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FUNCTIONAL TRAITS AND CLIMATE CHANGE SHAPING FRUGIVORY NETWORKS IN THE BRAZILIAN ATLANTIC FOREST

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Sumário

Resumo

A Mata Atlântica, um hotspot de biodiversidade global, enfrenta ameaças críticas devido às mudanças climáticas, à defaunação e à fragmentação de habitat. Nesta tese, investigamos como meta-redes de interação entre aves frugívoras e plantas se estruturam e variam espacialmente e como podem responder a futuras mudanças climáticas, integrando ecologia de redes, traços funcionais das aves e modelagem espacial. No primeiro capítulo, mostramos que o papel das aves na meta-rede de frugivoria na Mata Atlântica Brasileira é moldado por traços ecológicos e morfológicos. Espécies mais especialistas em dieta e com menor capacidade de dispersão tendem a formar interações mais fortes, enquanto espécies especialistas em dieta e amplamente distribuídas atuam como conectores na rede. No segundo capítulo, apresentamos o “net.raster”, um pacote em R que espacializa métricas de redes ecológicas bipartidas, permitindo mapear e visualizar a diversidade de interações em escala macroecológica. Essa ferramenta vincula dados de distribuição de espécies com registros de interação, facilitando a análise de padrões biogeográficos tanto em mutualismos, como dispersão de sementes e polinização, como em redes de interações bipartidas antagônicas. No terceiro capítulo, utilizamos essa abordagem metodológica para projetar espacialmente a meta-rede de frugivoria no bioma tanto no presente como no futuro (2050, projeções otimista e pessimista). Investigamos o impacto das mudanças climáticas, revelando que o norte e o litoral da Mata Atlântica devem sofrer simplificação estrutural acentuada, enquanto áreas mais internas e meridionais apresentam maior resiliência devido a processos históricos e traços funcionais das espécies. Observamos que massa corporal, maior grau de frugivoria e distribuição restrita das aves favorecem a estabilidade das interações, enquanto a eficiência de voo se torna um diferencial sob extremos climáticos. Em síntese, demonstramos que a conservação da frugivoria na Mata Atlântica depende da proteção de espécies-chave, como aves frugívoras obrigatórias e de grande porte, e da manutenção de áreas climaticamente estáveis. A integração entre traços funcionais, redes de interação e abordagens espaciais é promissora ao prever e mitigar os impactos das mudanças climáticas em sistemas mutualistas tropicais.

Palavras-chave: redes de interação, traços funcionais, frugivoria, mudanças climáticas, Mata Atlântica, modelagem espacial.

Abstract

The Atlantic Forest, a global biodiversity hotspot, faces critical threats due to climate change, defaunation, and habitat fragmentation. In this thesis, we investigate how interaction meta-networks between frugivorous birds and plants are structured and vary spatially and how they may respond to future climate change, integrating network ecology, bird functional traits, and spatial modeling. In the first chapter, we show that the role of birds in the frugivory meta-network in the Brazilian Atlantic Forest is shaped by ecological and morphological traits. Species that are more diet-specialists and have lower dispersal capacity tend to form stronger interactions, while diet-specialist and widely distributed species act as connectors in the network. In the second chapter, we present “net.raster”, an R package that spatializes metrics of bipartite ecological networks, allowing mapping and visualization of the diversity of interactions at a macroecological scale. This tool links species distribution data with interaction records, facilitating the analysis of biogeographic patterns in both mutualisms, such as seed dispersal and pollination, and in networks of antagonistic bipartite interactions. In the third chapter, we use this methodological approach to spatially project the frugivory meta-network in the biome both in the present and in the future (2050, optimistic and pessimistic projections). We investigate the impact of climate change, revealing that the northern and coastal areas of the Atlantic Forest are expected to undergo marked structural simplification, while more inland and southern areas show greater stability due to historical processes and functional traits of the species. We observe that body mass, a higher degree of frugivory, and a restricted distribution of birds favor the stability of interactions, while flight efficiency becomes a differential under climate extremes. In summary, we demonstrate that the conservation of frugivory in the Atlantic Forest depends on the protection of key species, such as obligate and large frugivorous birds, and the maintenance of climatically stable areas. The integration of functional traits, interaction networks and spatial approaches holds promise for predicting and mitigating the impacts of climate change in tropical mutualistic systems.

Keywords: interaction networks, functional traits, frugivory, climate change, Atlantic Forest, spatial modeling.

General Introduction

Seed dispersal is a crucial ecological process for forest regeneration and the maintenance of species diversity in tropical forests (Jordano, 2000; Herrera, 2003), where plants rely mostly on animals to disperse their seeds (Jordano, 2000). In the Atlantic Forest, this function is predominantly carried out by birds, especially in defaunated areas where large mammals have been locally extinct (Galetti et al., 2013; Emer et al., 2020). By linking plants and frugivores, these mutualistic interactions sustain plant communities and their regenerative processes but are increasingly threatened by deforestation, fragmentation, defaunation, and climate change (Emer et al., 2019; Galetti et al., 2013; Bomfim et al., 2018; Tylianakis et al., 2008).

Understanding the mechanisms and patterns underlying frugivory interactions is therefore critical to inform conservation and restoration strategies, especially in highly threatened biodiversity hotspots. These anthropogenic pressures not only reduce species diversity but also reshape the structure of mutualistic networks, with potential implications for ecosystem stability and functionality (Bascompte & Jordano, 2007; Valiente-Banuet & Verdú, 2013). Ecological network theory provides a powerful framework to understand how these interactions are organized and how they respond to disturbances, both at local and regional scales. Applying this theory to seed dispersal allows researchers to assess the relative importance of individual species (e.g., keystone species), the structural complexity of communities, and the robustness of interactions under environmental change (Memmott et al., 2004; Landi et al., 2018).

Within network ecology, we can use different levels of organization to describe the structure of mutualistic systems. Species-level metrics, such as species strength and centrality (closeness and betweenness), reflect each species' functional position in the network and its importance for the flow of interactions (González et al., 2010; Trøjelsgaard & Olesen, 2016). Network-level metrics, such as species richness, links per species, generality, and vulnerability, describe the complexity and functional redundancy of the network as a whole (Tylianakis et al., 2007; Montoya et al., 2006). Especially when considering a metanetwork, these levels are complementary: the functional role of species helps us understand how networks remain structured, while large-scale patterns reveal how environmental forces and biological traits shape the network regionally.

Ecological and morphological traits of frugivores are key determinants of the formation and stability of these networks; for instance, beak and body sizes, dietary specialization, mobility and flight ability, and geographic range size of species distribution (Dehling et al., 2016; Sebastián-González et al., 2017; Vizentin-Bugoni et al., 2021). The functional composition of communities influences both interaction diversity and system stability, and specific traits can predict patterns of connectivity, redundancy, or specialization (Ramos-Robles et al., 2018; Correa et al., 2016). Therefore, understanding how functional traits influence network structure, at different levels and scales, is crucial to predicting the maintenance of the ecological service of seed dispersal in the context of degradation and climate change.

This thesis investigates how ecological and morphological traits of frugivorous birds, spatial gradients, and climate-driven changes influence the structure and cohesion of frugivory networks across multiple scales in the Brazilian Atlantic Forest (AF). Three integrated chapters address this central question: (1) the first analyzes how traits determine the functional role of bird species in a frugivory metanetwork; (2) the second develops a new computational tool to calculate network metrics from spatial data; and (3) the third applies this spatial approach to assess the effects of current and future climate, in adition bird traits, on the structure of the frugivory metanetwork in the Brazilian Atlantic Forest.

In Chapter 1, we examine how bird traits determine species roles in a frugivory metanetwork built from 26 local networks across the AF. The traits are beak width, body mass, frugivory degree, hand-wing index (HWI, associated with avian flight efficiency and dispersal ability), and range size. We used betweenness and closeness centralities and species strength to quantify the ecological importance of each bird species in the network. Based on existing evidence (Dehling et al., 2016; Malanotte et al., 2019; Ramos-Robles et al., 2018), we hypothesized that species with greater morphological versatility (e.g., larger body and beak sizes) and ecological generalism (higher frugivory degree and broader ranges) would be more central and exert stronger effects on the network. These species commonly act as hubs or connectors, potentially buffering the network against disturbances (González et al., 2010; Morán-López et al., 2019; Moulatlet et al., 2023). The focus on species-level descriptors allows a mechanistic understanding of how trait variation translates into functional roles within the interaction system.

Chapter 2 presents the R package *net.raster*, developed as part of this thesis to overcome a methodological gap in spatial network ecology. While existing tools (e.g., *bipartite* and *bmotif* packages) compute network metrics from interaction matrices, they do not support large-scale or spatialized analyses based on raster data. Our tool integrates rasterized species distribution data with known interactions to produce raster maps of network metrics across regions. This innovation enables macroecological analyses of interaction networks, responding to recent calls to include spatial and temporal dynamics in network ecology (Guimarães, 2020; Poisot et al., 2021; Windsor et al., 2022). By combining species co-occurrence and interaction data, *net.raster* allows the inference of network properties at local and regional scales, bridging ecological theory and spatial conservation planning.

In Chapter 3, through *net.raster* we assess how frugivory networks in the AF may reorganize under climate change. We generate SDM for 192 bird species and 320 plant species, for present and future scenarios (2050, optimistic and pessimistic). Then, we filter the metanetwork matrix used in Chapter 1 for the projected species pool, modelling five key network-level metrics: number of species of each level (plants and frugivores), links per species, generality (mean partners per frugivore), and vulnerability (mean partners per plant). Our hypotheses include that historically stable areas host more complex networks and that future scenarios will induce functional simplification of the metanetwork, favoring generalist and widely distributed frugivores (Carnaval et al., 2014; Huang et al., 2025; Emer et al., 2019). Furthermore, we examined how the same bird traits from Chapter 1 predict spatial variation in network metrics across scenarios, integrating trait-based and macroecological perspectives (Li et al., 2020; Huang et al., 2025; Zhang et al., 2025).

The hypotheses developed in Chapter 3 extend those from Chapter 1. While Chapter 1 tested whether traits predict species-level roles in a static metanetwork, Chapter 3 asked whether those traits also explain spatial variation in network complexity and interaction diversity under dynamic climatic scenarios. For instance, if highly frugivorous, widely distributed birds are central species in current networks (as shown in Chapter 1), their projected range shifts may determine the future persistence and redundancy of interactions in specific regions. Thus, the trait-network relationships established in Chapter 1 provide a foundation for the predictive analyses in Chapter 3, despite some different results regarding which traits are important for different network properties' descriptors. In addition, unlike the single metanetwork of the first chapter, in the third chapter, we have one network per pixel, built based on the input metanetwork and the SDMs.

The network metrics used in this thesis span two levels of organization: species-level (Chapter 1) and network-level (Chapter 3). Species-level metrics describe how individual species contribute to network cohesion, redundancy, and connectivity (Bascompte & Jordano, 2006; Trøjelsgaard and Olesen, 2016). In contrast, network-level metrics such as number of species, links per species, generality, and vulnerability, yet simple descriptors, can summarize structural properties of local or regional networks, allowing comparisons across space and scenarios (Guimarães, 2020; Poisot et al., 2021). By combining these perspectives, the thesis addresses both “who” maintains frugivory networks (Chapter 1) and “where” and “how” these networks persist or deteriorate (Chapter 3), offering an integrated multi-scale understanding, enabled by the developed tool (Chapter 2).

