogeography and pollination interaction can enhance our understanding of macroecological patterns, allowing us to test hypotheses about the drivers of species distributions and ultimately guide strategies for biodiversity management and conservation (Soberón & Peterson, 2009; Wiens, 2011).

In order to comprehend the drivers of species distributions and develop an efficient biodiversity management (Cumming *et al.*, 2010), networks of interaction represent a powerful tool. Ecological networks allow us to visualize geographic patterns and changes within biogeographic regions and across ecological gradients (Montoya & Galiana, 2017; Tylianakis & Morris, 2017). Over the last few decades, a significant advance in our understanding of pollination networks (Martín González *et al.*, 2015; Zanata *et al.*, 2017; Maruyama *et al.*, 2018) has revealed latitudinal patterns (Rech *et al.*, 2016), and enable comparisons across tropical and temperate environments (Schleuning *et al.*, 2012; Sonne *et al.*, 2020), climatic regimes (Dalsgaard *et al.*, 2013), and biomes (Araujo *et al.*, 2018). These studies highlight how environmental conditions, both contemporary and historical, may affect the evolution of interactions, including the evolution of specific traits connected to specific environments (Herrera, 2002; Lanuza *et al.*, 2023). For instance, wind pollination generally evolves under unstable conditions, such as temperate regions with historically and currently fewer stable climates (Ackerman, 2000). In contrast, in dense and closed areas, like tropical forests, the probability of pollination by wind decreases drastically, increasing the importance of biotic pollination (Regal, 1982; Rech *et al.*, 2016). Therefore, to further enhance our understanding of how species interactions are shaped by environmental conditions, it is crucial to investigate how shared biogeographic processes shaped the evolution of ecological interactions and their network structure, shedding light on the adaptive and evolutionary processes that sustain ecosystem interactions.

In the Neotropical region, species that overlap their distribution probably have experienced similar historical geographic events, however their response to these events might be different, originating distinct patterns of interaction in the community and consequently different network structures. There are two main evolutionary processes hypothesized to explain species distribution range and, consequently, their coexistence: niche conservatism and niche evolution (Wiens & Graham, 2005). The former process, i.e. niche conservatism, reflects the retention of ancestral traits in species, even in the face of environmental changes, resulting in greater niche overlap (Wiens & Graham, 2005). The latter process, i.e. niche evolution, on the other hand, reflects changes in species' responses to environmental alterations, leading to greater specialization in resource use and, consequently, less niche overlap. Species that faced similar historical contingencies may converge or diverge between niche conservatism and niche evolution composing distinct proportions of the interactions in one community (Wiens & Graham, 2005; Wiens, 2011). This study synthesizes four decades of research on plant–vertebrate pollination interactions in Neotropical rainforests to examine how shared biogeographic history has shaped these interactions. We characterize how biogeographic processes influence network structure, species turnover, interaction turnover, the distribution of key morphological traits, and the role of interacting species in linking network interaction patterns predicted by niche conservatism or niche evolution. Our study aims to answer two overarching questions: (i) How do Neotropical biogeographic processes (such as the biogeographic history of Caribbean islands, area colonization, the uplift of the Andes, and the emergence of the Isthmus of Panama) shape network structure, composition, trait distributions, and species functional roles across regions? (ii) Are interaction patterns constrained by evolutionary history (niche conservatism) or shaped by local adaptation (niche evolution)? We expect biogeographic processes to be reflected in a degree of variation in network topology. Although certain structural patterns may be conserved, regions with distinct biogeographic histories are likely to exhibit differences in network configuration, including variation in levels of nestedness, modularity, connectance, and indirect interactions. These differences are expected to reflect both variation in species composition and the ecological and evolutionary contexts of each region (Dalsgaard *et al.*, 2021; Vollstädt *et al.*, 2025). Similarly, the distribution of functional traits — such as bill length, corolla depth, and other morphological features mediating interactions, is also expected to vary across biogeographic regions. Additionally, we expect that if niche conservatism is the dominant process, phylogenetically similar species will maintain similar ecological interactions (that is, tand to interact with same species), even when occurring in different biogeographic regions (Gómez, Verdú & Perfectti, 2010; Peralta, 2016). After dispersing outside their center of origin, species are likely to retain ancestral traits that shape how and with which partners they interact. In such cases, when their original partners are absent, species may exhibit interaction turnover but with low rewiring, interacting instead with ecologically similar partners. Conversely, if interaction dissimilarity is not related to the phylogenetic dissimilarity of the species involved, this suggests that niche evolution, that is, the divergence of ecological traits over time, is the main driver. Under this scenario, even closely related species may form different interactions due to local adaptation.

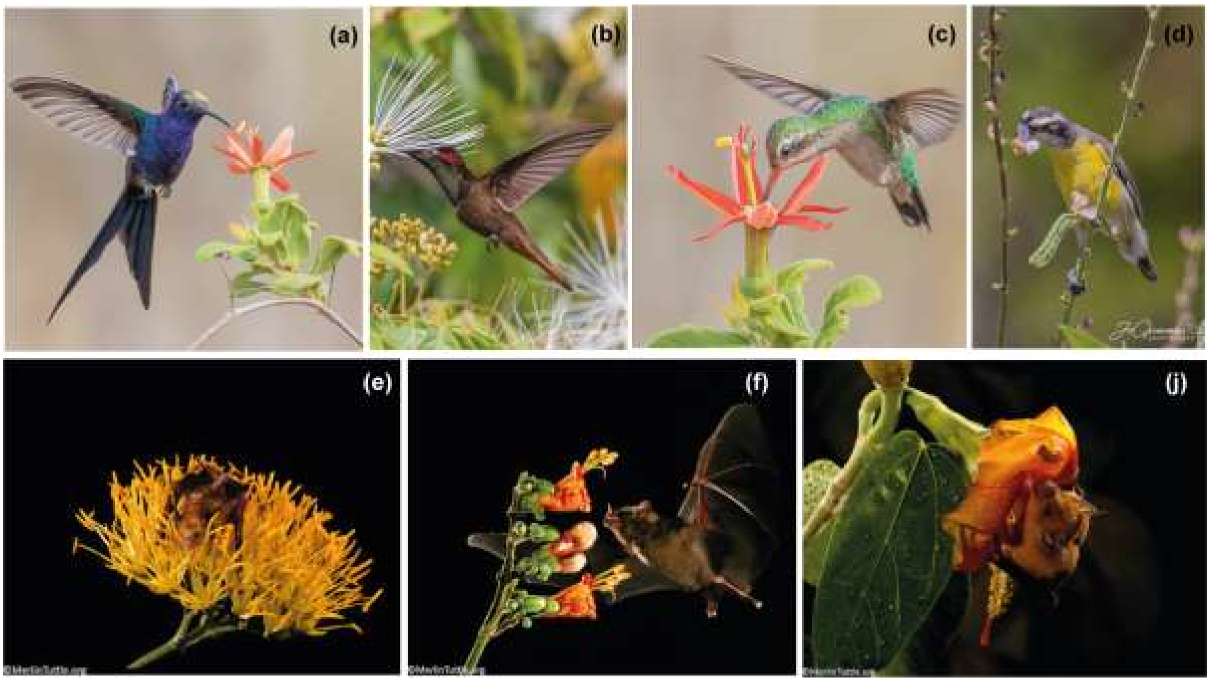

Figure 1: Species of birds and bats visiting flowering plants in the Neotropics. In (a) *Eupetomena macroura*; (b) *Chrysolampis mosquitus*; (c) *Chlorostilbon lucidus;* (d) *Coereba flaveola*; (e) *Erophylla sezekorni;* (d) *Glossophaga comissari* and (f) *Phyllonycteris poeyi*. The bird and bat photographs are respectively authored by João Victor Fernandes, and merlintuttle.org

2. Historical biogeography of vertebrate pollination in the Neotropics

The equatorial positioning of the Neotropics, coupled with its ancient geological history, has given rise to a remarkable diversity of environments, climates, and topographies. The geological history of the Neotropics began with the breakup of Gondwanaland approximately 100 million years ago (Mya) during the Mesozoic, which led to the complete isolation of South America from Africa and set the stage for distinct evolutionary trajectories on each continent (Sanmartín & Ronquist, 2004). Consequently, the Neotropical biota evolved under a spatially and temporally diverse landscape (Hoorn *et al.*, 2010; Antonelli & Sanmartín, 2011). This diversity is reflected in its classification into three primary subregions — Antillean, Brazilian, and Chacoan — along with two transition zones: the Mexican Transition Zone, bridging the Nearctic and Neotropical regions, and the South American Transition Zone, connecting Lowland South America to the Andes (Morrone, 2014; Morrone *et al.*, 2022). In this study, we take advantage of this characterization to establish a framework for identifying shared patterns of ecological interactions within each biogeographic region and assessing whether distinct historical processes have led to divergent network structures across regions. If species within a given region have been shaped by similar geological and climatic histories, we might expect ecosystems to converge in the properties exhibited by their interaction network structure. These dynamic landscapes have undoubtedly spurred species diversification (Barreto *et al.*, 2023; Dellinger *et al.*, 2024), but this approach allows us to disentangle how biogeographical history has also influenced the architecture of flowering plants and vertebrate pollinators across the Neotropics, a hallmark of Neotropical biodiversity. To understand how biogeographical history has influenced the evolutionary pathways of species interactions in the Neotropics, we first present the major geological events known to have shaped the Neotropical Biota.

The first key aspect of this history is the breakup of Gondwanaland, which profoundly influenced the independent evolution of the main vertebrate pollinators in the Neotropics (Giannini & Velazco, 2020; Fleming & Muchala, 2008). Within the Neotropics, nectar-feeding bats evolved independently in two subfamilies (Lonchophyllinae and Glossophaginae), illustrating convergent adaptations to nectarivory (Datzmann, von Helversen & Mayer, 2010). Hummingbirds, however, may have originated in Eurasia (McGuire et al., 2014). After their diversification in South America, some hypotheses suggest that hummingbirds went extinct in both Eurasia and North America (McGuire et al., 2014). Consequently, following their establishment in South America, hummingbirds recolonized North America and expanded their range into the Caribbean islands. During the Cenozoic, the emergence of major land connections, such as the Isthmus of Panama, the Antillean archipelago, and the uplift of the Andes, facilitated dispersal and gene flow, thereby shaping the ecological interactions and niche breadth of both bats and hummingbirds (Sexton et al., 2009).

A pivotal land bridge was the formation of the Isthmus of Panama (~3 Mya), which facilitated the Great American Biotic Interchange (GABI), enabling the movement of flora and fauna between North and South America (Dávalos, Velazco and Rojas, 2020). Although it may not have been the main driver for the colonization of nectarivorous bats and hummingbirds in North America, due to a possible earlier colonization during periods of low sea level (overwater dispersal) prior to the uplift of the Isthmus (McGuire et al. 2014; Morgan et al. 2023; Dávalos, 2009), this geological event still had important consequences. For hummingbirds, it opened a route for expansion into Central and North America, promoting rapid diversification and colonization of new habitats (Marshall et al., 1982; McGuire et al., 2014), potentially leading to homogenization among regions.

Similarly, for bats, it facilitated adaptation to diverse climatic zones in North America and contributed both to increased species richness and the development of ecological specialization (Woodburne, 2010; O'Dea et al., 2016). In both groups, niche evolution may have played a role in enabling adaptation to novel environments and diversification of ecological interactions, while niche conservatism may have reinforced allopatry in geographic distributions and driven species turnover (Holt & Gaines, 1992; Peterson, Soberón & Sánchez-Cordero, 1999; Wiens & Graham, 2005; Wiens, 2011).

Nectarivorous bats and hummingbirds likely expanded into the Caribbean islands through overwater dispersal (Rojas et al., 2016). For bats, this expansion may have been facilitated by exceptionally low sea levels during Miocene transitions, which enabled two-way biotic exchange between the South American continent and the Caribbean islands (Dávalos et al.). In the Caribbean, bat diversity is comparatively low, likely as a result of high extinction rates driven by climate fluctuations and sea-level changes, particularly during deglaciations (Dávalos & Russell, 2012), and further influenced by the species–area relationship (Stevens, Weber & Villalobos, 2020). Hummingbirds, in turn, appear to have colonized the Caribbean more recently, around 5 Ma. Their low diversity in the region may be due to a combination of extinction events and the relatively short time since their arrival, which may have limited the group's opportunity to achieve the diversification peaks observed in other regions (McGuire et al., 2014).

Even before establishment of the land bridges, the uplift of the Andes, beginning around 65 Mya in the Late Cretaceous, profoundly shaped South America's landscape, climate, and biodiversity (Hoorn et al., 2010; Antonelli & Sanmartín, 2011), creating altitudinal gradients and diverse niches that promoted adaptive radiations among nectarivorous bats and hummingbirds (Baker *et al.*, 2003; Datzmann *et al.*, 2010; McGuire *et al.*, 2014). These organisms adapted to varying resources and climates, with hummingbird pollination becoming more prevalent in montane forests than in lowland rainforests, likely due to temperature constraints on ectothermic pollinators (Classen *et al.*, 2015; Dellinger *et al.*, 2023). The Andes acted as biogeographic barriers, promoting allopatric speciation and diversification in clades such as Brilliants, Coquettes, Hermits, Mangoes, Bees, and Emeralds (McGuire et al., 2014) alongside adaptations in nectar plants, fostering co-evolution and evolutionary divergence (Graham et al., 2006; Hinkelmann & Schluter, 2018).

The uplift of the Andes influenced the diversification of phyllostomid bats, including nectarivorous species (Villalobos & Arita, 2010). Patterns of bat richness reveal a strong geographical gradient: regions such as the southwestern United States, northern Mexico, and northern Argentina and Chile exhibit low species richness, whereas the Amazon Basin harbors high diversity, with the tropical Andes representing the peak of bat richness (Villalobos & Arita, 2010), particularly at mid-elevations (Stevens, Weber & Villalobos, 2020). However, bat richness declines sharply with increasing altitude, as observed in the Peruvian Andes, where only 10 out of 101 species occur above 3,200 m (Graham, 1983). In clear contrast to hummingbirds, which tend to become more prominent in montane forests, bats show a reduction in species richness with altitude, likely due to physiological constraints and niche conservatism (Stevens, Weber & Villalobos, 2020). These patterns reflect complex interactions among ecological, geographic, and historical factors, including range cohesion, phytogeographic domains, and climatic history (Villalobos & Arita, 2010).