Together, the three chapters contribute to ecological network science by linking trait-based approaches, spatial modeling, and climate projections. They emphasize the need to conserve not only species but also their interactions, particularly in functionally diverse mutualistic systems vulnerable to global change. In addition, the *net.raster* tool offers a replicable and scalable framework for future studies in other biomes or taxa, paving the way for spatially explicit network studies focused on bipartite interactions, whether mutualistic or antagonistic.

This integrative approach aligns with growing efforts to understand biodiversity beyond species lists, recognizing the centrality of interactions and functional traits in maintaining ecosystem services such as seed dispersal. As tropical forests face accelerated transformation, identifying the traits and conditions that sustain interaction networks becomes increasingly urgent. This thesis responds to that challenge by offering insights into the spatial and functional reorganization of frugivory in one of the world's most threatened and biodiverse biomes.

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Capítulo 1. Ecological and morphological traits of frugivorous birds drive species strength and centrality in frugivore-plant metanetwork in the Brazilian Atlantic Forest

O presente capítulo será submetido para a revista *Oikos*. Portanto, a formatação segue as normas da revista.

Ecological and morphological traits of frugivorous birds drive species strength and centrality in frugivore-plant metanetwork in the Brazilian Atlantic Forest

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Abstract

Seed dispersal is a fundamental mechanism for the diversity maintenance of tropical plant communities. Species' ecological and morphological traits determine different species roles in mutualistic networks mediating the interactions between frugivores and fleshy fruits. We assessed how frugivorous bird traits affect species roles in a metanetwork in the Atlantic Forest (AF). We built a metanetwork based on 26 plant-frugivore networks comprising 214 bird species and 309 plants, compiled functional and ecological traits for all bird species, and used three species-level metrics - species strength (henceforth strength), betweenness centrality, and closeness centrality - to represent species roles in the metanetwork. We found that strength was positively correlated with frugivory degree and negatively correlated with hand-wing index (HWI), a proxy for bird species dispersion capacity. Thus, besides more diet-specialized frugivores, species with lower HWI and lower dispersion capacity make the strongest interactions and may provide an important proportion of the seed dispersal service in AF. Closeness centrality was positively correlated with frugivory degree and with range size, indicating that more frugivorous and geographically distributed bird species potentially act like hubs when interacting with many network generalist plants across the AF. Thus, birds with higher closeness centrality can contribute more in terms of richness maintenance, in addition to the possibility of them quickly affecting the entire network in situations of disturbance. Betweenness centrality was also positively correlated with the range size of species distribution, indicating widespread birds as possible connectors of different parts of the frugivory system. Therefore, the more specialized frugivores and those species with larger distributions form the central core of the metanetwork, being network generalists and important for maintaining plant diversity throughout the biome. Through the regional-scale metanetwork approach our study highlights that strength and centrality are not only driven by frugivory degree but also by species' HWI and range size. Therefore, a macroecological perspective on frugivory networks can improve our understanding of the role and importance of key species traits for ecosystem process maintenance and forest biodiversity.

Keywords: bird traits; network species role; network metrics; tropical frugivory; seed dispersal.

1. Introduction

More than 80% of tropical forest plants depend on frugivorous animals to disperse their seeds (Jordano 2000). Frugivory is an important early-stage diversifying mechanism for plant communities where zoochoric species predominate, and even relatively low rates of seed dispersal can maintain populations of rare species in forests (Carlo and Morales 2016). Frugivory is highly vulnerable to forest disturbance, as the groups of animals involved in this mutualistic interaction have been suffering a major decline in recent decades (Neuschulz 2016, Emer et al. 2020). Fragmentation and defaunation often lead to the functional extinction of large frugivorous birds and mammals and long-lived shade-tolerant plants, while small frugivores and pioneer plants tend to thrive in disturbed areas (Galletti et al. 2013, Bello et al. 2015, Silva et al. 2016). Such disturbance can lead to significant losses of species diversity that carry over to losses or changes in species interactions (Tylianakis et al. 2008, Naeem et al. 2009, Emer et al. 2020). A multi-network approach revealed that in mutualistic networks species interaction loss can cause ecosystem collapse through synergistic perturbations (Valiente-Banuet and Verdú 2013). This might undermine the dynamical stability of ecosystems, as both species diversity and their interactions are essential for the maintenance of ecological processes (Naeem et al. 2009; Bascompte; Jordano 2007).

Functional redundancy also seems important for the maintenance of fish-plant seed dispersal networks, where high overlap among generalists appears to mitigate the loss of any given species, even though these networks were sensitive to the loss of the most connected species (Correa et al. 2016). The architecture of these networks, analyzed based on the network structure regarding nestedness and modularity, seems to be maintained by larger fish species in general, which are central and connectors of the network due to their larger range of fruit size exploitation. The same overlapping pattern of resource use by generalists was found among frugivorous birds, resulting in greater network centrality for species with larger gapes (which can eat both small and larger fruits)(Malanotte et al. 2019). On the other hand, plants with smaller fruits (such as widely distributed pioneers, generally intolerant to shade) may also contribute to the stability of frugivory networks, as birds of different sizes can consume them, resulting in a greater number of interactions in the network (Ramos-Robles et al. 2018; Malanotte et al. 2019). This reinforces the hypothesis that size correspondence influences ecological interactions but also reveals the importance of the most connected species, which may be the strongest or most central. Moreover, regarding the potential functional redundancy attributed to the different roles of species in the network, it is crucial to investigate whether there is a loss of specific ecological functions associated with seed dispersal, which could result in the functional homogenization of interactions (Emer et al. 2020).

Network stability can be described throught many theoretical approaches and metrics, for example persistence, temporal stability, and robustness (see Landi et al. 2018 for a theoretical review). Here, we draw on one of the most common concepts used in ecological network research, the deletion stability: the tolerance of the network to sequential removal of species, simulating coextinction cascades (Memmott et al. 2004). Network stability appears to depend both on the number of interactions and on the presence of morphologically corresponding interaction partners (Dehling et al. 2016; Morán-Lopez et al. 2019). Therefore, besides the potential effects from human disturbances, the interactions between frugivorous and fleshy fruits are influenced by the traits of the species involved, such as abundance and morphology (Ramos-Robles et al. 2018; Malanotte et al. al. 2019).

Different plant traits, such as seed and fruit sizes, determine different species-level roles for birds in frugivory networks, like species strength and centrality metrics (Ramos-Robles et al. 2018; Malanotte et al. al. 2019). Therefore, it is important to investigate how different ecological characteristics of species influence the role played by these species in networks, which can be crucial for the stability of the ecosystem process (Dehling et al. 2016; Morán-Lopez et al. 2019). Besides morphological attributes (like the sizes of body, beak, and wings), bird ecological traits can be very important for frugivory and seed dispersal, for example, the dietary specialization degree (i.e., frugivory degree: proportion of fruits on diets), and the range size of geographical distribution (Sebastián-González et al. 2017; Malanotte et al. 2019; Carreira et al. 2020; Pizo et al. 2021; Vizentin-Bugoni et al. 2021). Indeed, a recent study comparing species-level drivers of avian centrality between local networks and a global metanetwork revealed that the influence of these factors differ between the two levels of organization of seed dispersal systems (Moulatlet et al. 2023). Geographic traits were more important than morphological or evolutionary traits in explaining the centrality of species only in the metanetwork (global scale), indicating that the process governing species centrality depends on the network level (Moulatlet et al. 2023).

To assess the species role on ecological networks, three important species-level network descriptors are species strength (SS), closeness centrality (CC), and betweenness centrality (BC). The use of species level measures is relevant for a more accurate identification of "keystone species", which might perform different topological roles and maintain network structure, fundamental for ecosystem functioning and conservation (González et al. 2010; Ramos-Robles et al 2018). In ecological terms, higher SS values reflect the relevance of a particular bird in the whole fleshy-fruited plant (meta)community for seed dispersal (Morán-Lopez et al. 2019; González-Varo et al. 2021). In turn, greater CC values imply that bird species interact with many network-generalist plants, being part of the central core of the Atlantic Forest metanetwork and more important for plant diversity maintenance (González et al. 2010; Morán-Lopez et al. 2019). Finally, positive values of BC identifies species that act as network connectors, which indicates that the species may play a key role to the cohesiveness of mutualistic networks (González et al. 2010).

The metanetwork is formed by the regional pool of species and their potential interactions, by aggregating local networks, sampled at different times, in different locations or under different environmental conditions (Poisot et al. 2014). Therefore, whenever two species interact in at least one local network, they receive an interaction in the metanetwork (Poisot et al. 2014). Thus, building a regional metanetwork represents an opportunity to assess species contributions to ecosystem functions from a macroecological perspective (Araújo et al. 2018; Moulatlet et al. 2023). It is necessary to understand the regional scale context in which species and interactions are inserted for adequate conservation planning of the ecosystem service of seed dispersal in response to anthropogenic threats (Li et al. 2020; Santini et al. 2021). Indeed, it can raise awareness among States and the general public, enabling biodiversity research and conservation to remain on the priority agenda despite economic uncertainties and political fluctuations (Santini et al. 2021). Besides that, as network structure seems to be scale dependent (Galiana et al. 2019; Li et al. 2021; Moulatlet et al. 2023), focus on regional scales can help to better understand the drivers of network metrics and guide conservation efforts of ecosystem functioning in fragmented landscapes of biomes or domains (Li et al. 2020).

The Brazilian Atlantic Forest (AF) is an important biodiversity hotspot that has been suffering deforestation and fragmentation, currently a complex mosaic of small fragments and clusters of neighboring fragments (Joly et al. 2014, Myers et al. 2000, Ribeiro et al. 2009). The detrimental effects of habitat loss on the number of plant-frugivore interactions has been previously documented in this domain (Emer et al. 2020, Pinto et al. 2021, Bonfim et al. 2022). The number of interactions decreases and the remaining ones are carried out by smaller-sized generalist species in anthropogenic landscapes, suggesting that the AF is losing specific ecological functions associated with seed dispersal, which can cause functional homogenization of interactions in the medium and long term (Emer et al. 2020).

Few studies assess how ecological and functional species characteristics influence the role of species in bird-plant frugivory metanetworks (see Li et al. 2020 for a subtropical fragmented forest landscape and Moulatlet et al. 2023 for a global metanetwork, both comparing local networks with the metanetwork derived from them). Therefore, there is an urgent demand for investigations focusing on the species roles and their interactions in space across regional scales such as biomes, especially in Neotropical forests, where zoochory is the priority process of seed dispersal (Jordano 2000). Here, we assess how ecological and morphological traits of frugivorous birds affect their network species' roles in a metanetwork. In order to do this, we gathered a robust dataset on 26 published plant-frugivore networks across the Atlantic Forest to build a metanetwork. We evaluate how bird species traits (frugivory degree, range size of spatial distribution, body mass, beak width, and hand-wing índex – HWI) relate to species-level network metrics (species strength, closeness, and betweenness centralities). We expect that the more specialized frugivorous are on their diet (i.e., with high proportion of fruits on diet) the higher SS will be, thus occupying the central position in the metanetwork (higher CC), as they are more dependent on fruits for life and regularly feed on a greater variety of fruit species, especially those network-generalists plants with smaller, sugar-rich and lipid-poor seeds (Mello et al. 2015; Malanotte et al 2019; Pizo et al. 2021). We predict the same effect (higher SS and CC) for large-bodied frugivorous compared to small-bodied ones, as larger birds are expected to feed on a greater number of plant species, and can morphologically match with both smaller and larger seeds (Ramos-Robles 2018; Correa et al. 2016; Carreira et al. 2020). As beak width is correlated with body mass and to the bird's ability to consume fruits below a certain size threshold (Dehling et al. 2016; Sebastián-González et al. 2017), we expected similar effects on SS and CC. Furthermore, we expected frugivorous with greater HWI (often used as a proxy for dispersal ability) and with larger geographic ranges to have higher SS and be more central than frugivorous with smaller HWI and narrowly distributed, as the first ones also feed on a broader number of plants (Vizentin-Bugoni et al. 2021). About BC, it is expected that only the network-generalist bird species would present positive values of BC (González et al. 2010). Thus, we expected that birds acting like connectors of the entire metanetwork should be those with higher levels of frugivory, larger body size, greater beak sizes, and with larger HWI values and geographic ranges.