In this study, to assess the biogeographical mediated network patterns, we consider four neotropical subregions: a simplification of Morrone's (2014) classification (Figure 2). In this simplified classification, we merged the Brazilian and Chacoan regions to form Lowland South America, extending to the southern portion of the Isthmus of Panama. Additionally, the Mexican transition zone was integrated into Central America, giving rise to what we refer to as the North and Central America subregion. The South American transition zone, here described as the Andes, encompasses the Andean mountains of South America. Finally, we have the oceanic islands of the Antilles, referred to as the Caribbean subregion. This classification, suggested in a biogeographical network study conducted by Dalsgaard et al. 2021, also proved suitable for the interaction networks addressed in this study and reflect the irradiation time of nectar feeding bats and hummingbirds.

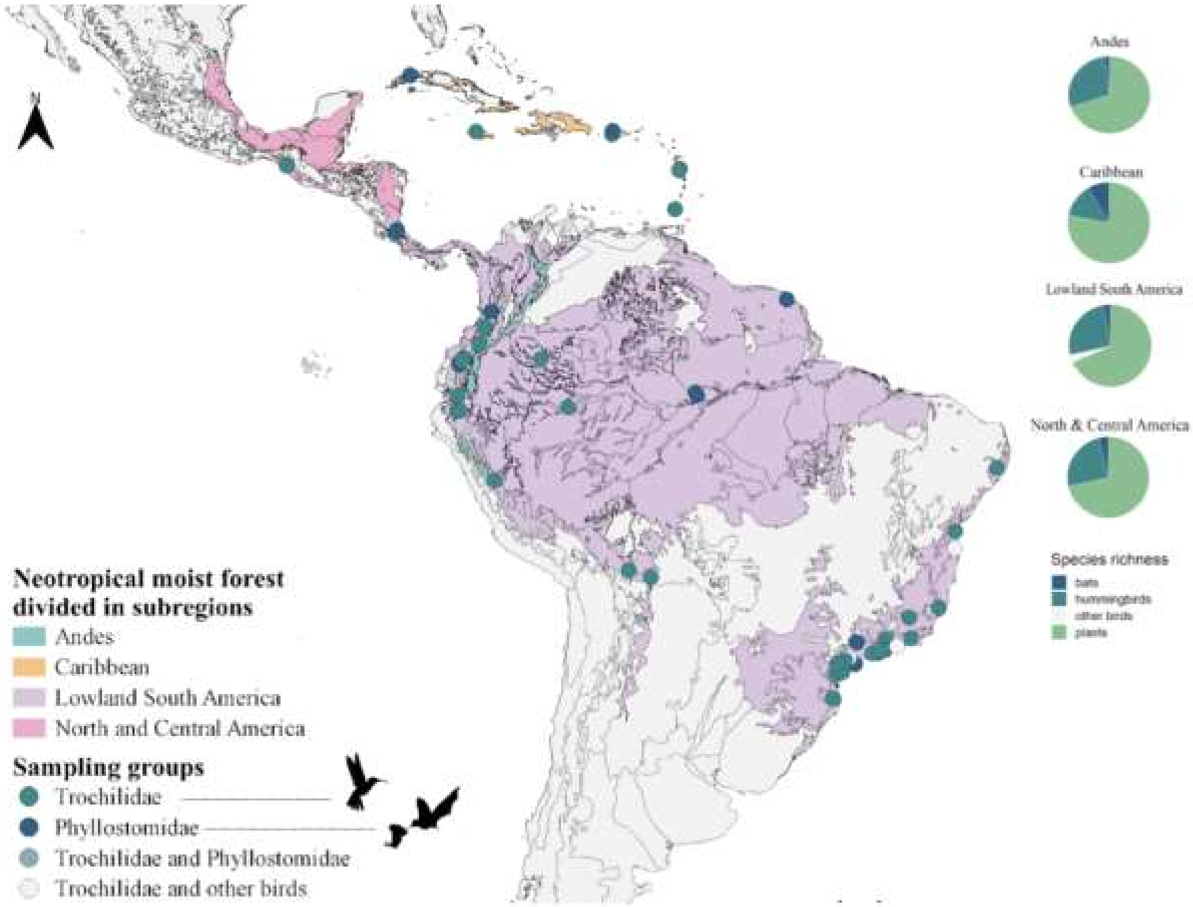

Figure 2: Neotropical moist forest map divided into four biogeographical subregions: i) Andes in light green; ii) Caribbean in light orange; iii) Lowland South America in light purple; iv) North and Central America in light pink. The white represents the area not covered by tropical moist forest. The dots represent networks sampled on the area, and the color dot represents the pollinator group used to build the network: Trochilidae networks are in light green; Phyllostomidae are in dark blue and networks with both groups are in bluish green; lastly, networks with Trochilidae and other birds are in white. The pie charts represent the species richness for each biogeographical subregion. Animal silhouettes are from PhyloPic (URL: https://phylopic.org/) under an open access license
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3. Methods

3.1. Data compilation

To investigate network biogeographical patterns, we gathered data on pollination interactions involving flying vertebrates in neotropical rainforests. We conducted an extensive search across four available databases: Web of Life (Fortuna et al., 2014), Interaction Web Database (http://www.ecologia.ib.usp.br/iwdb), Atlantic Pollination (Iamara-Nogueira *et al.*, 2022), and Neobat Interactions (Florez-Montero *et al.*, 2022). Additionally, we searched in DRYAD (https://datadryad.org/), Scopus, and Web of Science using the following terms: "plant-pollinator network," "pollination network," "floral visitation network," or ("mutualistic interaction network" AND pollinator) AND "tropical." We only included empirical studies conducted in tropical moist forests that examined interactions at the community level.

The search returned a dataset comprising 67 pollination networks (*lato sensu* - including floral visitor networks), belonging to 47 different studies conducted between 1979 to 2019 (table S1). These networks span 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).

3.2. Predictors of networks structure and composition

To compare network structure patterns accross biogeographic regions, we examined network nestedness, modularity, connectance, the proportion of indirect links in the networks, and interactions beta diversity. We computed network nestedness using the NODF index (Almeida-Neto *et al.*, 2008), with values ranging from 0 (no nestedness) to 100 (perfect nestedness), and modularity using Stephen Beckett's algorithm (2016), which measures the formation of cohesive subgroups of species, ranging from 0 (no modules) to 1 (perfectly modular). Additionally, we computed the connectance, representing the proportion of observed interactions compared to possible interactions. To assess statistical significance, we generated 1000 null models using the Patefield algorithm, and calculated z-scores to compare observed values against these models (see details in supplementary materials). To estimate the potential for indirect effects in plant–pollinator networks, we first used matrix **A** to generate a square matrix **B**, in which all species (plants and pollinators) appear in both rows and columns, with row *i* and column *i* referring to the same species. While matrices A and B contain the same interaction information, matrix B is structured to enable the matrix operations required for estimating indirect effects. Each row of B was then standardized to sum to one, producing the matrix **B'**. Using B', we computed the total effects matrix by using $\mathbf{T}=(\mathbf{I}- \mathrm{R}\mathbf{B'})^{-1}$, where **I** is the identity matrix with the same dimensions as B', and **R** is the probability (or dependence) between interacting species. In our analysis, **R** was kept constant at 0.95 (Gama et al. 2025; Pires et al., 2020). The matrix T summarizes the potential for both direct and indirect effects to propagate through the network, under the assumption that effects decay along longer pathways.

The overall potential for indirect effects in a network was then calculated as:

$$U = \sum_i^N \sum_j^N t_{ij} \,(1 - b'_{ij}) \;/\; \sum_i^N \sum_j^N t_{ij}$$

where t_{ij} comes from the total effects matrix **T** and represents the potential influence of the species in column *j* on the species in row *i*. The term 1 - b_{ij} removes the contribution of direct interactions. In addition, T allows the estimation of each species' influence in propagating both total effects (T_{out}) and purely indirect effects within the network (see Pires et al., 2020 for details). This provides a measure of how much a species affects others through paths of varying lengths, from direct connections to longer indirect chains.

We assessed the dissimilarity among networks within the same biogeographic region (i.e., we compared the dissimilarity between pairs of networks belonging to the same biogeographic subregion, excluding comparisons between different regions, as higher dissimilarity would already be expected in those cases). Specifically, we assess four components: dissimilarity in species composition within communities ($\boldsymbol{\beta}_{S}$); dissimilarity of interactions ($\boldsymbol{\beta}_{WN}$), which is subdivided into two components: rewiring ($\boldsymbol{\beta}_{OS}$), representing the dissimilarity of interactions established between species common to both networks; and turnover ($\boldsymbol{\beta}_{ST}$), representing the dissimilarity of interactions due to species substitution (Novotny, 2009; Poisot *et al.*, 2012).

3.3. Morphological traits and species-centred analysis

To analyze how the mean trait values of interacting species vary according to the biogeographic area, we collected the traits associated directly or indirectly with the pollination process. First, the species names of plants and animals of networks were verified and, when necessary, updated using the *taxize* and *flora* packages (Chamberlain et al. 2020; Carvalho, 2020), and also the Plant of the World online repository (https://powo.science.kew.org/). For hummingbirds, we collected body mass, bill length and curvature (Dalsgaard et al. 2021; Tobias et al. 2022). For flowers, we compiled corolla length or petal length in the case of some tubular flowers (Dalsgaard et al. 2021; Iamara-Nogueira et al. 2022). We also classified each species of hummingbird according to the nine clades (McGuire et al. 2014). Finally, for bats, we compiled body mass (Gonçalves et al. 2018; Iamara-Nogueira et al. 2022; Garcia-Garcia et al. 2014; Farneda et al. 2015; Mancina et al, 2005; Ganon et al. 2005; Tschapka, 2005; Molinari et al. 2014).

3.4. Unique pairwise of interactions and species's roles

To understand the role of species and their positions within the networks, as well as their prevalence as central species in biogeographic regions, we calculated two centrality metrics: (i) closeness that reflects how close a species is to all other species in the network, representing its potential for efficient information or resource transfer and (ii) betweenness that captures the extent to which a species acts as a bridge or intermediary in the network, highlighting its role in connecting different species or groups.Using these metrics, we assessed the frequency at which species exhibited high levels of centrality in each network within the subregions.

Moreover, to assess the contribution of specific interactions to the biogeographical structure of pollination networks, we built a meta-network based on the 67 local networks compiled in this study. In this meta-network, nodes represent unique species interactions (i.e., plant–pollinator pairs), and links connect each interaction to the local networks where it occurs, forming a bipartite structure between interactions and local networks (Emer *et al.*, 2018). A link indicates the presence of a given interaction in a particular local network. Based on this meta-network, we calculated centrality metrics to quantify the relative importance and distribution patterns of interactions across the Neotropics. Specifically, we computed degree centrality, which reflects how widespread an interaction is (i.e., the number of local networks where the interaction occurs), and betweenness centrality, which indicates the extent to which an interaction connects different networks, acting as a bridge between biogeographical regions or ecological contexts.

3.5. Phylogenetic and interaction dissimilarity

Finally, to evaluate whether the phylogenetic composition of communities influences the establishment of plant–hummingbird interactions, and whether these patterns are shaped by niche conservatism or niche evolution, we quantified phylogenetic dissimilarity between networks for both groups. The plant phylogeny was derived from the GBOTB.extended tree (Jin & Qian, 2019) using the V.PhyloMaker package, while the hummingbird phylogeny followed McGuire et al. (2014). Bat phylogeny was not included due to insufficient data for nectar-feeding bats, which would be necessary to ensure reliable estimates.

From these phylogenies, we generated pairwise phylogenetic dissimilarity matrices for plants and hummingbirds using cophenetic distances, defined as the sum of branch lengths connecting two taxa on a phylogenetic tree. These distances were combined with species presence–absence data from the networks to calculate phylogenetic beta diversity via the "comdist" metric (Webb, Ackerly & Kembel, 2008), which measures phylogenetic turnover between communities.

We then integrated the resulting phylogenetic dissimilarity matrices with the interaction dissimilarity matrices described earlier. To account for biogeographical structure, networks were grouped into four bioregions: Lowland South America, Andes, Caribbean, and North and Central America. The relationship between phylogenetic dissimilarity and interaction dissimilarity was tested using linear models and linear mixed-effects models, with bioregion as a random effect, for each component of interaction dissimilarity (β_{WN}, β_{ST}, and β_{OS}), considering plants and hummingbirds separately. Detailed methods are provided in the supplementary material.

4. Biogeography of Vertebrate Pollination in the Neotropics

Across the 67 Neotropical plant-vertebrate networks we found variation in species richness and interaction patterns. Species richness varies both within these networks and across the four Neotropical subregions, with the lowland South America region exhibiting the highest richness, followed by the Andes (see Table 1). The number of interactions follows the same trend as species richness (Table 1).

Table 1: Species richness and total number interactions distributed in four subregions of Neotropics in 67 plant-vertebrate interaction networks.

	Andes	***Caribbean***	***Lowland South America***	***North & Central America***
Bat richness	10	7	24	8
Hummingbird richness	128	11	223	49
Plant richness	325	64	596	143
Other bird species	-	-	27	-
Total species richness	463	82	870	200
Total number of interactions	958	92	1505	276
Number of networks	14	8	37	8

These networks include a total of 740 plant species distributed across 76 botanical families. We found significant variations in the main plant families pollinated by vertebrates, both among different groups (hummingbirds and bats) and subregions (Figure 3). For bats, we observed that the most prevalent visited families were Fabaceae, followed by Malvaceae, and Bromeliaceae. However, when considering the different subregions, the patterns change: in the Andes, the most visited family is Campanulaceae; while in the Caribbean and North and Central America subregion, interactions are predominantly with flowers of Malvaceae. In the South America region, Fabaceae predominates among interactions. Also, Bawa (1990) indicated other botanical families commonly visited by bats in the tropics, such as Bombacaceae and the genera *Passiflora* in Passifloraceae, *Parkia* (subfamily Mimosaceae) and *Bauhinia* (subfamily Caesalpiniaceae) in Fabaceae.

As for hummingbirds, the most frequently visited families are Bromeliaceae, Gesneriaceae, and Rubiaceae. We also noticed variations in plant families visited by subregion, with Ericaceae being the most visited family in the Andes; Bromeliaceae in South America; and Rubiaceae in the Caribbean and North & Central America subregion. A similar pattern was recorded in another study, with the most frequently visited families being Acanthaceae, Bromeliaceae, Gesneriaceae, Marantaceae, Musaceae, Rubiaceae, and Zingiberaceae (Bawa, 1990; de Oliveira et al., 2025).