2. Methods

2.1 Study area

The Atlantic Forest originally covered more than 1.5 million square kilometers ranging from northeast Brazil to Argentina (Joly et al 2014). Since the European colonizers disembarked on the Brazilian coast in 1500, this tropical forest has been exposed to high levels of deforestation and fragmentation (Joly et al. 2014). Currently, its landscape is a complex mosaic of small fragments (<50 ha, c. 80% of the remaining area) and clusters of neighboring fragments (<200 m apart) (Ribeiro et al. 2009). Also, it is considered one of the top five biodiversity hotspots in the world due to the high species diversity, high levels of endemism and the presence of threatened species (Myers et al. 2000). In this domain, zoochoric seed dispersal is carried out mainly by a diverse set of bird species, especially in defaunated areas, without large mammals (Galetti, 2013; Emer et al., 2020).

2.2 Data collection

The dataset on the local plant-frugivore networks was published elsewhere (Bonfim et al. 2022) but a brief overview is given here. The authors gathered data in the largest published database on interactions available for the Brazilian Atlantic Forest, the ATLANTIC FRUGIVORY (Bello et al. 2017). This database has more than 8000 interactions from 331 vertebrates and 788 plant species recorded in 166 studies, encompassing studies that recorded a particular animal feeding on fruits, animal diet and network studies (reporting interactions among plants and frugivorous in specific sites). They selected only the last type of studies, filtering on bird-plant networks, which resulted in 12 studies. Hence, the dataset includes only community-level studies in forest fragments, using different methodologies such as focal observations, feeding bouts, etc. Thus, the authors completed the data with the results of additional search of bird-plant networks studies in the Web of Science and Scopus, using the following search terms: ("ecological network*" OR "mutualistic network*" OR "frugivor*") AND ("bird*") AND (“Atlantic Forest”) in TOPIC. In addition, they only included network studies that had the coordinates of the sample fragment and provided the interaction matrix, resulting in another 13 studies accounted for. The authors additionally shared to us a compiled network that was not included in their original publication due to the absence of sampling effort data, which we do not evaluate. Thus, our final database comprised 26 plant-frugivore networks from different forest fragments across the biome (Fig.1; SM). In addition, the set of networks includes phytocentric studies (based on observations of fruit consumption by birds in each plant species in the field) and zoocentric studies (based on the analysis of feces of each bird species). Due to the time lapse among publications (from 1994 to 2019), we checked the scientific nomenclature of bird and plant species to standardize the data in the metanetwork. Thus, we corrected the names of birds and plants from the 26 studies with the help of the Brazilian Biodiversity Information System (SiBBr), after checking incorrectly spelled names and synonyms in local networks. For birds, we also checked the full correspondence with the names listed in the AVONET (Tobias et al. 2022) and, in case of divergence (only for *Aburria jacutinga*), we considered the name listed as accepted in SIBBr and in the current ornithological literature. We maintained on the dataset the birds from Psittacidae family (11 species), as their role as endozoochorous dispersers is debated, with recent studies pointing that this is a neglected mutualism, especially regarding larger-seeded plants (Tella et al. 2019; Blanco et al. 2016). Among the plants, we excluded nine records that were not identified at least at the family level, even after trying contact with the authors where they appeared. Therefore, we excluded from metanetwork one bird species (*Dysithamnus mentalis*) present at only one local network, since it lost all its connections after this plant exclusion. Finally, it is important to highlight that our dataset possibly aggregates many local networks of disturbed areas, which may have already lost their larger frugivorous birds.

2.3 Bird traits

We collected data on bird ecological and morphological traits related to frugivory and seed dispersal. We used frugivory degree, range size of spatial distribution, body mass, beak width, and the hand-wing index (HWI) (see the Supplementary Table 1 for definitions) as possible determinants of bird species' role on our Atlantic Forest metanetwork. We tested the correlation between all the ecological and morphological birds`traits (Supplementary Table 2), thereby excluding two categorical traits that we previously included (degree of dependence on forests and forest stratum generalism/specialization). The importance of using ecological and morphological traits in network studies relies on many reasons. For instance, the correspondence between morphological and functional differences between species is consonant with the differences in resource use (Dehling et al. 2016). In addition, functional trait matching in bird-plant species strongly influences whether the species interact or not (Dehling et al. 2016; Morán-Lopez et al. 2019), being a general mechanism regulating interactions in mutualistic networks (Rezende et al. 2007; Sebastián-González et al. 2017; Albrecht et al. 2018, Moulatlet et al. 2023).

About the chosen traits, frugivory degree, (i.e.dietary specialization), seems to be the main driver of keystone central species in seed dispersal networks (Mello et al. 2015) and seems to be correlated with the importance in terms of species role on frugivorous network (Vizentin-Bugoni et al. 2021). Body mass is an important and well-used trait for seed dispersers of many taxa (e.g. Mello et al. 2015; Correa et al. 2016; Malanote et al. 2019; Carreira et al. 2020). The range size of spatial distribution seems to be a major trait to the Atlantic Forest birds, where the apparent predominance of geographical widespread species appears to impact frugivorous networks (Pinto et al. 2021; Fuzessy et al. 2022). We also choose to test HWI because it shows positive and significant relationships with geographical and ecological traits related to dispersal abilities (Sheard et al. 2020; Arango et al. 2022). The beak width is related both to fruit choice preferences and to the bird's ability to consume fruits that are below a certain size threshold (Dehling et al. 2016; Sebastián-González et al. 2017). We used the Elton Traits database (Wilman et al. 2014) for diet information and the AVONET (Tobias et al. 2022) database for the other traits. In this way, we were able to collect the traits of interest for 200 bird species (93.5%).

2.4 Network species level descriptors

We built a metanetwork by pooling the 26 plant-frugivore networks in a single weighted A_{mn} adjacency matrix in which m is each plant species (rows), n is each bird species (columns) and the cells contain the number of interactions of the bird-plant pairwises (edges) (Moulatlet et al. 2023). In this way, each cell of the matrix presents the interaction frequency, which was determined by the sum of the unique pairwise combination of each bird and plant species recorded interacting in each network. Thus, our matrix is weighted by the frequency of studies in which each interaction occurs. Then, we estimated species strength (SS), weighted closeness centrality (CC) and weighted betweenness centrality (BC) focusing on bird species. SS is based on the sum of relative frequencies of interaction/visit on plant species (Bascompte & Jordano, 2006; Morán-Lopez et al. 2019), quantifying the relevance of frugivorous in the whole fleshy-fruited plant community: higher values reveal that much of the dispersal services depend on this particular disperser (Morán-Lopez et al. 2019; González-Varo et al. 2021). In turn, CC describes how close (in number of interactions) a particular species is to all other species in the system (Trøjelsgaard and Olesen, 2016). Thus, a frugivorous with greater CC interacts with many network-generalist plants, acting like a hub, and being important to the overall connectance and stability of the network (González et al. 2010; Trøjelsgaard and Olesen, 2016; Malanotte et al. 2019). Hence, dispersers with higher CC are network-generalists, part of the central core of the network, and key to the maintenance of plant richness (González et al. 2010; Morán-Lopez et al. 2019). Finally, the BC is “a measure of the number of shortest paths (between all species pairs) that passes through a focal species” (Trøjelsgaard and Olesen, 2016). Therefore, species with positive BC can be keystone species by connecting different parts of the system, acting as a bridge between different parts of the network and being crucial species to the cohesiveness of mutualistic systems (González et al. 2010).Both CC and BC range from 0 to 1. These three metrics at the species level complement each other in the identification of ecologically fundamental species, either by the strength of their interactions in the metacommunity, or by their centrality for the maintenance of the diversity of the plant community and cohesion of the network (proxy for the maintenance of the ecosystem service seed dispersal). All these network metrics were estimated by the species.level function in the bipartite package (Dormann et al. 2011).

2.5 Model selection

We tested the normality of the data distribution of each network metric performing the Shapiro-Wilk test. Because data distribution was not normal we built a global generalized linear mixed model fitted by maximum likelihood (Laplace Approximation) using each bird trait as predictors and network metrics as response variable, through the glmmTMB function of glmmTMB package (Brooks et al. 2017). In each model we included the information on the taxonomic Family as a random effect. We used the Gamma family and log link for SS and the zero-inflated Beta family and logit link for CC and BC. The models were validated based on residual analysis (Pearson). To do so, we transformed the geographic range size by means of a square root and used a log of body mass. Due to the zero inflation and lower values, we needed to transform the both centrality metrics to perform the model selection, transforming 0 values of closeness centrality and using the square root of weighted betweenness. Then, to fit a mixed effects model for each metric, we performed the automated model selection with the aid of the function dredge of the MuMIn package (Bartoń 2020), building the average model and thus identifying which traits actually had an effect on our species level metrics. The best performing models were chosen based on the lowest value of Akaike Information Criterion (AIC, *Akaike Information Criterion*, AKAIKE, 1974). Afterward, we rebuilt the model with these chosen predictors and used the effect_plot function of jtools package (Long 2022) and ggplot2 (Wickham 2016) to generate predictor effect plots of SS, BC and CC. All analyses were run in R v. 4.2.2 (R DevelopmentCore Team 2022).

3. Results

The Brazilian Atlantic Forest frugivorous bird-plant metanetwork was composed of 214 bird and 355 plant species. Six birds (2.8%) are identified only at the genus level, while 10.4% of the plants in the metanetwork are identified at the genus level, besides 2.5% of plants identified at family level. Birds were distributed in 128 genera and 30 families. The genera *Tangara* and *Turdus* were the most frequent (12 and nine species, respectively). Plants were distributed in 22 families and 37 genera. The most important genus was *Miconia*, with 23 species and one record at the genus level. Frugivorous bird species strength ranged from 0.01053 to 25.62093 (mean=1.84579), being *Chiroxiphia caudata* the species with highest SS value (Supplementary Table 3). In addition to *C. caudata*, *Thraupis sayaca, Penelope obscura*,*Turdus rufiventris*, and *Turdus albicollis* also presented values of SS greater than 12. Weighted closeness centrality (CC) ranged from 0 to 0.00654 (mean=0.004609). *Dacnis cayana* presented the greater value of CC. Besides *D. cayana*, the more central species in terms of closeness were *T. albicollis*, *C. caudata*, *T. rufiventris*, *Tachyphonus coronatus, and T. sayaca*. Weighted betweenness centrality ranged from 0 to 0.195 (mean= 0.00467), with 45.3% of species presenting positive values of BC. The most central species and metanetwork hubs were *D. cayana*, *Turdus albicollis*, *C. caudata*, *Turdus rufiventris*,and *T. sayaca*. We also present all the values for both binary and weighted values of CC and BC in Supplementary Table 3.