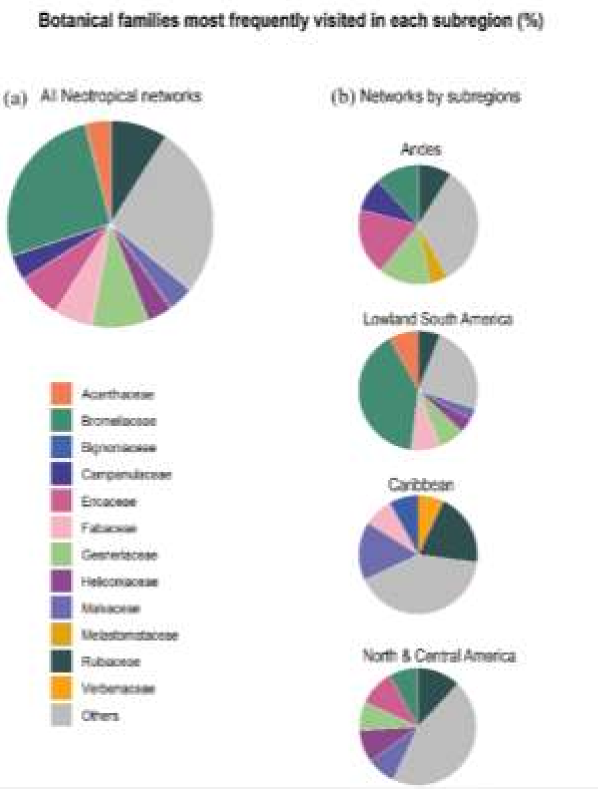

Figure 3: Percentage of interaction events (visits) by bats and hummingbirds to different botanical families in 67 plant-pollinator networks across the Neotropics. (a) Most representative plant families across all networks. (b) Most frequently visited plant families in each Neotropical subregion (Andes, Lowland South America, Caribbean, North & Central America). Colors represent plant families, indicating their relative frequency of visits.

Our database encompasses a variety of bird and bat species that interact with plants across the Neotropical subregions. The networks included 179 species of vertebrates, of which 135 are Trochilidae species, 19 belong to other groups of birds (such as Thraupidae, Icteridae, Cotingidae, and Picidae and 25 are bat species. The most common bird species interacting with plants are from the family Trochilidae (135 species), while 18 species belong to other bird families (Thraupidae, Icteridae, Cotingidae and Picidae). Phyllostomidae was the only bat family interacting with plants. From this compilation, a pattern emerges showing that Caribbean networks exhibit lower species richness both for plants and pollinators and fewer interactions, as well as a smaller number of networks documented in the region. These patterns may be related both to the lower inherent richness characteristic of this insular region and to potential undersampling.

5. Similarities and divergence in network structural patterns

The plant-pollinator networks in the Neotropics are generally nested (figure 4a). Following this pattern, the networks present an average high proportion of indirect effects (figure 4b), that is, interactions occurring through intermediary species rather than direct contact between the two species involved. On the other hand, we did not find an evident pattern of modularity, as most of the Z-modularity values are below zero, indicating that the observed modularity is less than expected by chance (figure 4c). The connectance was similar among subregions, except for the Caribbean networks, which exhibit highest connectance values (figure 4d). Pollination networks are expected to exhibit a nested structure (Bascompte *et al.*, 2003). The nested pattern is observed when specialist species interact with a subset of species that generalist species also interact with (Bascompte & Jordano, 2007). This results in the presence of highly connected generalist species, which lead to the proliferation of paths, especially indirect ones (Guimarães *et al.*, 2017; Cosmo *et al.*, 2023). Consequently this explains our results for nestedness and the proportion of indirect paths, as these metrics are correlated (Guimarães *et al.*, 2017).

Overall, the network structure varied among the subregions for all predictors evaluated (Table S1-Table7). Although the networks are predominantly nested across all subregions, the degree of nestedness was different between the Andean and Caribbean subregions (Figure 4a). Remarkably, Andean networks exhibit higher nestedness compared to Caribbean, while the opposite is observed in terms of modularity. The degree of nestedness is, in some cases, positively correlated with species richness (Bascompte et al., 2003). Thus, the observed pattern in Andean ecological networks might be explained by the high species richness in this subregion. The Andes are distinguished for hosting the highest average number of plant and pollinator species (Andes= μ 33.5; Caribbean= μ 10.6; lowland South America = μ 25.8 and North and Central América = μ 25.3) potentially fostering the coexistence between generalist and specialist species. This coexistence, in turn, may contribute to a more pronounced nestedness than observed in Caribbean networks (Bastolla *et al.*, 2009). It is noteworthy that, in the studied networks, the South America and North America subregions, also exhibited a considerable degree of nestedness, with high variance in the lowlands of South America (Figure 4a). In addition, the observed patterns in network connectance might also be explained by species richness in both cases, referring to the low connectance values found in the Andes and the high values in the Caribbean. Such a pattern is expected, as this index calculates the number of interactions performed among all possible ones, and there is a tendency for this value to increase with decreasing species richness (Olesen & Jordano, 2002). In the case of the Caribbean, referring to the high connectance values, is due to the increased probability of performing all possible interactions in a species-poor network

The structural distinctiveness of Caribbean networks may be linked to island-specific processes, such as those mentioned earlier, including extinction events during periods of sea-level rise and species–area relationships, which have been shown to be important factors limiting species richness (Dávalos, 2009; Stevens et al., 2020) and, consequently, shaping the structure of interactions. The Caribbean subregion is recognized as a biodiversity hotspot due to its remarkable levels of endemism. Although overall species diversity is lower in the Caribbean compared to the Andean subregion, the islands host a higher proportion of endemic species (Myers et al., 2000). This pattern is also evident in the groups analyzed here, where interacting hummingbird species are exclusively endemic to the Caribbean or to specific islands. Examples include *Anthracothorax dominicus*, restricted to certain islands in the subregion, and *Trochilus polytmus*, endemic to Jamaica. A similar trend is observed for bats, with species such as

Erophylla sezekorni and *Phyllonycteris poeyi* among the endemics recorded in our networks (Mancina, 2010; Simmons, 2005).

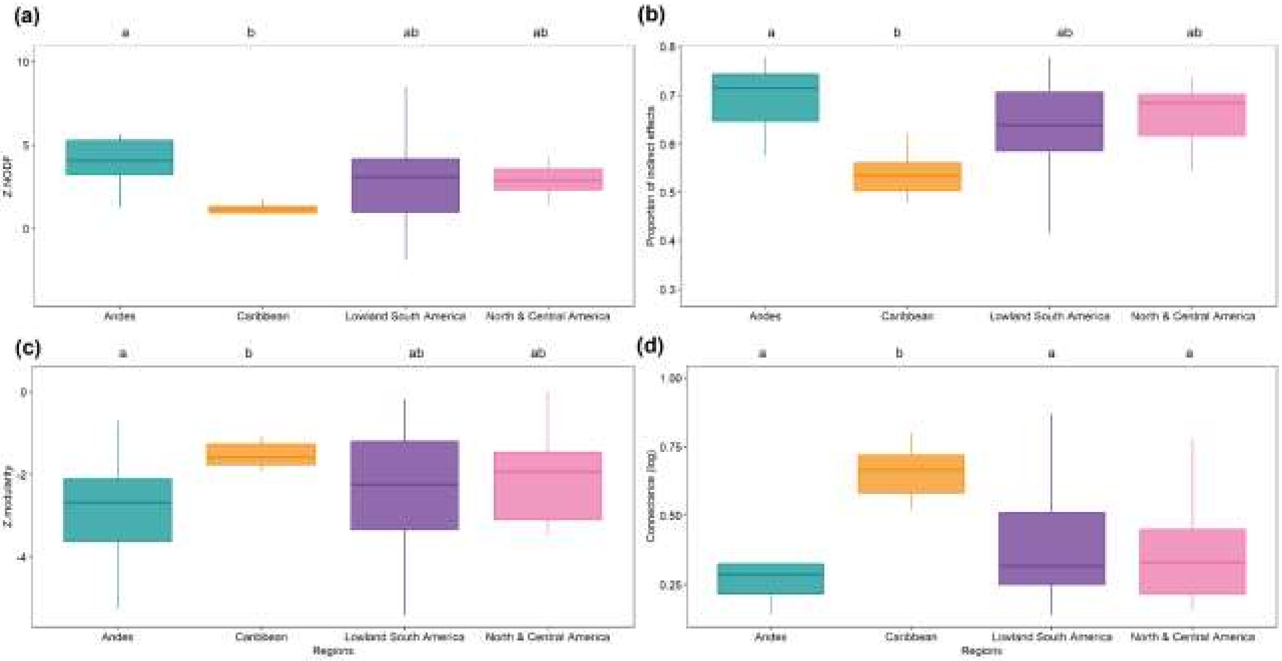

Figure 4: Values of four network metrics according to the biogeographical subregion (Andes, Caribbean, South America and North-Central America). We show the Z-score for the nestedness (a); the proportion of indirect effects cascading on the network (b); Z-score for modularity (c) logarithmic of the connectance (d). The letters at the top of each graph represent the results of pairwise comparisons conducted through Tukey's test, where different letters indicate statistical difference ($p < 0.05$).

When combining all the networks' metrics into a Principal Component Analysis (PCA), we observed a high overlap between subregions (Figure 5a; Table S5). However, the Caribbean occupied a much smaller space, indicating how this subregion differs significantly from the others, specially from Andes and Lowland South America (Figure 5b).

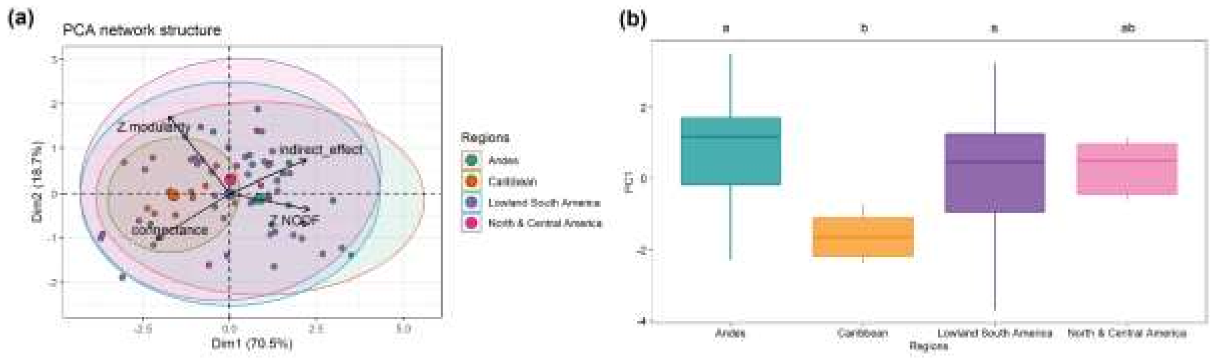

Figure 5: a) PCA graph combining the four-network metrics for the biogeographical subregions. b) First component of PCA for each subregion; Andes are in light green;

Caribbean in orange; Lowland South America in light purple; North and Central America in light pink. The letters at the top of (b) graph represent the results of pairwise comparisons conducted through Tukey's test, where different letters indicate statistical difference ($p < 0.05$).

For a more comprehensive understanding of variations in network structure, we examine their dissimilarity through beta-diversity of interactions. When assessing the dissimilarity among networks within a subregion, we observe that, in general, these networks exhibit relatively high dissimilarity (Figure 6). Both $\boldsymbol{\beta}_{\mathrm{WN}}$ and $\boldsymbol{\beta}_{\mathrm{S}}$ maintained elevated values in almost all subregions. Even though the compared networks originate from the same subregion, they display considerable distinction in terms of total interaction dissimilarity ($\boldsymbol{\beta}_{\mathrm{WN}}$) - values close to 1 (see Figure 6). This dissimilarity appears to be primarily associated with differences in community composition ($\boldsymbol{\beta}_{\mathrm{S}}$) and, consequently, species turnover ($\boldsymbol{\beta}_{\mathrm{ST}}$), as these two components are positively correlated (Poisot et al., 2012). Additionally, in communities where common species exist, they appear not to interact similarly, as evidenced by high values of $\boldsymbol{\beta}_{\mathrm{OS}}$. High $\boldsymbol{\beta}_{\mathrm{OS}}$ values reflect a low number of shared interaction pairs between networks, both in the general context of Neotropical networks and within subregions (Fig. 6).

When comparing the four subregions, the Caribbean exhibited the lowest values of interaction rewiring ($\boldsymbol{\beta}_{\mathrm{OS}}$), close to zero. This indicates that, when the same species co-occur across networks, they tend to maintain very similar interaction patterns, showing a strong conservation of ecological roles. Despite this, the total dissimilarity of interactions ($\boldsymbol{\beta}_{\mathrm{WN}}$) and the components related to species turnover ($\boldsymbol{\beta}_{\mathrm{S}}$ and $\boldsymbol{\beta}_{\mathrm{ST}}$) remain high. This pattern suggests that interaction dissimilarity in the Caribbean is primarily driven by species replacement rather than by changes in the way shared species interact. This is consistent with the fact that while vertebrate species like *Orthorhyncus cristatus*, present in three out of five hummingbird networks, and *Monophyllus redmani*, present in all bat networks, are widespread across islands, plant species composition varies substantially. This leads to high species turnover and, consequently, high dissimilarity of interactions despite the ecological consistency among shared vertebrate species.