Species strength was positively correlated with frugivory degree (β =0.0175, t value = 10.40, p < 2e-16; Figure 2A) and negatively correlated with hand-wing índex – HWI (β = -0.0228, t value = -11.56, p < 2e-16; Figure 2B). The weighted closeness centrality of birds was positively correlated with frugivory degree (β = 0.00457, z value = 3.46 , p = 0.00053; Figure 2D), as well as with the range size of species distribution (β = 0.00007, z value = 2.03, p = 0.04253; Figure 2E). Weighted betweenness centrality was positively correlated only with range size (β = 0.00013, z value = 2.22, p = 0.0267; Figure 2C). Body mass and beak width did not influence any species level descriptors on our metanetwork. Accordingly, we found a positive effect of the degree of frugivory on both SS and CC, as expected. Also, frugivorous with larger geographic areas were more central in terms of closeness and betweenness, but this characteristic did not explain the SS. Finally, HWI did not explain centrality and, contrary to what we expected, it was negatively related to SS. Contrary to our predictions, body mass and beak width were not related to any bird species-level metric evaluated in the metanetwork.

4. Discussion

Using a metanetwork approach we unveiled how ecological and morphological traits are correlated with frugivorous bird roles in the Brazilian Atlantic Forest. Specifically, our results showed that bird species with higher frugivory degree and lower hang-wing índex (HWI) are stronger seed dispersers within this macroecological system, whereas species with higher frugivory degree and larger geographical ranges occupy central roles in the metanetwork. This means that species with lower HWI, which often have a lower dispersal capacity, make the strongest interactions and provide an important proportion of the seed dispersal service (Morán-Lopez et al. 2019). On the other hand, widely distributed species, which are more likely to be present even in disturbed local communities and to be observed interacting with the fruits, form the central core of species in the metanetwork, being of greater regional importance for the maintenance of plant diversity (Morán-Lopez et al. 2019). Widespread species are also the hubs of the metanetwork, that is, their interactions connect different parts of the network in space, revealing that their populations are crucial for the cohesion of the AF frugivory system (González et al. 2010). Therefore, our study reveals that, despite the congruence of frugivory degree's importance for SS and CC, other divergent traits also drive these two metrics in the metanetwork approach. Additionally, range size was positively important to both centrality metrics, CC and BC, confirming that in the macroecological scale of interactions, this is a key trait of central frugivory birds, while neither morphological trait had an influence on avian centrality. Thus, in a regional macroecological perspective of frugivory networks, our study contributes to improving the understanding of the different traits, the role and importance of different species of frugivorous birds for the maintenance of both the ecosystem process of seed dispersal and the entire community associated with this mutualism in extensive areas and disturbed forests and regions.

In terms of key bird species, *Chiroxiphia caudata, Thraupis sayaca, Turdus albicolis*, and *Turdus rufiventris* were the strongest and most central species, despite the low values of metanetwork centrality measures. *Penelope obscura* had the highest species strength and also showed above-average values for centrality. *Dacnis cayana* proved to be the most central of the species and has above average, albeit relatively low, species strength. Thus, we can consider these six species key species for the frugivorous system in the AF, apparently an important core of bird assemblage for the maintenance of the seed dispersal service and the plant community diversity. In a recently investigated global metanetwork (Moulatlet et al. 2023), four of this set of species also showed greater centrality (*Thraupis sayaca, Turdus albicolis, Turdus rufiventris,* and *Dacnis cayana*). Moreover, *Turdus* was the strongest and most central genus of bird species in the AF metanetwork, in addition to being the most frequent in local networks (along with the genus *Tangara* in this last characteristic). Indeed, Turdidae and Thaupideae are often the most representative families in Neotropical frugivorous networks, including the Atlantic Forest (Silva et al. 2016; Emer et al. 2018), lower humid forests in Venezuela (Buitrón-Jurado, Snaz 2021), and across the Andes (Bender et al. 2018). Moreover, these two families were also the most central species in the global metanetwork (Moulatlet et al. 2023), corroborating their frugivory keystone species status (Escribano-Avila et al. 2018). These families are generally tolerant to humans, generalists in their diets, and widespread throughout the Neotropical region (Tobias et al. 2022, Moulatlet et al. 2023). Thrushes (*Turdus)* are also regional, altitudinal or long-distance migrants that can contribute with the seed dispersal service (Emer et al. 2018). *Chiroxiphia caudata*, *Turdus rufiventris* and *Turdus albicollis* were key species in terms of strength, being important as potential seed dispersers. The three species have forest habitats and are broadly distributed across the AF. These two *Turdus spp.* present generalist primary lifestyle and medium degree of frugivory, while *C. caudata* is classified as highly frugivorous (Tobias et al. 2022). Another strong species within the network was *Penelope obscura*, a large, forest-dependent, and highly specialized frugivorous (Tobias et al. 2022). In turn, *Thraupis sayaca* showed higher strength and was a connector of different parts of the metanetwork, revealing its potential to seed dispersal service on the flesh-fruited plant species. This species is small-bodied and broadly distributed across the biome, exhibiting medium level of frugivory degree (Tobias et al. 2022). Finally, *Tachyphonus coronatus* was one of the more central species, even being less specialized on frugivory and adaptable to many types of habitats (Tobias et al. 2022).

As expected, the degree of frugivory was positively correlated with SS and CC, being the only characteristic shared by the best explanatory models for both network metrics. The proportional amount of fruits in the diet is well known and extremely important for seed dispersal systems, making fruit-eating birds with high levels of frugivory degree important for the structural robustness of ecological communities (Mello et al. 2015; Malanotte et al. 2019; Sazima et al. 2010). However, another study of a bird-plant frugivorous metanetwork, composed of 16 local networks from fragments of the Atlantic Forest, found different conclusions, revealing the demand for new investigations. Despite the convergent importance of small-seeded, fast growing plant species, the less frugivorous, small-bodied bird species were the more important (Emer et al. 2018). The higher SS associated with greater frugivory degree rely on the prominent relevance of birds with more diet specialization in the whole fleshy-fruited plant community for the seed dispersal service (Morán-Lopez et al. 2019; González-Varo et al. 2021). Fruit chemistry can possibly explain this finding because as suggested by Pizo et al. (2021), birds that eat more fruits tend to interact more with plant genera producing lipid-poor (that is, sugary) fruits, while less specialized frugivorous tend to prefer lipid-rich fruits. Therefore, we believe that the more frugivorous species need to increase their interactions with many lipid-poor seeds to reach their energy requirement (as postulated by the optimal foraging theory of MacArthur & Pianka 1966). In fact, the main plant genera in our study, *Miconia*, is a great example of a plant that often produces small lipid-poor fruits, being capable of connecting with many bird species and possibly dependent on those birds (Pizo et al. 2021). As well, the most important bird genera in terms of interaction frequency and strength, *Tangara*, is often heavily frugivorous with small-body size (Pizo et al. 2021), thus having this morphological correspondence only with small seeds. Therefore, the relationship between SS and the increase in the frugivory degree possibly depends on the dominance, in the metanetwork, of both more specialized frugivorous and small sugar-rich fruits. Hence, our results corroborate that the bird species that appear to be important for plants, due to their high species strength values, are predominantly more specialized frugivorous and may favor the seed dispersal of the species they feed on, as they need to interact with many plants to reach their nutritional demands (Mello et al. 2015; Ramos-Robles et al. 2018; Vizentin-Bugon et al. 2021).

Contrary to our expectations, body mass did not relate to strength and centrality species metrics, even though the most frequent birds in local networks showed small-to-medium body-size. The same lack of relationship appears in a global seed dispersal metanetwork, although they found a negative association between body mass and avian centrality at the scale of local networks (Moulatlet et al. 2023). Moreover, a previous study in AF showed that large species are less central to seed dispersal at small spatial scales in fragmented areas (Emer et al. 2018). Another study showed little explanatory power of body mass in the variation of centrality metrics in plant frugivorous networks when bird and bats species are combined (Mello et al. 2015). One reason for the result that we found may be our metanetwork approach, as our dataset aggregates many local networks of disturbed areas, which may have already lost their larger frugivorous birds. Indeed, in disturbed landscapes such as the Atlantic Forest, larger frugivorous birds are the first to vanish when the small forest fragments do not support the number of fleshy fruits required for their population's maintenance (Emer et al., 2018). Small-bodied frugivorous often become key actors in defaunated environments, with outstanding importance for the smaller birds (Galetti et al. 2013; Carreira et al. 2020; Fuzessy et al. 2022). Regarding understory plant-frugivore networks, Pinto et al. (2021) found that even at sites immersed in more forested landscapes in the AF, most interactions reported were exclusively shaped by a few small frugivorous birds and pioneer plants that are abundant and widely distributed in those sites, resulting in similar networks between sites regardless of landscape or local levels of disturbance. On the other hand, defaunation may compromise the removal of seeds from some plant species in the medium to long term, particularly in plant species with large seeds (Neuschulz 2016; Fuzessy et al. 2022), which can produce evolutionary changes in ecological time (Galletti et al. 2013). Thus, these divergent conclusions of body mass effects highlight the need to carry out further studies at macroecological scales, relating this well-known morphological feature to species-level network metrics, preferably for different taxa in mutualistic systems. Furthermore, this reveals the importance of deepening our knowledge about the roles of species in the context of metanetworks, also covering the plant trophic level, to better understand this feedback between larger seed plants and larger frugivorous in disturbed scenarios.

As with body mass, we found no effect of beak width determining the species roles on the network. Previous studies have shown positive correlations between corresponding morphological traits of bird and plant species interacting in mutualistic networks (e.g. Rezende et al. 2007; Dehling et al. 2014; Sebastián-González et al. 2017). In addition to this different finding, our results for the Atlantic Forest metanetwork appear to diverge from previous evidence that interaction patterns for birds are better described by passive rules driven by morphological constraints on fruit, seed, and bird size (Sebastián-González et al. 2017). Working in an undefaunated multi taxa seed dispersal assemblage in the Brazilian Pantanal, these authors found that none of the non-size-related traits was important factors for interaction patterns. This suggests that the drivers of the role of high-level species in the mutualistic networks, such as their strength and centrality, may not be related to the drivers of interaction patterns or may be different when only birds are evaluated as frugivorous or seed dispersers. A complementary explanation may be that the macroecological scale that emerged from the metanetwork approach, added to the fragmented and disturbed scenario of the domain, should highlight ecological rather than morphological traits driving the species’ strength and centrality of frugivorous birds. Indeed, this appears to be corroborated on a global scale, as beak width was also not correlated with avian centrality in the seed dispersal metanetwork (Moulatlet et al. 2023).

Related to the dispersal ability proxy, bird species with higher HWI presented lower SS, but this index was not related to centrality, besides being the only morphological trait affecting a species-level metric on the AF metanetwork. This underscores the importance of maintaining the diversity of local frugivorous assemblages, as those species with the lowest potential capacity to cross larger areas throughout the biome are the ones with the greatest strength in the metanetwork, providing a large part of the seed dispersal service (Morán-Lopez et al. 2019). Similarly, HWI also had no influence on avian centrality in the study of the seed dispersal metanetwork on a global scale, as well as any morphological trait investigated (Moulatlet et al. 2023). Contrary to our expectation and the evidence of a recent global synthesis about this morphological index (Sheard et al. 2020), HWI and geographical range size did not respond in the same way, neither to SS nor to centralities. Indeed, working with extensive data from marine taxa (thus, on a much broader scale), Lester et al (2007) suggest that dispersal is not a general determinant of range size, but can play an important role in some circumstances - and this appears to be our case. About SS, we believe that species with lower HWI (therefore, with broader wings and lower dispersion capacity) are able to explore more foraging niches as they have higher maneuverability. In other words, bird species with lower HWI seem to be more important for the whole fleshy-fruited plant community for seed dispersal (Morán-Lopez et al. 2019; González-Varo et al. 2021) when we use the metanetwork approach. Bird species with higher HWI values (thus, with elongated wings) often have larger range sizes, even for sedentary species because they seem to have greater ability to cross barriers or gaps fragmentation (Sheard et al. 2020; Arango et al. 2022). Furthermore, even though these species with lower HWI were not central to the metanetwork, their importance for plant point of view is critical: they make stronger interactions and apport important proportion of the seed dispersal service on the Atlantic Forest fragments.