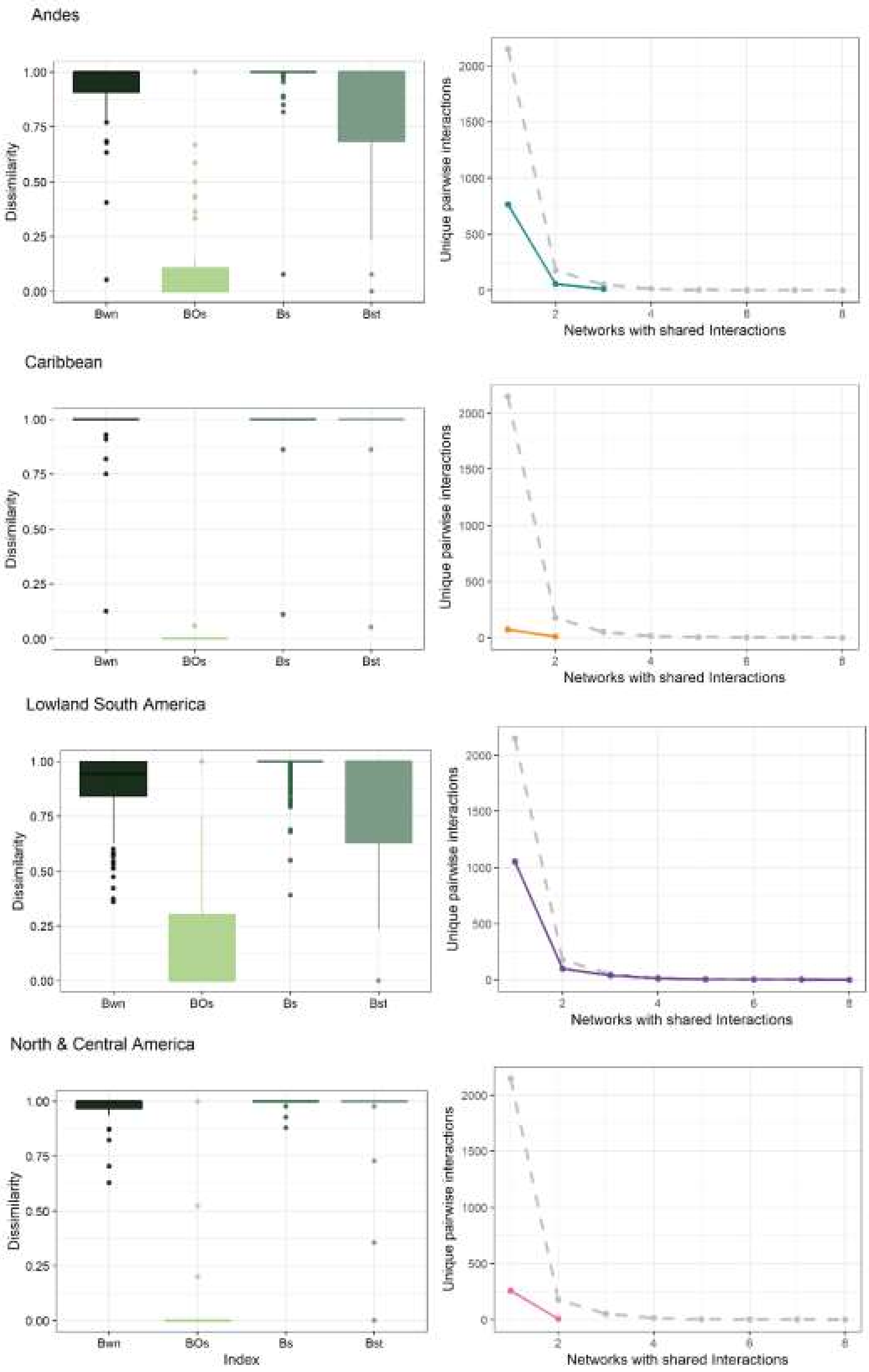

Figure 6: Dissimilarity of interactions in the networks belonging to the Neotropical subregions. The dissimilarity is represented in boxplot graphs by indices: Dissimilarity in species composition within communities ($\boldsymbol{\beta}_{\mathrm{S}}$); dissimilarity of interactions ($\boldsymbol{\beta}_{\mathrm{WN}}$), which

is subdivided into two components: rewiring ($\boldsymbol{\beta}_{\mathrm{OS}}$), representing the dissimilarity of interactions established between species common to both networks; and turnover ($\boldsymbol{\beta}_{\mathrm{ST}}$), representing the dissimilarity of interactions due to species substitution. The line graphs represent the sharing of pairwise interactions between local networks belonging to the Neotropical subregions. The number of networks sharing a unique interaction varies from 1 (when the pair occurs in only one local network) to 8 (when the pair is shared across 8 networks).

6. Morphological biogeographic patterns in interacting species

Hummingbird traits varied among subregions (Table S6-S9). We observed a pattern where hummingbirds from the Andes differed from the Caribbean subregion by presenting longer and less curved bills (Figure 7a-b). Additionally, hummingbirds from the Caribbean subregion showed a smaller body size (Figure 7c). On the contrary, bat traits were similar between subregions (see Figure 8a; Table S10).

Interestingly, when looking at the average corolla length per biogeographic region, the differentiation is not as clear as it is for hummingbird's bill (Figure 8b; Table S11). It may be a consequence of the interaction effects for plants combined with the result of net selection. For instance, plants of the genus *Callianthe* (formerly classified as *Abutilon*, Malvaceae) and the species *Siphocampylus sulfureos* E.Wimm. (Campanulaceae), present mixed pollination syndromes between bats and hummingbirds, being effectively pollinated by both groups. Consequently, it may generate intermediate characteristics as these animals will exert different selective pressures. The species *Callianthe rufinerva* (A. St.Hil.) Donnel (formerly *Abutilon rufinerve*), during the night, presents flowers fully open (shaped like a bowl) to receive visits from bats; and during the day, the flowers narrow their opening, adopting a bell shaped to receive visits from hummingbirds. At dusk, the flowers open again, repeating these changes throughout the period in which they are available to pollinators (about 30 hours) (Buzato, Sazima & Sazima, 1994). On the other hand, local adaptation within one species of plant may help in generating more variation inside each subregion. For instance, differences in hummingbird assemblages in the Caribbean islands appear to influence the characteristics of flowers, leading to morphological variations within the same plant species (*i.e. Heliconia bihai*), across different islands. On the island of Hispaniola, where *Eulampis jugularis* is found, a morphological similarity between *Heliconia bihai* and *H. caribaea* is observed, which coincides with the morphology of this hummingbird. Therefore, the similarities between the flowers of these Heliconia species may result from floral convergence driven by selection mediated by a common pollinator species, which varies according to the presence of the pollinator (Martén-Rodríguez *et al.*, 2011). The same is true for plant species pollinated by different functional groups, throughout its distribution area, which the consequence could be the formation of a geographic mosaic (Thompson, 1994).

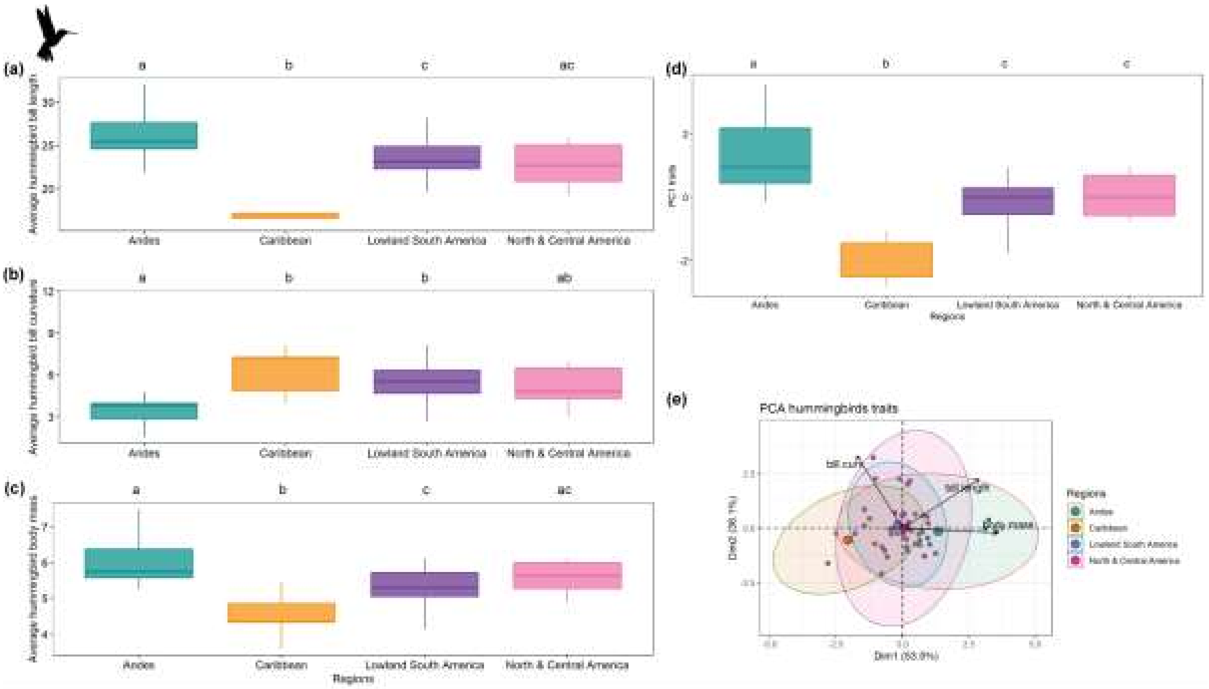

Figure 7: Differences in hummingbird traits between biogeographical subregions (Andean, Caribbean, Lowland South America and North & Central America). The figure (a) represents the average bill length; (b) average bill curvature; (c) average body mass; (d) PCA graph combining the three hummingbird traits for each biogeographical subregion, and (e) the first component of PCA for each subregion; Andes are in light green; Caribbean in orange; Lowland South America in light purple; North and Central America in light pink. The letters at the top of each graph (figures (a) to (d)) represent the results of pairwise comparisons conducted through Tukey's test, where different letters indicate statistical difference ($p < 0.05$). Hummingbird silhouettes are from PhyloPic (URL: https://phylopic.org/) under an open access license.

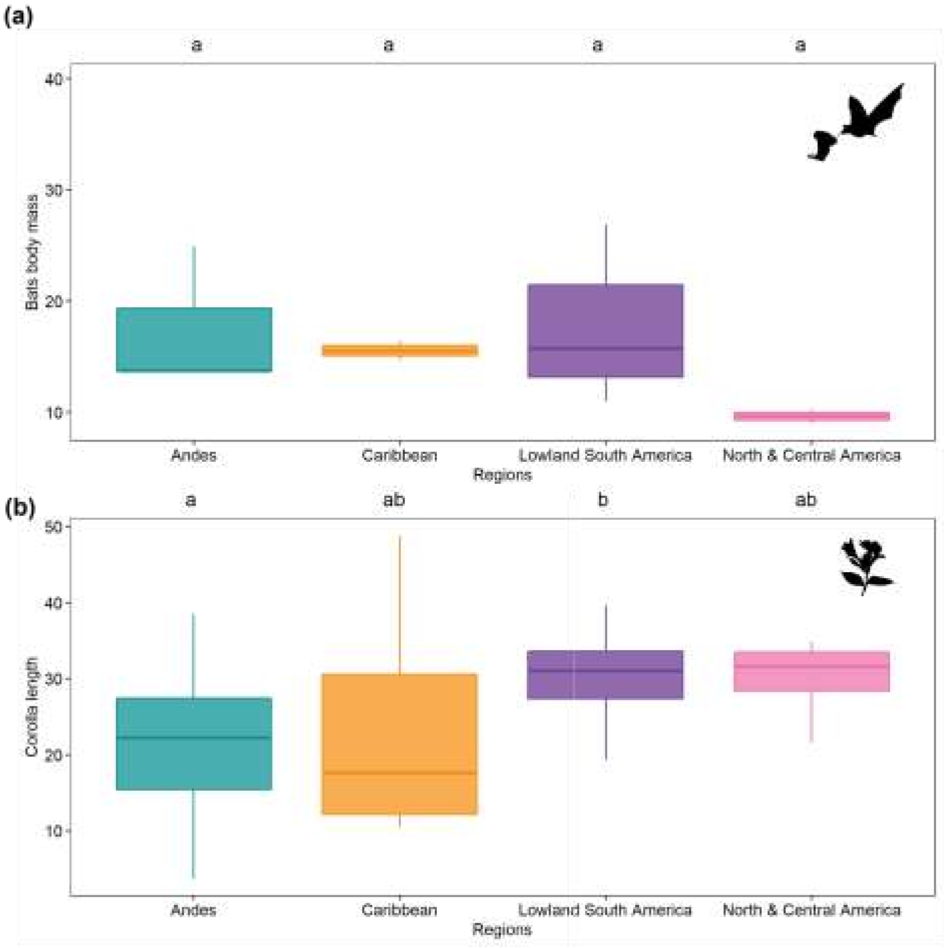

Figure 8: Differences in flower and bats traits between biogeographical subregions. Where in (a) we represent the average bat's body mass; and in (b) the average corolla length in biogeographical subregions: Caribbean in orange; Lowland South America in light purple; North and Central America in light pink. The letters at the top of each graph represent the results of pairwise comparisons conducted through Tukey's test, where different letters indicate statistical difference ($p < 0.05$). Bat and flower silhouettes are from PhyloPic (URL: https://phylopic.org/) under an open access license.

7. Unique interactions and species's roles across Neotropical subregions

When evaluating species roles, we found that in networks from North and Central America, as well as the Caribbean, no species stood out as central (that is, higth closeness or betwenness centrality). However, in terms of closeness centrality, *Thalurania glaucopis* stood out in lowland South America, while in the Andes, *Coeligena wilsoni*. Regarding betweenness, *T. glaucopis* remains prominent in lowland South America. In the Andes no species showed high betweenness centrality values, although the genus *Coeligena* stands out. Notably, no bat species emerged as central, likely due to the limited number of bat networks in the dataset. Species with high centrality values play a crucial role in the structure and stability of the network. Identifying these central species can help determine their importance to the network (Martín González, Dalsgaard & Olesen, 2010) and provide tangible information on which species should be conserved to ensure the maintenance of the network. For example, species centrality has been used in the field of landscape ecology to understand which species and specific pairwise interactions are important for connecting habitat fragments (Emer et al., 2018).

We also assessed the role of species in interaction pairs through a metanetwork approach. Specifically, when evaluating interaction pair centrality, we observed variations compared to previous analyses that focused solely on centrality frequency. Considering closeness centrality, the interaction pair with the highest value was between *Thalurania glaucospis* and *Aechmea nudicaudalis.* On the other hand, using the betweenness centrality, the interaction pair with the highest value was *Galucis hirsutus* and *Centropogon cornutus* (Figure 9).

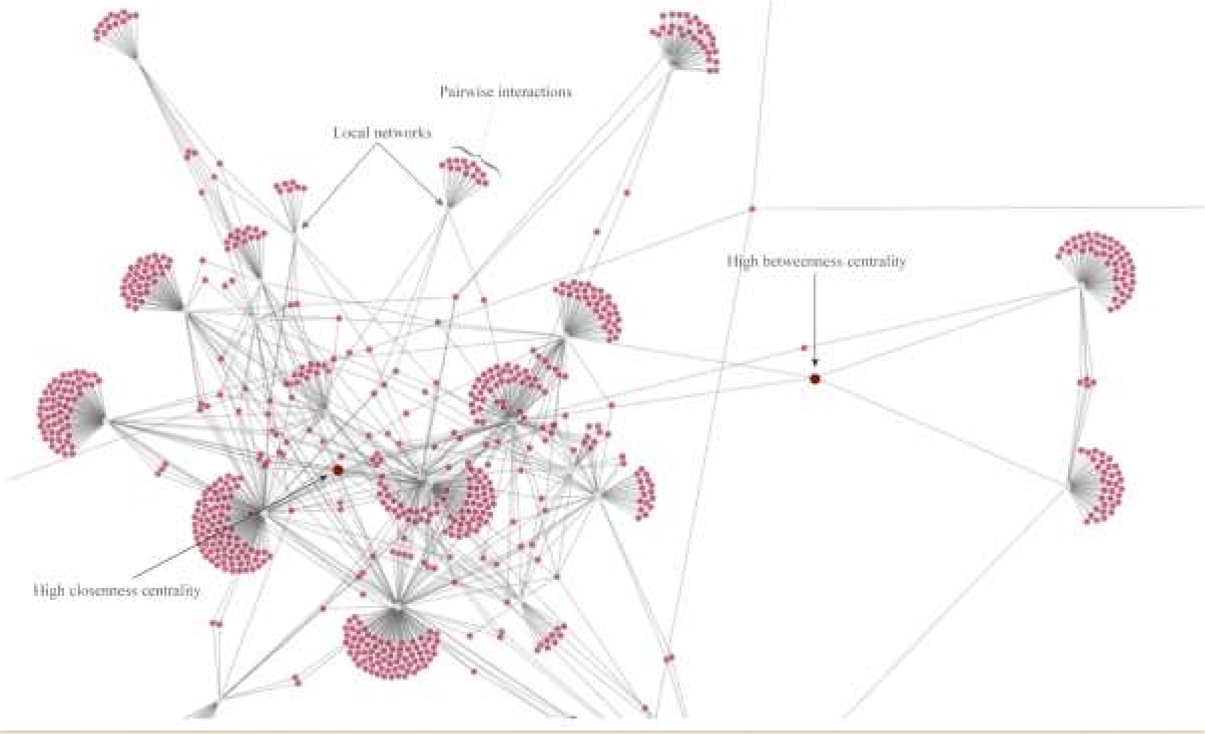

Figure 9: Section of the Neotropical metanetwork of vertebrate pollinators, highlighting in red the two pairwise interactions *Thalurania glaucopis-Aechmea nudicaudalis* and *Galucis hirsutus-Centropogon cornutus*, which stand out in terms of closeness and betweenness, respectively. Pink dots represent the interaction pairs, while white dots indicate the local networks.

The assessment of species centrality at different scales reveals roles of species and their pairs, both locally and regionally. For the closeness metric, a species that connects to many other nodes within its networks may indicate potential generalism in its interactions. Frequent observation of this pattern in local networks suggests that the species interacts with a wide range of partners, reflecting generalism across various local contexts. The betweenness metric, on the other hand, highlights a structural role within the network by connecting different parts of local networks. Species with high betweenness play a crucial role in linking distinct subgroups within the network, maintaining the integrity and flow across these sections.

At the metanetwork level, the role of species highlighted by closeness is similar to that observed in local networks. Achieving a high closeness value requires the species and its interaction pair to be present in multiple local networks, indicating generalism related to broad distribution and diverse habitats. This pattern explains the recurrent presence of species such as *Thalurania glaucopis*, which, due to its generalist nature and wide distribution, exhibits high closeness values at both local and regional scales. In the context of the metanetwork, the betweenness metric underscores a structural role in connecting different parts of the network on a regional scale. Species with high betweenness are found in distinct networks that belong to different subgroups within the metanetwork. For example, the interaction between *Galucis hirsutus* and *Centropogon cornutus* connects various parts of the metanetwork (Figure 9), playing a crucial role in maintaining network integrity and preventing fragmentation into separate compartments.

8. Niche Conservatism in Plant-pollinator networks

Our results reveal that the evolutionary history of species shapes the interaction patterns in plant–hummingbird networks across Neotropical subregions. The positive relationship observed for β_{WN} and β_{ST} (Figure 10 and see Table S12) indicates that phylogenetically distant communities tend to exhibit more distinct interaction patterns, mainly driven by species turnover. In contrast, β_{OS} shows a negative relationship with phylogenetic distance. We observed that communities that are more phylogenetically dissimilar tend to exhibit more distinct interaction patterns, especially when considering the β_{WN} component, that is, the total interaction dissimilarity in the network. This pattern is consistent with the niche conservatism hypothesis, in which functional traits associated with the evolutionary history of species constrain or guide their interaction possibilities (Wiens & Donoghue, 2004; Thompson, 2005). In the case of hummingbirds and the plants they visit, traits such as bill and floral morphology, physiological adaptations, or trophic preferences appear to be strongly conserved within lineages and therefore directly influence patterns of interactions. When we look at more specific components such β_{ST} (species turnover), the relationship with phylogenetic dissimilarity remains strong, particularly for hummingbirds. Both components show significant slopes, indicating that phylogenetic distance continues to explain a substantial part of the variation not only in overall dissimilarity (β_{WN}), but also in how species turnover and interaction rewiring occur across communities. For plants, the association is also significant but comparatively weaker, especially for β_{WN}, suggesting that factors beyond phylogenetic relatedness may play a larger role in shaping interaction patterns among plants. The negative relationship observed for β_{OS} indicates that closely related communities tend to have more similar interaction arrangements, with less rewiring, reinforcing the role of evolutionary history in constraining interaction flexibility.

Supporting the expectations often reported in mutualistic networks where animals tend to maintain stronger fidelity to ancestral interactions due to physiological specialization (Rezende, Jordano & Bascompte, 2007), our results reveal that hummingbirds exhibit higher phylogenetic fidelity in their interactions. This pattern likely reflects evolutionary constraints related to morphological and physiological traits, such as bill shape and foraging behavior, which limit the range of floral partners. Furthermore, the differences in patterns across subregions, such as the stronger phylogenetic effects observed in the Andes compared to the more diffuse patterns in the Caribbean or North & Central America suggest that the relative importance of evolutionary and ecological processes is not spatially homogeneous. Interestingly, only the Caribbean subregion sometimes exhibits distinct patterns, which could result either from the relatively low number of hummingbird species in this region or reflect genuine ecological differences. For example, even for plants β_{OS}, where diversity is high, the Caribbean still maintains a distinct pattern, suggesting that these differences are not solely due to species richness. This may reflect differences in biogeographic history, degrees of isolation, local species diversity, and region-specific environmental filters. Overall, our findings indicate that phylogenetic niche conservatism is an important factor in shaping plant–hummingbird interactions, particularly when considering the overall network dissimilarity (β_{WN}). However, there is also room for the influence of contemporary ecological processes that promote flexibility in interactions, especially regarding partner replacement (β_{OS}). This highlights a dynamic balance between evolutionary legacies and local ecological contingencies in shaping interaction networks across Neotropical bioregion

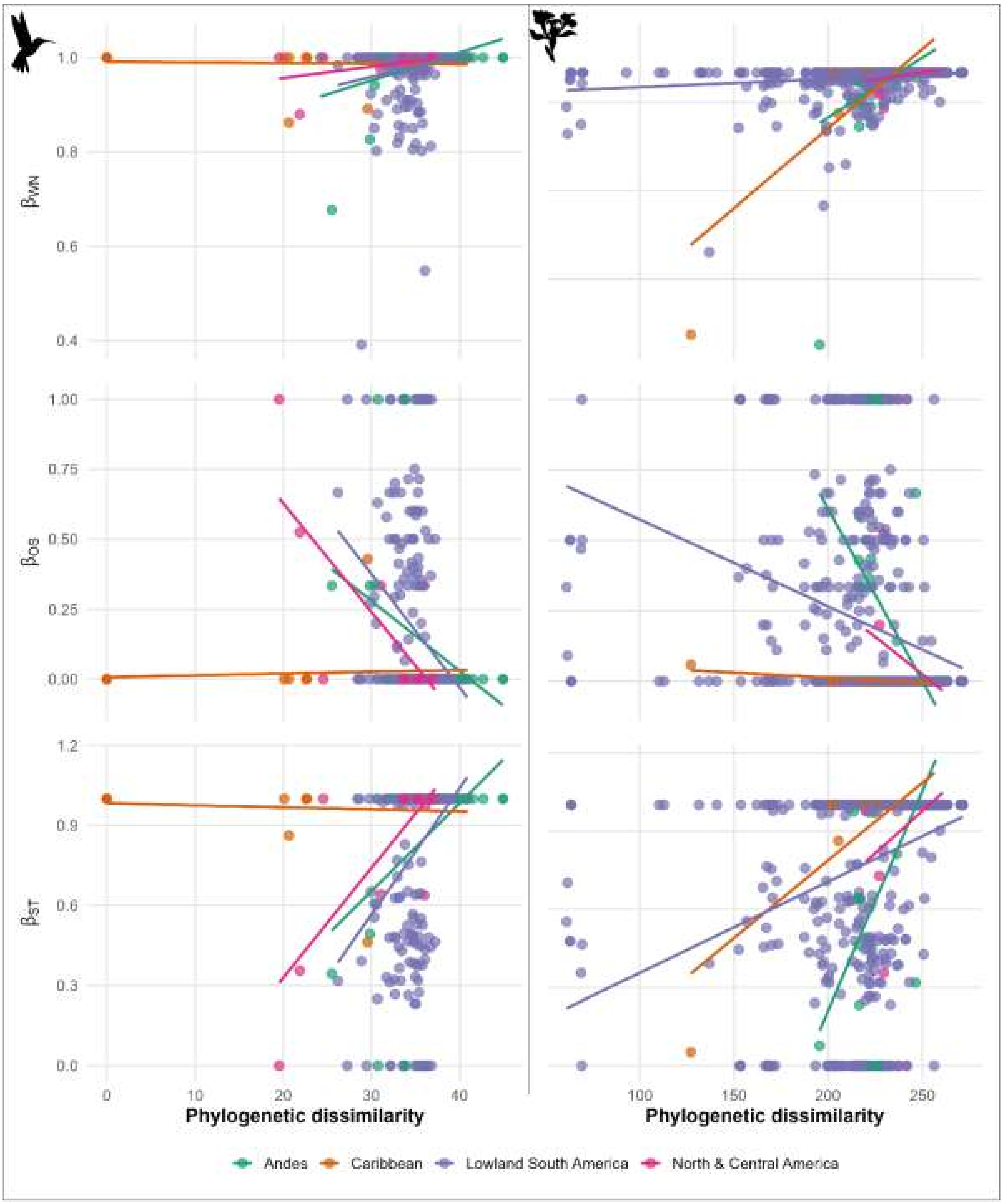

Figure 10: Relationship between phylogenetic dissimilarity and interaction dissimilarity in plant–pollinator networks across Neotropical subregions. Panels on the left correspond to hummingbirds, and panels on the right correspond to plants. Each panel shows the relationship for a different component of β-diversity: total interaction dissimilarity (β_{WN}), species turnover (β_{ST}), and interaction rewiring (β_{OS}).

9. Concluding Remarks

We conducted a comprehensive analysis of Neotropical plant-pollinator interaction networks using an extensive database accumulated over approximately 40 years of research. Our findings reveal general patterns characterizing these interactions, including predominantly nested networks with low modularity, low connectance, and a high proportion of indirect effects. The networks also exhibit significant dissimilarity in both species' composition and interactions, consequently high beta diversity within and across biogeographic subregions. Notably, the Caribbean and the Andes emerge as contrasting extremes. In the Caribbean, networks have lower diversity, reduced interaction dissimilarity, and less nested structures. This differentiation is evident not only in network architecture but also in the morphology of hummingbirds, with Caribbean species exhibiting larger body sizes but comparatively smaller bill lengths than those in other regions. These patterns likely result from island-specific processes such as extinctions (Vollstädt *et al.*, 2025), the relatively recent arrival of lineages, and diversification rates that have yet to reach their peak (McGuire *et al.*, 2014). In contrast, the Andes exhibit extremely high diversity, attributed to geological uplift events that drove rapid diversification (McGuire *et al.*, 2014).

Our study also reveals that despite distinct biogeographic differences across Neotropical subregions, niche conservatism emerges as a important process shaping plant–pollinator interaction patterns. Our findings demonstrate that evolutionary history is not simply a backdrop, but an active force shaping ecological interactions across the Neotropics. The fact that more phylogenetically distant communities exhibit greater dissimilarity in their interaction patterns (driven primarily by species turnover) reveals how deep-time evolutionary processes continue to reverberate in contemporary ecological networks. In essence, the determination of interaction partners is not a random outcome of ecological availability, but rather the result of a complex equation that integrates species' evolutionary history and the constraints imposed by ancestral traits. Ultimately, our results highlight that Neotropical plant–vertebrate networks are shaped by a dynamic interplay between evolutionary legacies and ecological flexibility. This interplay is not spatially uniform, but it is modulated by the biogeographic histories and ecological conditions unique to each subregion. Understanding this balance is crucial not only for explaining the patterns we observe today but also for anticipating how these networks may respond to future environmental changes.

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Supplementary Materials

Biogeography of Vertebrate Pollination on the Neotropics

Detailed description of the methodological procedures

1. Network descriptors

To assess the existence of general patterns in the network structure that could be explained by biogeography, we examine general aspects of the structure of plant-pollinator networks that we compiled. To achieve this, we evaluated nestedness, modularity, connectance, and also the proportion of indirect links in the networks. The nestedness were computed through the NODF index (Almeida-Neto et al., 2008). This metric delineates the extent of network nestedness on a scale from 0 (absence of nestedness) to 100 (perfectly nested) (Bascompte and Jordano, 2013). Modularity was determined using the algorithm proposed by Stephen Beckett (2016), which describes the formation of cohesive subgroups of species within the network, interacting significantly among themselves (Bascompte and Jordano, 2013). Modularity ranges from 0 (no modules) to 1 (perfectly modular networks). We computed connectance, which also ranges from 0 to 1 and represents the proportion of observed interactions compared to the all-possible interactions in the network. Both nestedness and connectance were calculated using the 'networklevel' function from the bipartite package. Specifically for modularity, we utilized the 'ComputeModules' function, from the same package (Dorman et al. 2023).

To assess the statistical significance of the obtained nestedness and modularity values, we generated null models to mitigate the effect of variation in network richness. This procedure involved generating null networks where the number of links per species was held constant using the Patefield algorithm (Dormann et al., 2009). In other words, interactions were randomly redistributed among species while ensuring an equal number of connections for each. Subsequently, we recalculated the nestedness and modularity values for each null network. The z-score was employed to evaluate the statistical significance of the observed values, thus controlling for the effect of variation. The z-score was computed using the formula $(X - \mu) / \sigma$, where X represents the observed value, μ is the mean of the null distributions, and σ is the standard deviation of these distributions. Z-scores significantly different from zero indicate statistically significant deviations from expected randomness, considering the constancy of the number of links per species. The values obtained here were utilized in subsequent analyses.