Bird species with larger geographical range size were more central and seemed to connect with network-generalist plants that often are more frequent in local networks. This same trend was also found both in the global-scale metanetwork (Moulatlet et al. 2023) and in other studies in AF, focusing on fragmented landscapes (Emer et al. 2018; Pinto et al. 2021) or comparing conserved and disturbed fragments (Fuzessy et al. 2022). As previously found for this biome (Emer et al. 2018), several species (e.g.*Turdus* spp.) recorded in our metanetwork are regional, altitudinal or long-distance migrants, able to move to large distances that may eventually result in seed dispersal. Furthermore, due to the larger area size that allows them to interact with more plants, core species appear to be able to maintain the cohesion of metanetworks even in fragmented landscapes (Moulatlet et al. 2023). As closeness centrality is related to the generalism of the other level, it is also necessary to highlight that plants widely distributed are often pioneers with smaller fruits and may contribute to the stability of frugivory networks, because of its greater number of interactions by trait-matching (Ramos-Robles et al. 2018; Dehling et al. 2016; Morán-Lopez et al. 2019).

Furthermore, from a conservation perspective, species with greater CC and BC values are important because they are highly connected and considered a network hub, then they can be important elements in maintaining the stability of the network in terms of disturbances (Martín González et al. 2010; Mello et al. 2015; Malanote et al. 2019). That is why centrality metrics may be useful to understand coextinction cascades in a mutualistic network (Sazima et al. 2010; Fuzessi et al. 2022), which is further important for disturbed regions. As high CC values indicate species that are close to many other species in the network (in terms of direct and indirect paths), the loss of high CC species, increases the probability of a coextinction cascade through the network, compromising seed dispersal services (Sazima et al. 2010; Fuzessi et al. 2022). Also, widely distributed species can be hubs of the metanetwork, connecting different parts of the network across the domain, turning them into key species and populations for the cohesion and maintenance of the AF frugivory system (González et al. 2010). Thus, both the widely distributed and more specialized frugivorous birds seem to be key species of the remaining forests within the Atlantic Forest, and should be prioritized in conservation policies aimed at maintaining and improving the seed dispersal service, despite the pervasive effects on largest seed plants already reported.

Finally, we expected that only the most generalist bird species would show positive values of the other centrality metric (BC), as found in pollination networks from different geographic and environmental settings (González et al. 2010). In our study, most bird species exhibited positive BC, potentially acting as connectors for different parts of the metanetwork, but the values were remarkably low. Perhaps there are two reasons for this, both related to the dimensions of our metanetwork. The first is the intrinsic characteristics of this metric itself, as a measure of the number of shortest paths between all species pairs for each focal species (Trøjelsgaard and Olesen, 2016). The second reason is our large macroecological scale, as we used distant spatial and temporal local networks to build a model for the entire biome, resulting in a wider mutualist network than usual. Thus, in a large network resulting from many sites with different plant and bird communities and different combinations of interactions for each site, it is reasonable to expect BC to dissolve at extremely low and zero values. In addition, species' distribution range size turned out to be the only crucial trait to affect the ability of a species to connect parts of the network on a macroecological scale. Furthermore, the same centrality metric was not related neither to the dietary specialization group (Malanotte et al. 2019) nor to the body mass (Emer et al. 2018, also with a metanetwork approach) of frugivorous birds from the same biome.

5. Concluding Remarks

On the Atlantic Forest bird-plant frugivory metanetwork, stronger interactions seem to be particularly carried out by more specialized frugivorous with lower HWI and dispersal ability. Also, the more central bird species embrace more specialized frugivorous and those with broader geographical range sizes. In such manner, it is clear the importance to conserve and restore the remaining forested fragments, especially those large ones, despite the notorious defaunation damage particularly addressed to the larger seed dispersers (Galletti et al. 2013; Emer et al. 2018; Pinto et al. 2021; Fuzessy et al. 2022). Because these large forest fragments potentially hold key interactions between animals and plants, they can act as important exchanging sources of species and functions for the surrounding fragmented landscape, although the smaller fragments can serve as step-stones for the frugivorous avifauna of the biome on a landscape perspective (Emer et al. 2018; Fuzessy et al. 2022). Moreover, bird-plant networks on AF seem to be already shrinking with landscape-scale deforestation and defaunation (Pinto et al. 2021). In addition, those future disturbed landscapes from AF are predicted to select species with greater dispersal ability, so it is possible that bird species with lower HWI and stronger relevance on metanetwork will be more impacted, demanding focused conservation policies (Sheard et al. 2020). All these threats to frugivorous birds can lead to the selection of species that are more diet generalists and are more widely distributed, with greater potential for loss of the most specialized frugivorous and the species with lesser capacity for dispersal. That is, birds with greater species strength in the metanetwork and part of the more central core seem to be more subject to extinction and the cascading effect on the frugivory system of the AF at macroscale. By top-down control, such changes could lead to major shifts in the structure and dynamics of plant populations through the disruption of processes such as seed dispersal, even if some evidences show the flexibility of these mutualistic systems to disturbances (e.g. Sales et al. 2021 and Pinto et al, 2021). In the long term, this reported scenario may compromise the plant community, imposing long delays for the recovering of patches of the forest and for the functional integration of forest fragments within a cohesive metanetwork (Emer et al. 2018). Faced with an already disturbed scenario and with a worrying degree of defaunation, there are two apparently opposite characteristics of the frugivorous birds that are important for the cohesion of the frugivory system on a macroscale. Dietary specialized and less mobile (low HWI) birds are a crucial part of each local community's assemblage, while widely distributed species contribute to the overall cohesiveness of the system. Thus, they are all key species of the forest remnants of the Atlantic Forest, and should be prioritized in conservation policies aimed at maintaining and improving the seed dispersal service.

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Figure Captions

Figure 1 - Distribution of the 26 plant-frugivore networks in the Brazilian Atlantic Forest, based on studies carried out from 1994 to 2019.

Figure 2 - Effects of ecological and morphological traits of birds on species-level metrics of these disperser species in the frugivorous bird-plant metanetwork in the Brazilian Atlantic Forest. A) Effect of frugivory degree (%) on species strength (SS). B) Effect of hand-wing índex (HWI) on SS. C) Effect of geographical range size (km²) on weighted betweenness centrality (BC). D) Effect of frugivory degree (%) on weighted closeness centrality (CC). E Effect of geographical range size (km²) on CC. Both geographical range size and BC were transformed by extracting its square root during the selection of models, due to the difference in the amplitude of variation of its values in relation to that of other evaluated traits and species-level metrics. All these graphics of predictors effects were built with the effect_plot function of jtools package (Long 2022) and ggplot2 (Wickham 2016).

Figures

Figure 1

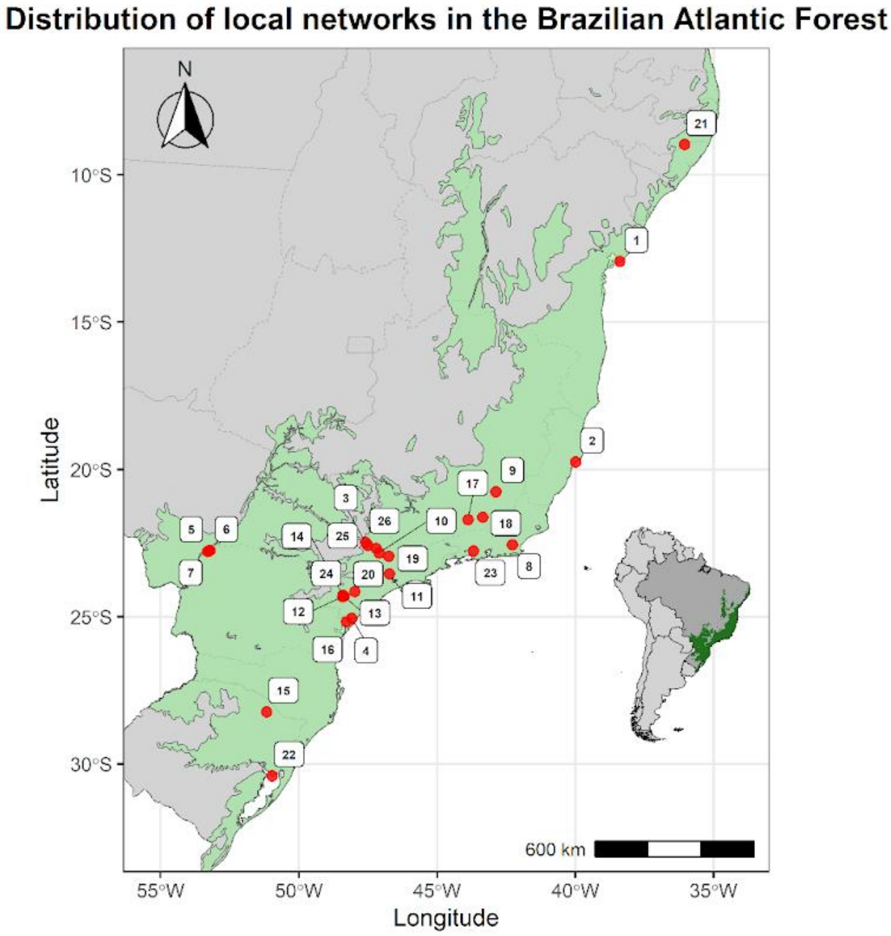
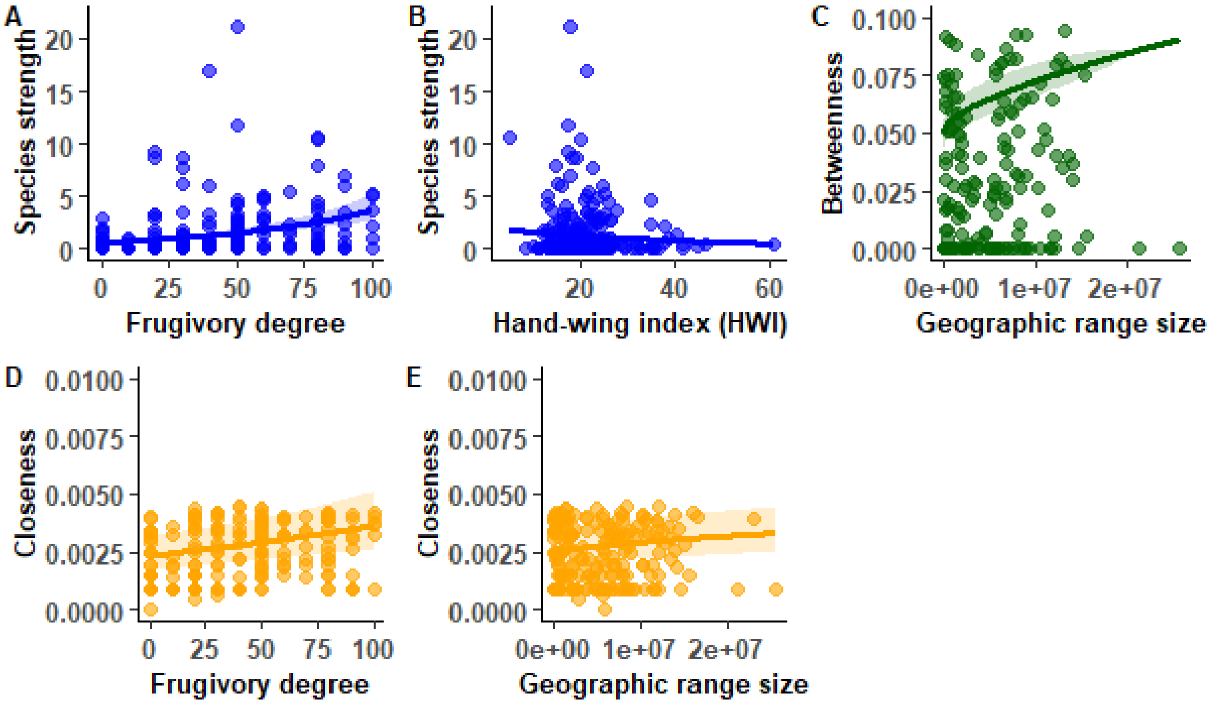


Figure 2


A
Species strength
0
5
10
15
20
0
25
50
75
100
Frugivory degree
B
Species strength
0
5
10
15
20
20
40
60
Hand-wing index (HWI)
C
Betweenness
0.000
0.025
0.050
0.075
0.100
0e+00
1e+07
2e+07
Geographic range size
D
Closeness
0.0000
0.0025
0.0050
0.0075
0.0100
0
25
50
75
100
Frugivory degree
E
Closeness
0.0000
0.0025
0.0050
0.0075
0.0100
0e+00
1e+07
2e+07
Geographic range size

Supplementary Material

Supplementary Table 1 - Definitions of ecological and morphological traits of bird species.

Bird trait	**Definition**
Beak width	Morphological beak measurement, sometimes called beak size (Rezende et al. 2007).
Body mass	Morphological measurement of the entire body of birds, measured in grams.
Frugivory degree	Ecological metric based on the degree of dependence on fruit in the overall diet (Fuzessy et al. 2022), expressed as a percentage (Wilman et al. 2014). We classified each bird species as occasional frugivorous, if it consumes less than 80% fruit in its diet, or obligate frugivorous, those that feed heavily on fruit and whose diet comprises equal to or greater than 80% fruit, following Wilman et al. (2014).
Hand-wing index (HWI)	A metric of bird wing shape and the most commonly used morphological proxy for dispersal (Arango et al. 2022).
Range size of spatial distribution	Geographic range of bird species distribution (Lester et al. 2007).

Supplementary Table 2 - Correlation analyses between ecological and morphological traits of bird species in the Brazilian Atlantic Forest plant-frugivore metanetwork: a) between continuous variables; b) between two categorical variables, “strata generalism” and “habitat preference”; c) between categorical variable “strata generalism” and continuous variables (p value from ANOVA); d) between categorical variable “habitat preference” and continuous variables (p value from ANOVA). HWI = Hand-wing índex.

a)

	Frugivory degree	**Beak Width**	**HWI**	**Body mass**	**Range size**
Frugivory degree	1.0000	0.1555	0.0910	0.0513	-0.2691
Beak Width	0.1555	1.0000	0.0838	0.4890	0.0396
HWI	0.0910	0.0834	1.0000	-0.0057	0.0550
Body mass	0.0514	0.4890	-0.0057	1.0000	0.1123
Range size	-0.2691	0.0396	0.0550	0.1123	1.0000

b)

	Strata generalism	**Habitat preference**
Strata generalism	2.00	0.004
Habitat preference	0.018	4.00

c)

	Strata generalism	**p-value**
Frugivory degree	Strataspecialist	0.00116**
Beak width	Strataspecialist	0.103
HWI	Strataspecialist	0.407
Body mass	Strataspecialist	0.583
Range size	Strataspecialist	0.0111 *

d)

	Human modified	**Open habitat**	**Wetland**
Frugivory degree	p=0.000974 *	p=3.66e-05 *	p=0.122542
Beakwidth	p=0.780	p=0.714	p=0.709
HWI	p=0.960	p=0.934	p= 0.839
Body mass	p=0.0323 *	p=0.6486	p=0.8110
Range size	p=1.92e-08 *	p=0.0256 *	p=0.8242

Supplementary Table 3 - Species-level network descriptors values of bird species in the Brazilian Atlantic Forest plant-frugivore metanetwork. SS: species strength, CC: weighted closeness centrality, and BC: weighted betweenness centrality.

Bird species	**SS**	**CC**	**BC**
Aburria jacutinga	2.46086E+14	0.00346686189771762	0
Amazona aestiva	0.0119047619047619	0.000930067049124471	0
Antilophia galeata	1.3697E+14	0.00321567260085442	0
Ara chloropterus	0.44	0.000920520854254837	0.0128811573276856
Aratinga aurea	0.4	0.000656646653071612	0
Aratinga leucophtalma	0.0119047619047619	0.000930067049124471	0
Arremon flavirostris	0.0222222222222222	0.000918442302587653	0
Arremon taciturnus	0.0135135135135135	0.000921443048951718	0
Attila phoenicurus	0.0566188197767145	0.00154119342812837	0
Attila rufus	0.601125308383373	0.00248379758790575	0
Baillonius bailloni	2.62614E+14	0.00358008337563064	5.11E+09
Baryphthengus ruficapillus	0.356939514936409	0.0026822873331406	0
Basileuterus culicivorus	0.111111111111111	0.000913775097978854	0
Brotogeris chiriri	0.345238095238095	0.00140374992724969	0
Brotogeris tirica	0.283397146863679	0.00247726114252401	6.13E+08
Cacicus chrysopterus	1.07061E+14	0.00316139478917544	3.58E+09
Cacicus haemorrhous	3.62184E+14	0.00414155393611886	0.0147630380021537
Camptostoma obsoletum	0.486017692178886	0.00352746486187406	0.000366921006977742
Capsiempis flaveola	0.0208333333333333	0.00092128680544233	0
Caracara plancus	0.25	0.000900340707147125	0
Carpornis cucullata	1.08256E+13	0.00409217009766534	0.00326629346523457
Carpornis melanocephala	4.12876E+14	0.00326367196496173	0
Celeus flavescens	1.84355E+14	0.00347986305960602	1.52E+09
Ceratopipra rubrocapilla	0.221465003005251	0.00270841059044576	0
Chiroxiphia caudata	2.1912E+14	0.00439970897587599	0.12776875539565
Chiroxiphia pareola	3.15406E+14	0.00230978614349499	3.83E+09
Chlorophanes spiza	0.0850090744101633	0.00196688588060968	6.39E+08
Chlorophonia cyanea	0.615591397849462	0.00150333000032073	0
Chrysomus ruficapillus	0.0909090909090909	0.000905837529619344	0
Cissopis leverianus	1.90362E+14	0.00344950281494798	0
Cnemotriccus fuscatus	0.119048986812145	0.00249694489028964	0
Coereba flaveola	2.09162E+14	0.00393349293310648	0.000192974863253739
Colaptes campestris	0.113717590645375	0.00251102773835341	6.67E+08
Colaptes melanochloros	0.0505596959085331	0.00196362276434785	3.83E+08
Columbina talpacoti	1	0	0
Conirostrum speciosum	1.03649E+14	0.00323237372731568	4.37E+09
Conopopha galineata	0.0792316926770708	0.0015060370075934	0
Coragyps atratus	0.25	0.000900340707147125	0
Coryphospingus cucullatus	0.140792209213262	0.00225948388334839	1.21E+09
Coryphospingus pileatus	0.037037037037037	0.000915735436229308	0
Corythopis delalandi	0.25	0.000887427966854087	0
Cranioleuca pallida	0.2	0.0009082056312121	0

Bird species	**SS**	**CC**	**BC**
Crotophaga ani	0.174122864223295	0.00186858761006997	1.38E+09
Crotophaga major	0.142857142857143	0.000909497676750484	0
Cyanerpes cyaneus	0.574305133051263	0.00322563358288472	8.90E+09
Cyanocorax caeruleus	0.216923076923077	0.0019370928397993	1.02E+09
Cyanocorax chrysops	0.2	0.00050927019210301	0
Cyanocorax cristatellus	0.923518255097202	0.0022172214965992	2.84E+08
Cyclarhis gujanensis	0.939585488850195	0.00307633348144723	1.95E+09
Dacnis cayana	6.21026E+13	0.00444637346095088	0.201397130439769
Dixiphia pipra	0.428384792355381	0.00310820036480963	1.89E+09
Dysithamnus mentalis	1	0	0
Elaenia	2.54489E+14	0.00353160191479359	0.000445259336922773
Elaenia flavogaster	3.10675E+14	0.00409978359241564	0.00904968482122879
Elaenia mesoleuca	2.11919E+14	0.00326341729950283	0
Elaenia obscura	0.341306326755594	0.0026583523827105	0
Elaenia spectabilis	0.114906832298137	0.00151792720909272	0
Empidonomus varius	0.573610927326098	0.00322917691018827	4.48E+09
Estrilda astrild	1	0	0
Euphonia chalybea	0.0714285714285714	0.000910787539563132	0
Euphonia chlorotica	1.12457E+13	0.00323865012455608	0.000118097452755238
Euphonia pectoralis	5.7928E+14	0.00398522397064905	5.32E+09
Euphonia violacea	3.85594E+14	0.00373206032451245	0.000545039446110235
Forpus xanthopterygius	0.050125313283208	0.00200105800224902	8.07E+08
Geothlypisa equinoctialis	0.0135135135135135	0.000921443048951718	0
Gnorimopsar chopi	0.0135135135135135	0.000921443048951718	0
Guira guira	1.10144E+14	0.0014932906056119	1.53E+09
Habia rubica	3.83977E+14	0.00393351432203568	0
Haplospiza unicolor	1.17606E+14	0.00225207331919835	0
Hemithraupis flavicollis	0.169795403541534	0.00226138139002126	0
Hemithraupis guira	0.04	0.000919911277133608	0
Hemithraupis ruficapilla	1.65808E+14	0.00383211254613816	7.12E+09
Hemitriccus diops	0.0588235294117647	0.000910090314470317	0
Hylophilus amaurocephalus	0.333333333333333	0.000903553571265374	0
Hylophilus poicilotis	0.324434544783382	0.00195603526875446	0
Icterus cayanensis	0.76463924963925	0.00293240201991983	0
Ilicura militaris	4.4426E+14	0.00379453648991673	4.41E+09
Laniisoma elegans	0.0169491525423729	0.000916109690170144	0
Lanio cristatus	1.38624E+14	0.00334848097591264	9.27E+08
Lanio melanops	1.85693E+14	0.00354796426629148	7.57E+08
Lathrotriccus euleri	0.0524572530692482	0.00197018714299706	0
Legatus leucophaius	0.221852629940865	0.00225370865646087	0
Leptotila rufaxilla	0.0105263157894737	0.000927385742722187	0
Leptotila verreauxi	0.105128205128205	0.00152132298244191	0
Lipaugus lanioides	4.72074E+14	0.00385909089279847	0
Machaeropterus regulus	0.115371148459384	0.00193752045989673	0