We also calculated the proportion of indirect effects in the networks. Indirect pathways represent the effects induced by species that are not directly connected as interacting partners. When analyzing an adjacency matrix of interactions, we consider the direct connections between species, i.e., whether species "i" interacts directly with species "j". However, it is possible to calculate indirect pathways from this matrix. For this, we use a matrix T, that is as a comprehensive effects matrix, summarizing the impact of each species in propagating effects through both direct and indirect connections. The characteristics of matrix T are determined by the pathway size and the dependence between interacting species (R). 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. 2022; Pires et al. 2020). To isolate the indirect effects from the total matrix T, we use the following equation: $U = \sum_i^N \sum_j^N tij \times (1 - bij) \, / \, \sum_i^N \sum_j^N tij$, Here, tij is derived from the total effects matrix (T) and represents the potential that a species in column j must affect a species in row i. Meanwhile, bij represents the presence of interactions between species, where b is the binary interaction matrix. Therefore, 1 - bij is used to determine whether there is a direct interaction between species "i" and "j" (if bij equals 0) or if there is no such interaction (if bij equals 1).

We assessed the dissimilarity among networks belonging to the same biogeographic region. In addition to assessing the dissimilarity in species composition of communities ($\boldsymbol{\beta}_{S}$) considering that each network represents a local community. Following Poissot et al. 2012, we decompose the dissimilarity of species interaction networks into three main components: the dissimilarity of interactions among species common to the compared networks ($\boldsymbol{\beta}_{OS}$), the dissimilarity of interactions due to species turnover ($\boldsymbol{\beta}_{ST}$), and the overall dissimilarity of interactions ($\boldsymbol{\beta}_{WN}$). The calculations are based on classic dissimilarity indices such as Whittaker's (1960), but with modifications to account for interactions within each network rather than the species composition in the community (see Poissot et al 2012 for details). The decomposition of dissimilarity into two components – one compositional and the other interactive – reveals not only the differences between networks but also the source of this variation (Poisot et al. 2012).

2. Phylogenetic and interaction dissimilarity

To assess whether the phylogenetic composition of local communities shapes the establishment of plant–hummingbird interactions—and thereby determine whether niche conservatism or niche evolution drives these patterns—we used the phylogenies of plants and hummingbirds as the basis for calculating phylogenetic dissimilarity between networks. The underlying hypothesis is that communities composed of more phylogenetically distinct species would tend to exhibit different interaction patterns, reflecting the influence of evolutionary history on network assembly. The plant phylogeny was constructed using the GBOTB.extended mega-phylogeny (Jin & Qian, 2019) through the *phylo.maker* function in the *V.PhyloMaker* package. This tree is based on a robust phylogenetic backbone for vascular plants and allows the placement of missing species based on higher-level taxonomic information (genus and family). For hummingbirds, we used the phylogeny proposed by McGuire et al. (2014), which represents one of the most comprehensive and updated phylogenetic hypotheses for Trochilidae.

From these adjusted phylogenetic trees, we calculated pairwise phylogenetic dissimilarity matrices for plants and hummingbirds separately. We extracted cophenetic distances, which represent the sum of the branch lengths separating each pair of species. These distances were then combined with species presence–absence matrices from the networks, allowing us to compute phylogenetic beta diversity between communities. This was calculated using the *comdist* metric (applied to both plants and hummingbirds), which measures the mean phylogenetic distance between pairs of species belonging to different communities (Webb et al., 2002). This metric is particularly sensitive to lineage turnover across spatial gradients, making it well suited to detect phylogenetic turnover. The phylogenetic dissimilarity matrix was then paired with the interaction dissimilarity matrix obtained from the beta diversity of interactions, as previously described. Additionally, we accounted for the biogeographical structure of the networks by grouping them into four bioregions: Lowland South America, Andes, Caribbean, and North and Central America. We tested the relationship between phylogenetic dissimilarity and interaction turnover using linear models and linear mixed-effects models, with bioregion as a random effect. Separate models were fitted for each turnover component (β_{WN}, β_{ST}, and β_{OS}), considering either plants or hummingbirds as the focal group for phylogenetic dissimilarity.

3. Statistical analyses

To investigate variations in network structure across different biogeographic regions, we employed generalized linear models (GLM). We used network structure predictors, such as nestedness, modularity, connectance, and the proportion of indirect effects, as response variables. The independent variable was represented by subregions of the neotropics (Andes, Caribbean, lowland South America, and North & Central America). In order to identify significant differences among the subregions, we conducted a post-hoc test, specifically the Tukey test. This procedure allowed revealing which subregions exhibited statistically significant distinctions in relation to the considered network structure metrics. To investigate the relationships among network predictors, we employed a principal component analysis (PCA). Subsequently, we selected the first principal component (PC1) as a summarized representation of network characteristics. We also conducted generalized linear models (GLM) using PC1 as the response variable to analyze how these components vary across different regions. To assess significant differences among the regions, we applied the Tukey test as a post-hoc. These same procedures were replicated to comprehend the variation in traits among groups (plants, hummingbirds, and bats) across subregions. Specifically for hummingbird traits, a principal component analysis (PCA) was exclusively applied. For analyses involving phylogenetic dissimilarity, we used linear mixed-effects models (GLMMs), incorporating biogeographical subregion as a random effect. This approach accounts for the hierarchical structure of the data and potential non-independence among networks within the same subregion. These models tested whether phylogenetic dissimilarity (plants and hummingbirds separately) predicts interaction dissimilarity components (β_{WN}, β_{ST}, and β_{OS}), thus assessing whether evolutionary history constraint interaction patterns. All models were adjusted according to the nature and distribution of each response variable.

TABLES

Table S1: Tukey’s multiple pairwise comparisons of nestedness (Z.NODF) between biogeographic regions. Significant differences ($p < 0.05$) are in bold.

Pairwise comparisons	Estimate	Std. Error	t value	p-value
Caribbean – Andes	-3.267	1.141	-2.863	**0.027**

Lowland South America – Andes	-1.604	0.808	-1.985	0.198
North & Central America – Andes	-1.689	1.141	-1.480	0.446
Lowland South America – Caribbean	1.663	1.004	1.657	0.346
North & Central America – Caribbean	1.578	1.287	1.226	0.604
North & Central America – Lowland South America	-0.085	1.004	-0.084	0.999

Table S2: Tukey's multiple pairwise comparisons of modularity (Z.modularity) between biogeographic regions. Significant differences ($p < 0.05$) are highlighted in bold.

Pairwise comparisons	Estimate	Std. Error	t value	p-value
Caribbean – Andes	1.548	0.570	2.718	**0.040**
Lowland South America – Andes	0.486	0.403	1.204	0.618
North & Central America – Andes	0.810	0.570	1.421	0.482
Lowland South America – Caribbean	-1.063	0.501	-2.120	0.153
North & Central America – Caribbean	-0.739	0.643	-1.149	0.652
North & Central America – Lowland South America	0.324	0.501	0.646	0.914

Table S3: Tukey's multiple pairwise comparisons of log-transformed connectance between biogeographic regions. Significant differences ($p < 0.05$) are highlighted in bold.

Pairwise comparisons	Estimate	Std. Error	t value	p-value
Caribbean – Andes	0.753	0.223	3.370	**0.007**
Lowland South America – Andes	0.187	0.158	1.185	0.630
North & Central America – Andes	0.037	0.223	0.167	0.998
Lowland South America – Caribbean	-0.565	0.196	-2.878	**0.026**
North & Central America – Caribbean	-0.715	0.252	-2.839	**0.029**
North & Central America – Lowland South America	-0.150	0.196	-0.764	0.866

Table S4: Pairwise comparisons of indirect effects among biogeographic regions from a beta regression mixed model. Significant differences ($p < 0.05$) are highlighted in bold.

Pairwise comparisons	Estimate	Std. Error	z value	p-value
Caribbean – Andes	-0.634	0.194	-3.266	**0.006**
Lowland South America – Andes	-0.232	0.141	-1.643	0.346
North & Central America – Andes	-0.222	0.197	-1.122	0.668
Lowland South America – Caribbean	0.402	0.168	2.395	0.075
North & Central America – Caribbean	0.413	0.217	1.899	0.222

North & Central America – Lowland South America	0.010	0.172	0.061	1.000

Table S5: Pairwise comparisons of the first principal component (Dimension 1) scores derived from PCA on network structure metrics across biogeographic regions.

Pairwise comparisons	Estimate	Std. Error	t value	p-value
Caribbean – Andes	-2.491	0.700	-3.557	**0.0039**
Lowland South America – Andes	-0.867	0.496	-1.748	0.300
North & Central America – Andes	-0.855	0.700	-1.220	0.608
Lowland South America – Caribbean	1.624	0.616	2.636	**0.0483**
North & Central America – Caribbean	1.636	0.790	2.071	0.168
North & Central America – Lowland South America	0.012	0.616	0.020	1.000

Table S6: Pairwise Tukey comparisons for average hummingbird bill length across biogeographic regions. Significant p-values are shown in bold

Pairwise comparisons	Estimate	Std. Error	t value	p-value
Caribbean – Andes	-8.933	1.454	-6.146	**<0.001**
Lowland South America – Andes	-2.754	0.969	-2.841	**0.0315**
North & Central America – Andes	-3.421	1.368	-2.501	0.0707
Lowland South America – Caribbean	6.179	1.316	4.695	**<0.001**
North & Central America – Caribbean	5.512	1.632	3.378	**0.0075**
North & Central America – Lowland South America	-0.667	1.221	-0.546	0.9450

Table S7: Pairwise Tukey comparisons for average hummingbird bill curvature across biogeographic regions. Significant p-values are shown in bold

Pairwise comparisons	Estimate	Std. Error	t value	p-value
Caribbean – Andes	2.315	1.079	2.145	0.1494
Lowland South America – Andes	1.761	0.720	2.446	**0.0796**
North & Central America – Andes	1.639	1.016	1.614	**0.3721**
Lowland South America – Caribbean	-0.555	0.977	-0.567	0.9390
North & Central America – Caribbean	-0.676	1.212	-0.558	0.9418
North & Central America – Lowland South America	-0.122	0.906	-0.134	0.9991

Table S8: Pairwise Tukey comparisons for average hummingbird body mass across biogeographic regions. Significant p-values are shown in bold

Pairwise comparisons	**Estimate**	**Std. Error**	**t value**	**p-value**
Caribbean – Andes	-1.5053	0.3305	-4.554	**<0.001**
Lowland South America – Andes	-0.7611	0.2204	-3.453	**0.0062**
North & Central America – Andes	-0.4389	0.3110	-1.411	0.4895
Lowland South America – Caribbean	0.7442	0.2993	2.487	0.0727
North & Central America – Caribbean	1.0663	0.3711	2.874	**0.0292**
North & Central America – Lowland South America	0.3222	0.2776	1.161	0.6456

Table S9: Pairwise comparisons of the first principal component (Dimension 1) scores derived from PCA on hummingbird traits across biogeographic regions.

Pairwise comparisons	**Estimate**	**Std. Error**	**t value**	**p-value**
Caribbean – Andes	-3.3910	0.4840	-7.006	**<0.001**
Lowland South America – Andes	-1.5213	0.3228	-4.713	**<0.001**
North & Central America – Andes	-1.2890	0.4554	-2.830	**0.03256**
Lowland South America – Caribbean	1.8698	0.4382	4.267	**<0.001**
North & Central America – Caribbean	2.1020	0.5434	3.868	**0.00176**
North & Central America – Lowland South America	0.2323	0.4064	0.572	0.93777

Table S10: Pairwise Tukey comparisons for average bat body mass across biogeographic regions. Significant p-values are shown in bold

Pairwise comparisons	**Estimate**	**Std. Error**	**t Value**	**p-value**
Caribbean – Andes	-1.910	6.676	-0.286	0.991
Lowland South America - Andes	1.929	5.642	0.342	0.985
North & Central America - Andes	-7.812	7.464	-1.047	0.723
Lowland South America - Caribbean	3.839	5.642	0.680	0.900
North & Central America - Caribbean	-5.902	7.464	-0.791	0.855
North & Central America - Lowland South America	-9.741	6.556	-1.486	0.472

Table S11: Pairwise Tukey comparisons for average flower corolla length across biogeographic regions. Significant p-values are shown in bold

Pairwise comparisons	Estimate	Std. Error	t Value	p-value
Caribbean – Andes	1.8511	4.1074	0.451	0.9680
Lowland South America - Andes	8.6241	2.8177	3.061	**0.0166**
North & Central America - Andes	8.9289	4.1074	2.174	0.1372
Lowland South America - Caribbean	6.7730	3.6828	1.839	0.2576
North & Central America - Caribbean	7.0777	4.7428	1.492	0.4387
North & Central America - Lowland South America	0.3048	3.6828	0.083	0.9998

Table S12: Results of generalized linear mixed models (GLMMs) evaluating the relationship between phylogenetic dissimilarity and the components of beta diversity (βwn, βst and βos) for hummingbirds and plants. Biogeographical regions were included as a random effect. For each model, we present the fixed-effect estimates (estimate ± standard error), *t*-values, and the R², which represents the proportion of variance explained by both fixed and random effects.

Variável Resposta	Intercepto (Est ± SE)	t value	R2
Hummingbird βwn	12.513 ± 4.206	2.975	0.65
Hummingbird βst	3.9103 ± 0.8671	4.510	0.67
Hummingbird βos	-3.7620 ± 0.9268	4.059	0.67
Plants βwn	129.02 ± 19.17	6.729	0.07
Plants βst	37.812 ± 3.660	10.33	0.15
Plants βos	-34.375 ± 3.885	-8.849	0.12

Capítulo II

Habitat loss, not fragmentation per se, drives structural changes and species turnover in plant–vertebrate pollinator networks[2]

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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.

keywords: deforestation, interaction, mutualism, landscape ecology, hummingbirds, bats.

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Highlights

- Habitat loss triggers species declines in plant–vertebrate pollination networks.
- Cascading structural changes follow, reducing network resilience to further extinctions.
- ~90% of interaction dissimilarity across landscapes is due to species turnover.
- Plant–pollinator networks are not influenced by fragmentation per se.

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., 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; Calos 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-Quinceno et al. 2024; Arina-Velez 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.