Bird species	**SS**	**CC**	**BC**
Manacus manacus	6.97158E+14	0.00387114521411161	0.0226301938270972
Megarynchus pitangua	1.14061E+14	0.00356178839385748	0.000139564126658385
Melanerpes candidus	0.0389317889317889	0.00153174294713625	3.83E+08
Melanerpes flavifrons	0.393309552483451	0.00291169890704631	0
Mimus gilvus	0.0384615384615385	0.000926860778965892	0
Mimus saturninus	1.59916E+14	0.00338642380798475	5.15E+09
Mionectes oleagineus	0.175924631806985	0.00250429462711928	0
Mionectes rufiventris	4.40639E+14	0.00395415601317008	0.00807102144981608
Myiarchus	0.0375533428165007	0.00153475654229312	2.84E+08
Myiarchus ferox	0.817948799682546	0.00344042995239826	1.61E+09
Myiarchus swainsoni	0.571175473483055	0.00331392257078702	1.28E+09
Myiarchus tyrannulus	0.0384615384615385	0.000926860778965892	0
Myiobius barbatus	0.0204081632653061	0.000913652811286029	0
Myiodynastes maculatus	3.67488E+14	0.00417394281474	0.0132525477179226
Myiophobus fasciatus	0.254070004070004	0.0019856067180298	3.47E+09
Myiothlypis flaveola	0.211904761904762	0.00147543466509789	0
Myiozetetes cayanensis	0.037037037037037	0.000917931648325309	0
Myiozetetes similis	3.35536E+14	0.00404900279987682	0.00189045738896307
Nemosia pileata	0.6711961527751	0.00344901184174755	8.20E+09
Neopelma aurifrons	0.5	0.000879737557811102	0
Neopelma chrysolophum	0.570140783586162	0.00248526123333188	0
Orchesticus abeillei	1.12899E+14	0.00339955632416474	0
Orthogonys chloricterus	4.258E+14	0.00382789964417507	0
Oxyruncus cristatus	1.14086E+14	0.00326630935149465	0
Pachyramphus castaneus	0.139423076923077	0.00150113727521327	0
Pachyramphus polychopterus	0.23869117986765	0.00253836777387238	1.36E+09
Pachyramphus validus	0.425536738036738	0.00306337824160287	7.35E+09
Pachyramphus viridis	0.0105263157894737	0.000927385742722187	0
Patagioenas	0.027027027027027	0.000922029477508903	0
Patagioenas cayennensis	0.414089896347961	0.00225538110843139	2.37E+08
Patagioenas picazuro	0.74796265486668	0.0029361253975923	6.01E+09
Patagioenas plumbea	2.47934E+14	0.00324575862555009	0
Patagioenas speciosa	0.0277777777777778	0.000918747445915126	0
Penelope	0.0588235294117647	0.000908842792463916	0
Penelope obscura	1.16592E+14	0.00385430837820997	0.00653068834718954
Penelope superciliaris	1.52934E+14	0.00268512241109506	0
Phaetornis eurynome	0.583333333333333	0.00150722466497998	0
Phibalura flavirostris	0.108187134502924	0.00151691530049178	0
Phyllomyias fasciatus	0.0135135135135135	0.000921443048951718	0
Phylloscartes oustaleti	0.0105263157894737	0.000927385742722187	0
Phylloscartes sylviolus	0.0263157894736842	0.000924583449202526	0
Pionopsitta pileata	0.0204081632653061	0.000913652811286029	0
Pionus maximiliani	0.0878136200716846	0.00145447429531012	0
Pipra fasciicauda	0.0454545454545455	0.00091519317825767	0
Pipraeidea melanonota	1.12846E+14	0.00189631715965192	3.07E+09

Bird species	**SS**	**CC**	**BC**
Pitangus sulphuratus	8.85078E+14	0.0042014814629713	0.0666488753492549
Platyrinchus mystaceus	0.0169491525423729	0.000916109690170144	0
Poospiza lateralis	0.125	0.000903363937603773	0
Procnias nudicollis	2.26621E+14	0.00374568498663284	6.39E+09
Pseudoleistes guirahuro	0.0105263157894737	0.000927385742722187	0
Pteroglossus aracari	1.90791E+14	0.00224172282318819	0
Pteroglossus bailloni	2.50811E+14	0.0030871979668112	0
Pteroglossus castanotis	2.02381E+14	0.0018996292563187	0
Pyroderus scutatus	3.2675E+14	0.00321227676245369	7.45E+08
Pyrrhura frontalis	1.63494E+14	0.00271438173337952	7.83E+09
Ramphastos dicolorus	4.2758E+14	0.00390362321301677	0.00129189464371929
Ramphastos toco	1.34524E+13	0.0014781373143319	0
Ramphastos vitellinus	5.11242E+14	0.00340049817404748	0
Ramphocelus bresilius	0.418778482749071	0.0033734857946359	0.000103888795330432
Ramphocelus carbo	2.34289E+13	0.00385834247128572	0.00645082006018752
Saltator fuliginosus	0.8125	0.00150965449220743	0
Saltator maximus	2.36326E+14	0.00360958179271001	0.000388285727888118
Saltator similis	6.16764E+14	0.00392193225588128	0.00135478661306346
Satrapa icterophrys	0.0784615384615385	0.00150955856710655	3.68E+09
Schiffornis virescens	3.96295E+14	0.00401101140683549	3.56E+09
Selenidera maculirostris	8.77691E+14	0.00399808401263294	0.00623356006393357
Setophaga pitiayumi	0.0507060333761232	0.00152205342791341	0
Sicalis flaveola	0.190909090909091	0.00148738561601455	0
Sirystes sibilator	0.0475633528265107	0.00151688440415402	0
Sittasomus griseicapillus	0.183823529411765	0.00149967176343608	0
Sporophila caerulescens	0.0384615384615385	0.000926860778965892	0
Sporophila leucoptera	0.0384615384615385	0.000926860778965892	0
Stephanophorus diadematus	4.71179E+14	0.00362996648468824	0.000109898762914778
Tachyphonus coronatus	1.03449E+14	0.0043525448025794	0.0440268817408537
Tachyphonus cristatus	0.54688316069895	0.00282372062660171	0
Tangara cayana	7.10842E+14	0.00407632499573357	0.00121962422245568
Tangara cyanocephala	5.8185E+12	0.00422835614438979	0.0104962378412667
Tangara cyanoptera	1.93804E+14	0.00356888141208452	3.06E+09
Tangara cyanoventris	0.555741397642487	0.00247072659365011	1.88E+09
Tangara desmaresti	2.13373E+13	0.00396968598498271	5.14E+09
Tangara mexicana	0.667646333404659	0.00302484074900662	4.34E+09
Tangara ornata	0.376896031622198	0.00268977850281557	0
Tangara palmarum	3.55085E+14	0.00299637127489337	0.000122312576665949
Tangara peruviana	0.024390243902439	0.000919478455922457	0
Tangara preciosa	2.76275E+14	0.00249942678726798	0
Tangara sayaca	2.6107E+14	0.00314528008478331	7.00E+09
Tangara seledon	4.5066E+13	0.00414917641708462	0.000725982239624479
Tangara	0.0178571428571429	0.00091740843962084	0
Tersina viridis	0.295729984739273	0.0027492694117689	0.00113826416713177
Thlypopsis sordida	1.21223E+13	0.00333899406932718	8.05E+09

Bird species	**SS**	**CC**	**BC**
Thraupis bonariensis	0.0769230769230769	0.000915550377869775	0
Thraupis cyanoptera	5.49818E+14	0.00398969241609069	0.00308994428753411
Thraupis episcopus	3.36499E+14	0.00289273995701275	0.000216730583608679
Thraupis ornata	2.73034E+14	0.00404504596648558	0.00336465702406676
Thraupis palmarum	1.87851E+14	0.00366263673290649	0.00362801920445987
Thraupis sayaca	1.15121E+13	0.00430436617822939	0.0887479755972906
Tinamus solitarius	0.543478260869565	0.00145045444148479	0
Tityra cayana	3.34011E+14	0.00387233096812318	0
Tityra inquisitor	1.37265E+13	0.00154119867901018	0
Tolmomyias flaviventris	0.240142210730446	0.00196403596429588	2.45E+09
Tolmomyias sulphurescens	0.0866494784257942	0.00231147930257183	0
Trichothraupis melanops	9.08159E+14	0.00415692090113648	0.00369588658897225
Troglodytes musculus	0.0263157894736842	0.000924583449202526	0
Trogon rufus	2.4735E+14	0.00350204446234804	0
Trogon surrucura	1.08162E+14	0.00352723644459368	0
Trogon viridis	6.003E+14	0.00388407323954089	1.54E+09
Turdus	0.027027027027027	0.000918872377536888	0
Turdus albicollis	1.84258E+14	0.00441322476303843	0.178363731839192
Turdus amaurochalinus	4.91439E+14	0.00405583001152847	0.00293437165250836
Turdus flavipes	4.88232E+14	0.00424550540103067	0.00894558797939895
Turdus fumigatus	0.127027027027027	0.00151005330314143	0
Turdus leucomelas	6.83801E+14	0.00417245133464033	0.0204246327471057
Turdus rufiventris	1.28369E+14	0.00435287751448805	0.115361271866388
Turdus subalaris	0.511229946524064	0.00222988944413196	0
Tyrannus melancholicus	3.05009E+14	0.0040458322542869	0.0023461518199624
Tyrannus savana	0.531742382354377	0.00257025514387376	6.07E+05
Tytira cayana	0.25	0.000909485171680954	0
Veniliornis spilogaster	0.0497542997542998	0.00150388811154222	0
Vireo chivi	0.313130325447374	0.00294326037488188	6.67E+08
Vireo olivaceus	2.92066E+14	0.00392983066695134	0.00343351822584463
Volatinia jacarina	0.369885644660998	0.00281712901614775	0.000112735545459795
Xolmis cinereus	0.0105263157894737	0.000927385742722187	0
Xolmis velatus	0.0669651075223831	0.00196693247280561	2.84E+08
Zenaida auriculata	0.024390243902439	0.000919478455922457	0
Zonotrichia capensis	1.8892E+14	0.00340096021201188	0.000131192061819173

Capítulo 2. net.raster: Interaction network metrics for raster data

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net.raster: Interaction network metrics for raster data

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Highlights

- An R package to calculate network and species-level metrics using rasterized presence-absence data and bipartite interaction networks as input.
- Calculate and visualise interaction patterns across space by allowing a raster layer of species interactions in addition to species distribution models (SDM).
- By integrating known interaction networks, net.raster moves beyond purely co-occurrence-based predictions.
- The package may help the understanding of the spatial and temporal variation of interaction networks.

Abstract

The interaction among species from different trophic levels is essential for ecosystem functioning and the use of bipartite networks is often useful for improving our understanding of multiple ecological processes, such as seed dispersal, pollination, and predation. Still, we are just paving ways to better understand spatial variation and macroecological aspects of interaction diversity. Here we introduce net.raster, an R package to calculate network and species-level metrics using rasterized presence-absence data and bipartite interaction networks as input, aiming to place species interaction studies into a spatial perspective. First, we focus on the spatialization of the functions and arguments from the bipartite R package using the terra package. Then, we enhance the visualisation of interaction patterns across space by allowing a raster layer of species interactions in addition to species distribution models (SDM). To date, all available packages that compute mutualistic network metrics rely only on matrices, or edge lists and network graphs derived from them. The net.raster package applies the calculations for each cell of a raster, allowing users to extrapolate known interactions across space and to visualise spatial patterns of bipartite network descriptors. The resulting rasters of interaction metrics are based mainly on the geographical extrapolation of interaction records between pairs of species and the resulting calculations use co-occurrence as a proxy for an interaction between species. Like other network analysis packages, net.raster allows users to calculate network topography indices using: a) the entire web, b) selecting the lower or upper level of each group, or c) selecting each species, choosing both levels or one level of interest at a time. Thus, the spatial processing and visualisation of fundamental bipartite networks provided by net.raster may fill a current gap in macroecological and biogeographical research and enable the understanding of the spatial variation of interaction networks. It also may open other questions in the macroecological and biogeographical study of networks, inspiring new insights into the conservation of important ecosystem services, such as seed dispersal and pollination.