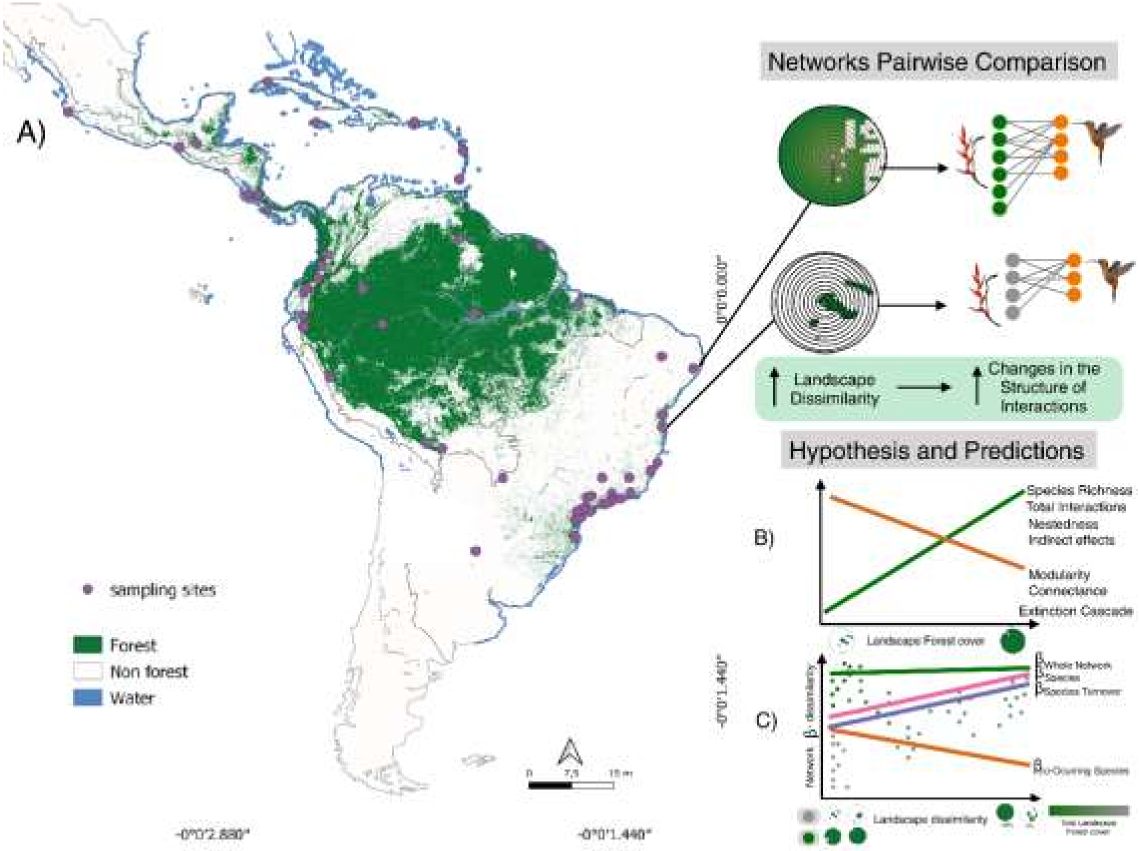

Figure 1: Predicted effects of forest cover and landscape dissimilarity on network structure and interaction beta-diversity on plant-vertebrate networks. (A) Study Area – Map of Neotropical Humid Forests. The map illustrates the forest cover in the Neotropical region, with purple dots marking the locations 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 meters 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).

. 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 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 – 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 1990-2022 (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 hectares (each pixel represents a 30 by 30-meter 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 3,000-meter, at 250-meter 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 3,000-meter 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); μ = average value of the metric obtained through the 1000 null model networks; and σ = 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 $\mathbf{T}=(\mathbf{I}- R\mathbf{B'})^{-1}$, 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:

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

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) $\beta_{wn,}$ 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 seconds 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 $\Delta AICc \leq 2$. 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 $\Delta\text{AICc} \leq 2$. 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 ≤ 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 3000m).

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). 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).

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**	**R²**
Plant richness	FC + sampling intensity	Negative binomial	3000	0.008	0.003	**2.871**	**0.54**
				2.276	0.400	**5.686**	
Pollinator richness	FC +Sampling intensity +precipitation	Negative binomial	3000	0.006	0.002	**2.170**	**0.38**
				1.478	0.363	**4.069**	
				-0.000	0.000	**-1.732**	
Number of interactions	FC + Sampling intensity	Gaussian (log transformed)	3000	0.006	0.002	**2.437**	**0.64**
				3.822	0.356	**10.716**	
Connectance	FC + sampling intensity	Gaussian (log transformed)	3000	-0.005	0.002	**-2.008**	**0.11**
				-0.731	0.336	**-2.176**	
Z-NODF	FC + sampling intensity	Gaussian	3000	0.000	0.000	**1.916**	**0.29**
				0.073	0.014	**4.960**	
Z-modularity	FC +sampling intensity	Gaussian	2750	-7.841e-05	5.157e-05	-1.520	**0.37**
				-4.222e-02	7.049e-03	-5.990	
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	0.003	**-2.507**	0.40
				-2.822	0.457	**-6.165**	

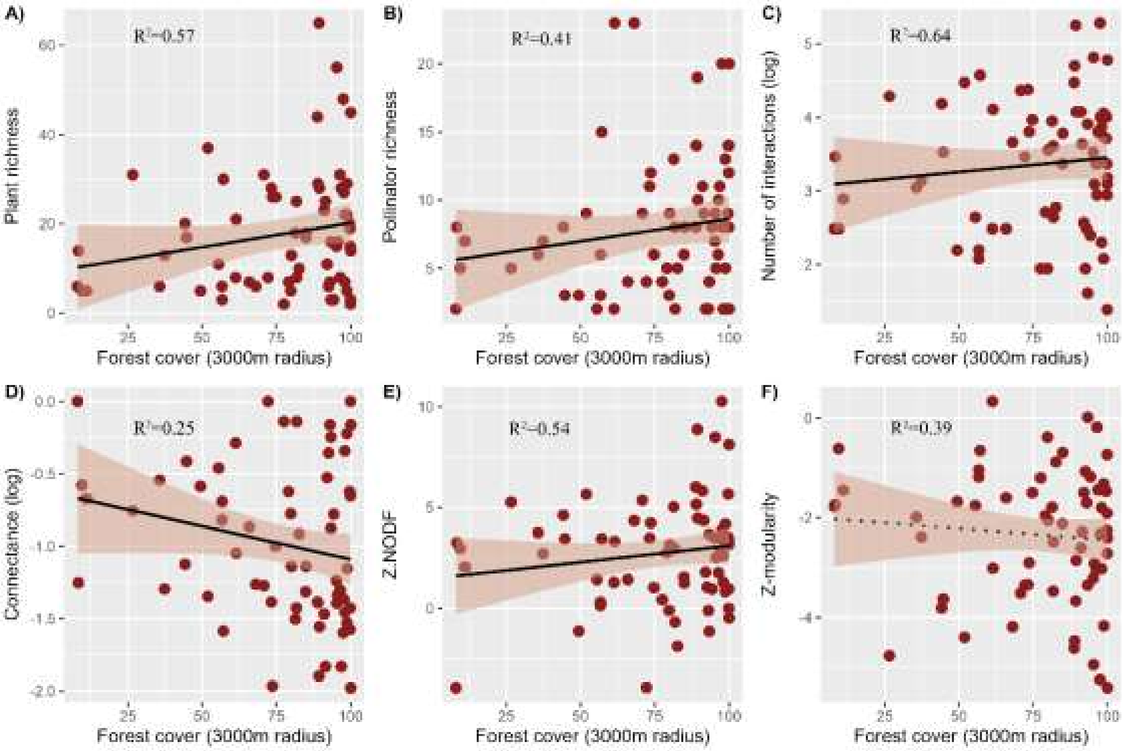

Figure 2: Effects of landscape changes on structure of Neotropical plant-vertebrate pollinator networks. The effects of forest cover (the opposite of habitat loss) are shown in A) Plant richness; B) Pollinator richness C) Number of interactions; D) Connectance, E) Nestedness (Z-NODF) and F) Modularity.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

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 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 (Figure S4). This suggests that variation in composition across functional groups may influence the overall pattern observed in the full dataset.

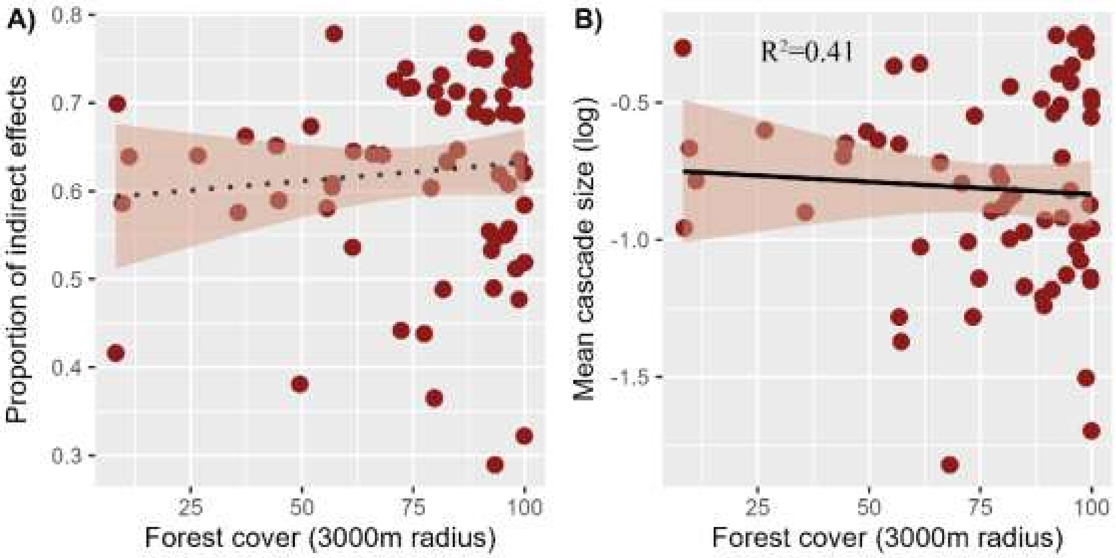

Figure 3: Effects of landscape changes on the indirect interactions within Neotropical plant–vertebrate pollination networks. The effects of percentage of forest cover are shown in A) Proportion of indirect effects, and B) Mean cascade size in networks. R^2 represents an estimate of how much the adjusted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

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).

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
βs ~landscape dissimilarity + (1|subregions)	3.305	2.190	1.509	0.131
βwn ~landscape dissimilarity + (1|subregions)	1.362	2.406	0.566	0.571
βos ~landscape dissimilarity + (1|subregions)	**-1.176**	**0.457**	**-2.571**	**0.010**
βst ~landscape dissimilarity	**1.079**	**0.393**	**2.746**	**0.006**

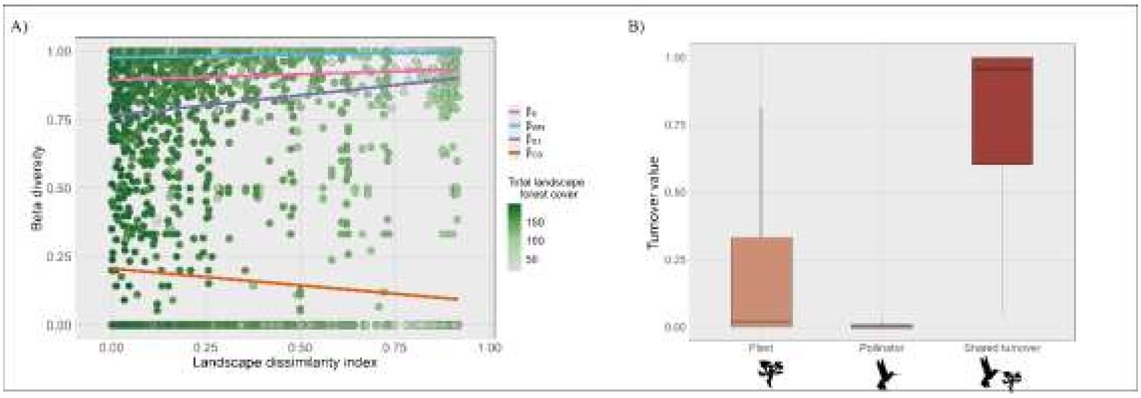

Figure 4. Beta diversity of plant-pollinator interactions along landscape dissimilarity gradient in the Neotropics. A) Relationship between beta diversity and landscape dissimilarity for the components of network dissimilarity. Each line represents a linear model fitted to a given component: βs - Dissimilarity 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.

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.

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 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 et al. 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.

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Supplementary Materials

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

TABLES

Table S1: Description of the 67 plant-vertebrate pollinator networks on Neotropics.

Network_ID*	lat	long	Plant richness	Pollinator richness	Interactions	Vertebrate group	Sampling_method
1	-16.96	-65.41	6	3	8	hummingbirds	transect
2	-17.51	-63.64	3	6	9	hummingbirds	transect
3	-20.75	-42.91	14	8	32	hummingbirds	focal observation
4	-20.75	-42.91	5	5	12	hummingbirds	focal observation
5	-22.50	-44.83	31	5	73	hummingbirds	focal observation
6	-13.81	-39.20	18	13	52	hummingbirds	focal observation
7	-3.82	-70.27	30	15	97	hummingbirds	focal observation
8	12.10	-61.70	7	2	10	hummingbirds	focal observation
9	15.35	-61.30	12	3	19	hummingbirds	focal observation

10	15.25	-61.37	11	2	14	hummingbirds	focal observation
11	18.35	-77.65	6	2	7	hummingbirds	focal observation
12	18.13	-66.76	11	2	13	hummingbirds	focal observation
13	-22.75	-47.11	6	2	12	bats	NA
14	-24.5	-47.25	2	2	4	bats	focal observation
15	-28833	-59.93	5	3	7	bats	focal observation + mist nets
16	-23.33	-44.83	29	5	42	hummingbirds	mist nets
17	-15.21	-39.20	6	23	39	birds	focal observation
18	4.83	-52.7	14	2	24	bats	pollen collection
19	-9.71	-76.16	26	12	45	hummingbirds	focal observation + transect
20	0.12	-78.63	29	14	110	hummingbirds	camera
21	0.12	-78.60	48	20	197	hummingbirds	camera
22	1.25	-77.43	31	9	79	hummingbirds	focal observation
23	-2.629	-60.050	3	8	11	bats	focal observation + pollen collection
24	-25.44	-48.92	8	10	19	hummingbird/bats	focal observation + mist nets

25	-27.26	-49.02	18	6	29	hummingbirds	focal observation
26	-27.26	-49.02	10	5	16	hummingbirds	focal observation
27	-27.27	-49.01	7	5	15	hummingbirds	focal observation
28	10.18	-84.11	20	9	41	hummingbirds	camera
29	10.44	-84.01	22	8	48	hummingbirds	camera
30	10.27	-84.08	25	8	37	hummingbirds	camera
31	-25.31	-48.70	28	10	59	hummingbirds	focal observation
32	22.855	-82.964	5	3	9	bats	feces collection
33	22.841	-82.924	5	4	8	bats	feces collection
34	-23.33	-44.83	16	5	22	hummingbirds	focal observation
35	-23.36	-44.85	22	13	58	hummingbirds	focal observation
36	-23.32	-44.94	28	11	80	hummingbirds	focal observation
37	3.87	-76438	6	6	21	bats	pollen collection
38	-0.204462	-79	7	2	12	bats	pollen collection

39	-0.416699	-79	8	2	14	bats	pollen collection
40	15.66	-92.81	28	11	45	hummingbirds	focal observation
41	15.63	-92.81	25	9	38	hummingbirds	focal observation
42	15.59	-92.85	7	4	12	hummingbirds	focal observation
43	-25.15	-48.27	13	7	23	hummingbirds	focal observation
44	2.51	-76.98	19	14	55	hummingbirds	transect
45	2.66	-76.95	27	8	55	hummingbirds	transect + mist nets
46	-24.25	-48.17	45	20	119	birds	focal observation
47	-24	-47.75	3	14	22	birds	focal observation
48	-23.07	-43.88	5	7	18	hummingbirds/birds	focal observation
49	0.07	-72.45	44	8	88	hummingbirds	focal observation
50	-24.2	-48.05	15	8	29	hummingbirds	focal observation
51	-24.45	-48.68	23	11	59	hummingbirds	focal observation
52	-23.56	-45.36	31	5	29	hummingbirds	focal observation
53	-23.596	-45.417	8	4	32	bats	focal observation

54	-8.71	-35.84	17	3	34	hummingbirds	focal observation
55	-23.63	-45.87	26	6	53	hummingbirds	focal observation
56	-3.97	-79.07	13	9	35	hummingbirds	focal observation + camera
57	-4.11	-79.17	17	8	44	hummingbirds	focal observation + camera
58	-4.11	-78.97	15	7	34	hummingbirds	focal observation + camera
59	18.41	-66.71	8	2	12	bats	feces collection
60	-22.41	-42.74	2	4	7	hummingbirds	focal observation
61	-2.86	-79.11	20	8	66	hummingbirds	focal observation + camera
62	10.423	-84.022	3	4	5	bats	focal observation + pollen collection
63	10.423	-84.022	16	4	50	bats	pollen collection
64	-19.98	-40.52	21	23	61	hummingbirds	focal observation
65	-23.40	-45.18	55	9	123	hummingbirds	focal observation
66	-0.02	-78.77	65	19	191	hummingbirds	focal observation
67	-19.95	-40.51	37	9	88	hummingbirds	focal observation

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Table S2: Results of model selection evaluating the relationship between landscape dissimilarity and beta diversity. ΔAIC values for different model types explaining the variation in interaction dissimilarity (β-diversity) across four dissimilarity indices: β_{S}, β_{OS}, β_{WN}, and β_{ST}. Lower ΔAIC values indicate better model parsimony. For each index, the model with the lowest ΔAIC is highlighted in bold.

	β_{s}	β_{wn}	β_{os}	β_{st}
	Δ AIC			
Linear model - GLM	104.56	8.56	3.6	**0.0**
Quadratic model	106.59	10.56	4.52	2.03
Linear mixed model - GLMM	**0.0**	**0.0**	**0.0**	0.28
Linear mixed model with quadratic term	1.88	1.46	1.33	0.26
Additive model - GAM	104.56	8,56	3.19	0.56

TABLE S3: Comparison of models assessing the effect of forest cover, and the effects of fragmentation *per se* (i.e. forest cover and patch density) on vertebrate pollinator networks in the Neotropical rainforest. Numbers after the model type indicate the scale of effect of each landscape predictor. AICc = Akaike Information Criterion corrected for small samples. SE = Standard error.

Network metric	Model	ΔAICc	df
Plant richness	**FC_{3000}**	**0.0**	**4**
	FC_{3000}+PD_{2270}	1.2	5
	Null	4.8	3
Pollinator richness	**FC_{3000}**	**0.0**	**5**
	FC_{3000}+ PD_{2270}	0.7	6
	Null	2.2	4
Number of interactions	**FC_{3000}**	**0.0**	**4**
	FC_{3000}+ PD_{2270}	1.4	5
	Null	65.2	3
Connectance	**FC3000**	**0.8**	**4**
	FC_{3000}+ PD_{2270}	0.0	5
	Null	4.2	2
Z-NODF	**FC_{3000}**	**0.0**	**5**
	FC_{3000}+ PD_{2270}	0.9	5
	Null	18.8	2
Z-modularity	**FC_{3000}**	**0.0**	**4**
	FC_{3000}+ PD_{2270}	1.9	5
	Null	0.0	4
Proportion of indirect effects	**FC_{3000}**	**0.0**	**5**
	FC_{3000}+ PD_{2270}	0.0	6
	Null	15.2	2
Mean cascade size	**FC_{3000}**	**0.0**	**4**
	FC_{3000}+ PD_{2270}	1.4	5
	Null	4.1	3

FIGURES

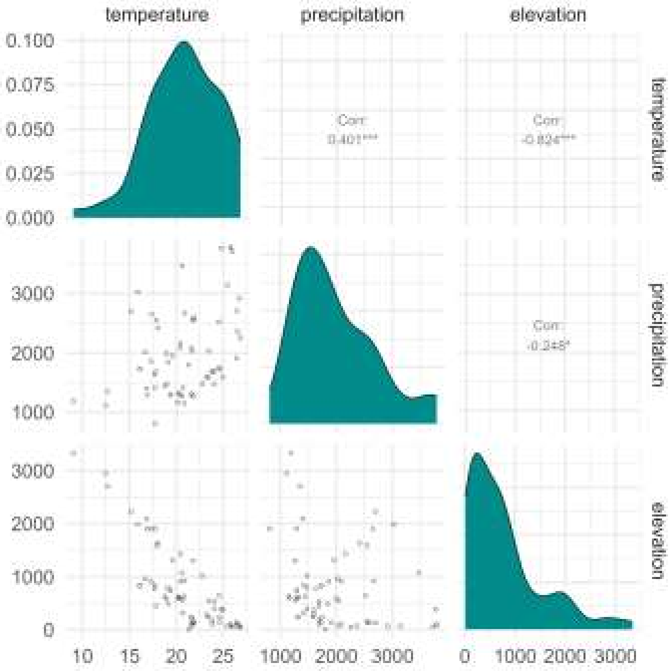

Figure S1: Pearson correlation among the environmental variables: temperature, precipitation and elevation. The values inside the figure represent the coefficient of correction. The * symbol indicates significant correlation. Negative values indicate a negative correlation between variables.

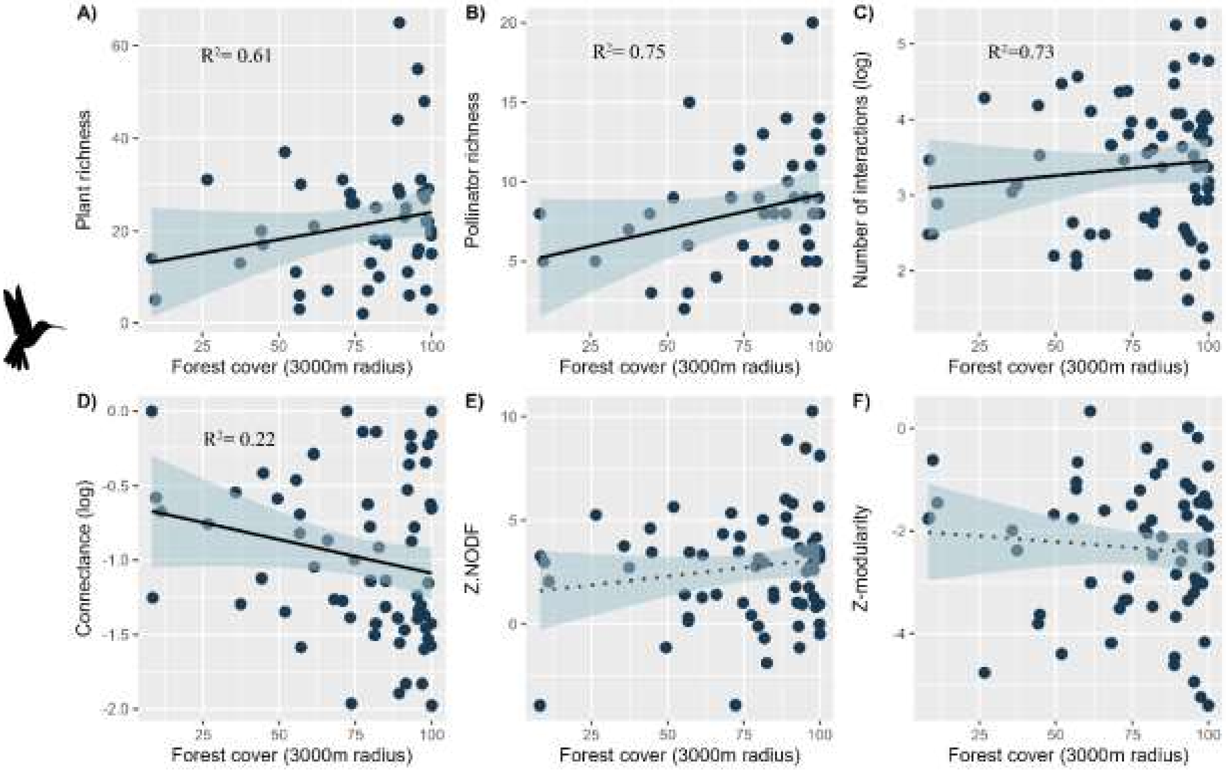

Figure S3: Effects of landscape changes on structure of Neotropical hummingbird pollination networks. The effects of edge density are shown in A) Number of plant species B) Number of pollinator species; C) Number of interactions; D) Connectance, and the effect of percentage of forest cover are shown in E) 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.

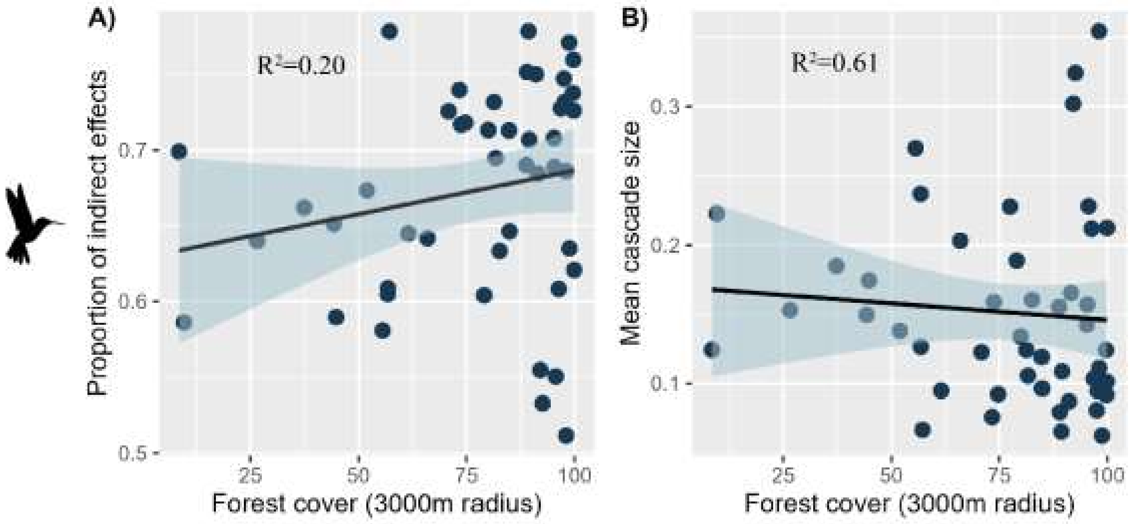

Figure S4: Effects of landscape changes on structure of Neotropical hummingbird pollination networks. The effects of percentage of forest cover are shown in A) Proportion of indirect effects, and the effects of forest edge density are shown in B) Mean cascade size in networks. R^2 represents an estimate of how much the adjusted model explains the variation.

CONSIDERAÇÕES FINAIS

Ao longo desta tese, buscamos entender como as redes de interações entre plantas e polinizadores vertebrados, especificamente beija-flores e morcego são moldados por forças que atuam em escalas diferentes: de um lado, os processos históricos e biogeográficos que ocorreram ao longo de milhões de anos; de outro, as transformações rápidas e intensas que nós, humanos, temos provocado nas paisagens tropicais. Os resultados mostram que essas interações são fruto de um delicado equilíbrio entre o legado evolutivo e ecológico dos organismos, hoje sob diferentes pressões devido a mudanças na paisagem. A história biogeográfica da região Neotropical é marcada por eventos como o soerguimento dos Andes, a formação de ilhas e pontes terrestres, o que deixou marcas profundas, determinando quem está presente hoje nas comunidades e as interações que se estabelecem.

O conservadorismo de nicho emerge como um fator importante, indicando que a história evolutiva segue moldando os padrões de interação, mesmo diante de ecossistemas dinâmicos e em constante transformação. Por outro lado, as mudanças nas paisagens, como o desmatamento, também são capazes de reconfigurar as redes ecológicas. Ao reduzir a quantidade de habitat disponível, essas transformações afetam diretamente quais espécies conseguem persistir naquele ambiente e, consequentemente, como elas interagem. Isso se reflete na alteração da composição e da estrutura das redes de interações. Um resultado particularmente importante deste trabalho é que o grau de fragmentação, ou seja, o quanto a paisagem está dividida em pedaços menores, não se mostrou um fator determinante para a estrutura das interações entre plantas e polinizadores. Isso sugere que, mesmo em paisagens fragmentadas, as interações ecológicas podem ser mantidas, desde que haja uma quantidade mínima de habitat disponível. Esse achado reforça o potencial valor de paisagens fragmentadas para a conservação da biodiversidade e dos processos ecológicos, especialmente nas florestas tropicais. Dessa forma, essa tese oferece uma visão integrada de como processos históricos e contemporâneos atuam juntos na construção e na manutenção das redes de interações. E, nesse contexto, compreender as forças que moldam essas redes, sejam elas geológicas, evolutivas ou antrópicas, é um passo essencial para planejar estratégias de conservação mais eficazes, sensíveis à história, à ecologia e às urgências do antropoceno.