Keywords

GIS; Software; Interaction patterns; Spatial patterns; Macroecology

1. Background

Trophic interactions provide several functional services that are key at the ecosystem scale such as seed dispersal and pollination (Bello et al., 2021; Wei et al., 2021). The information about species interactions can be transformed into binary networks and then evaluated through bipartite network theory to investigate interactions between higher and lower-tier species (e.g. seed dispersers and plants respectively). Nevertheless, we are just paving ways to better understand the spatial and temporal variation of interaction diversity and there are many unsolved questions about the geographic variation in network metrics, both on their structure (community level) and on the species/population level (Galiana et al., 2022; Guimarães, 2020; Poisot et al., 2021; Trøjelsgaard et al., 2015). This indicates the need to improve the investigation of bipartite networks from macroecological and biogeographical perspectives (Guimarães, 2020; Poisot et al., 2021; Windsor et al., 2022).

Several approaches from network ecology can establish and improve the exploration of large-scale ecological patterns and their drivers, allowing advances in a diversity of research fields such as biodiversity-ecosystem functioning, conservation, and restoration (Harvey et al., 2016; Windsor et al., 2022). Indeed, the exploration and monitoring of geographic patterns of interactions can help to predict and potentially prevent species extinctions, including results from interaction's partner mismatch, which might favour the strategic choice of priority areas for the conservation of important ecosystem services (Sales et al., 2021; Windsor et al., 2022). Expanding the network analyses to broader geographical scales can also help understand and project the disruption and reshaping of interaction patterns accelerated by anthropogenic causes, including species invasions, extinctions, deforestation, and climate change (Sales et al., 2021; Windsor et al., 2022).

The network structure or complexity can be described through many metrics (e.g. species richness, connectance, and link density), and consists of the “distribution patterns of links between nodes of an ecological network” (Guimarães, 2020), with the nodes being the species in bipartite networks (Guimarães, 2020; Landi et al., 2018). Across broad geographical scales, the network structure reflects the community level results from three community aspects: the local interaction patterns, the variation in species specialisation across space, and spatial processes that drive species occurrence (Guimarães, 2020). Furthermore, network complexity increases with area both at the level of species and connections taken in isolation (as network constituent blocks) and at the level of their combinations (links per species) (Galiana et al., 2022). As a result, fundamental trophic interactions can be predictably lost due to habitat modification (Galiana et al., 2022). However, the local network specialisation does not seem to be affected by species distribution, indicating that some community-level network properties may not vary with large-scale disturbance gradients (Emer et al., 2019). There is also evidence that some metrics of network structure remain conserved at extensive spatial scales, even with high species turnover across communities (Dallas and Poisot, 2017; Poisot et al., 2021). With this in mind, it is urgent to improve spatial tools for spatial pattern investigations and macroecological and biogeographical research into all network scopes: structure, trophic groups, and individual species. Here, we introduce net.raster, an R, Development Core Team (4.1.2) (2022) to calculate network-level and species-level metrics using rasterized presence-absence data and bipartite interaction networks as input. To estimate network interactions across space, we combine the species pool expected at a given location or region and the potential interaction networks composed from this species pool, based on previous interactions (Strydom et al., 2021).

2. Novelty and potential

Our package aims to insert species interaction studies into a spatial perspective by providing a spatialized framework for analysing species interaction data. The net.raster package combines the species distribution rasters and their recorded bipartite interactions. The resulting rasters of interaction metrics are based mainly on the geographical extrapolation of interaction records between pairs of species and the resulting calculations use co-occurrence as a proxy for an interaction between species. To date, all available R packages that calculate bipartite network metrics (e.g. bipartite, Dormann et al., 2008, and bmotif, Simmons et al., 2019) typically focus on a single community for a local network or a meta-network, relying solely on interaction matrices or objects generated from them, such as edge lists and graphs. Furthermore, other recent R packages allow handling and visualising multilayer networks (such as rMultiNet; Li et al., 2024 and one specific for ecological multilayer networks, the EMLN; Frydman et al., 2023). This type of network takes into account its variation in space or time through different layers, and allows working with multiple kinds of interactions on a single network (Frydman et al., 2023). However, although these packages can deal with the spatial and temporal variation of a single community, they cannot calculate network metrics from spatialised objects (e.g. raster data).

The availability and use of raster data have grown over time, along with the expansion of macroecological studies based on species distribution maps generated by species distribution models for several biological groups (e.g. Alves-Ferreira et al., 2022; Heming et al., 2022; Mota et al., 2022). From this perspective, there are recently released packages that are more computationally efficient (saving processing time and RAM) at calculating phylogenetic endemism, taxonomic, functional, and phylogenetic diversity metrics for raster data (Alves-Ferreira et al., 2024; Mota et al., 2023) when compared to tools based on matrix data of species presence-absence on multiple communities. Yet, there is also a demand for interaction diversity studies relying on large spatial variation (Poisot et al., 2021), which can be highly benefited from the calculation and visualisation of network metrics directly on raster data.

The net.raster is the first R package to calculate ecological network metrics using binary species distribution rasters and recorded bipartite interaction matrices as input, while also generating raster maps of each network metric as output. Therefore, our tool allows the calculation of several bipartite network metrics directly on spatial data, by applying calculations to multilayer SpatRaster objects (from terra package, Hijmans, 2022), which has proven to be an efficient memory-saving approach when dealing with several communities at large scales (Alves-Ferreira et al., 2024; Mota et al., 2023). To do so, we initially focused on rasterizing functions and arguments available in the bipartite R package (Dormann et al., 2008), an extensive tool for many types of bipartite ecological network analyses.

Another innovation is the spatial extrapolation of a local network or meta-network from the matrix of recorded interactions, using species distribution models (SDMs) to project known interactions across space and time. This approach generates multiple communities over space or time by mapping where interactions between species, already observed in the original network, may occur in a new spatial context. Rather than predicting new interactions between co-occurring species that do not interact in the known network, this method focuses on identifying spatially potential interactions - that is, places where documented interactions are likely to occur based on species co-occurrence and distribution patterns based on climate. Each raster's pixel is a subset of the interaction network recorded in the input matrix, following the species distribution, also provided as input (see Box 1). We identify the known and potential interactions of each pair of species that interacted at least once, extrapolating this interaction to each community (pixel) in which they co-occur.

The net.raster also improves the visualisation of interaction patterns across space, generating a new raster layer based on the species distributions. It calculates potential bipartite interactions in a grid by combining SDM, or even other raster data of species distributions from each trophic level. Furthermore, net.raster will contribute to understanding how the spatial structure of several ecological network metrics varies across space, as many community-level network properties seem to vary while some seem to be invariant across large-scale disturbance gradients (Emer et al., 2019). Our package can also help to improve understanding of the predicted impacts of climate change on ecological networks, such as the disruption and reshaping of interaction patterns, which can help prevent species extinctions and strategically choose priority conservation areas (Sales et al., 2021; Windsor et al., 2022). Some macroecological studies already rely on the integration of network structure with past and current climate data (Dalsgaard et al., 2013; Martín-González et al., 2015; Schleuning, 2014), but our package can expand the integration of species occurrence and potential interactions on future climate scenarios. In this way, the net.raster R package will contribute to opening a new path in the research of spatial patterns of interactions and in the macroecological and biogeographical study of interaction diversity, benefiting conservation and ecological research and policies.

3. Methods and features

The net.raster is written in R (version ≥ 3.5.0) language and environment and uses the packages bipartite (version ≥ 3.5.0) (Dormann et al., 2008) and terra (version ≥ 1.6) (Hijmans, 2022) as dependencies. We encourage users to report issues and make suggestions through the “Issues” topic in the GitHub repository. The package can be installed and loaded running the following code:

```
install.packages(“devtools”)
devtools::install_github(“CynOliveira/net.raster”).
```

The net.raster ecological network calculations are based on three steps. Initially, we need to carry out or compile field studies recording interactions between species, which can be binary (interactions presence-absence) or quantitative (matrices with estimations of pairwise interaction strength, usually interaction frequency, for weighted metrics). Whatever the nature of the interaction matrix data, net.raster will transform it into binary data, since we do not have a good understanding of species abundance prediction across space in SDM. It is known that this biotic factor directly impacts the frequency and strength of interactions, since more abundant species have more opportunities to interact with others (Vásquez et al., 2007). Moreover, interaction strengths can vary across space with abiotic conditions (Catella and Abbott, 2023). We then use species distributions (such as those estimated through SDMs) of each of the interacting species for the whole area of interest. At this step, we can also use other types of presence-absence distribution maps, like those provided by IUCN (International Union for Conservation of Nature). Finally, it is necessary to combine the distribution rasters of all species at both trophic levels with the information about their interactions.

The initial step requires stacking all species distribution rasters of each trophic level (lower and higher level - LL and HL) on two raster stacks (multi-layer SpatRaster objects from terra R package, Hijmans, 2022). Another required input is the network matrix, which records observed interactions between species. In the next step, the prep.web() function verifies if the species names in the raster stacks of both trophic levels match the species names in the interaction matrix. If the names do not match, an error message will be returned and the user must review the inputs.

Following the bipartite original features, the net.raster package allows users to calculate bipartite network topography indices in three ways: a) the entire web (default) using the networklevel.spat() function, b) each group level, selecting either the lower or higher level in this same function through the argument “level”, or c) for each species, with the specieslevel.spat() function, also choosing both (default) or one level of interest (higher or lower) at a time. Only binary (unweighted) calculations are allowed for all bipartite network metrics.

The indices that can be calculated using the function networklevel.spat() through the “index” argument are: connectance, web specialisation (H2’), web asymmetry, links per species, linkage density, number of compartments, compartment diversity, cluster coefficient, ISA (or interaction strength asymmetry or dependence asymmetry), SA (or specialisation asymmetry), Fisher alpha, interaction evenness, Alatalo interaction evenness, and Shannon diversity. These indices are equivalent to the ones from the networklevel() function of the bipartite R package. Also, networklevel.spat() provides two non-weighted metrics for nestedness, including NODF (an acronym for Nested Overlap and Decreasing Fill). Moreover, there are metrics invoked through “grouplevel” (higher or lower trophic level): number of species in the respective trophic level, mean number of links, mean number of shared partners, degree distribution, togetherness, C score, V ratio, discrepancy, extinction slope, robustness, niche overlap, generality, vulnerability, and fc (or alternatively functional complementarity).

The specieslevel.spat() metrics also follow arguments from the specieslevel() function of bipartite R package, which are: degree, normalised degrees, species strength, nestedrank as rank in a nested matrix, interaction push pull, PDI for Paired Differences Index, resource range, species specificity (or coefficient of variation of interactions), PSI for pollination service index (or pollinator support index, depending on the trophic level), NS for node specialisation index, betweenness, closeness, Fisher for Fisher's alpha index, partner diversity for Shannon diversity of interactions, effective partners, and d for Blüthgen's d’ (Dormann et al., 2008).

Other function provided by net.raster is related to an important, structural network-level measure: nestedness. The nested.spat() function provides additional features compared to the networklevel.spat() function by giving the results of three other nesting metrics and expanding the possibilities based on different null models and theoretical approaches for this web property. As output, in the case of community-level functions, the raster will have as many layers as metrics were required, while the specieslevel.spat() function generates a layer for each species in each indicated metric.

We invite users to learn more about these metrics and theoretical approaches by reading the net.raster package documentation, available on the GitHub repository. In addition, users may note that the processing time can vary significantly depending on several factors, such as the chosen metric and its algorithm, raster resolution, the geographical area covered, network size, and available computational resources. We suggest parallelization in data processing to speed up execution time. The complete workflow and examples of spatial views of metrics are outlined (Box 1).

4. Implementation example

We demonstrate the applicability of the net.raster by using a real plant-frugivore network dataset recorded in the Brazilian Atlantic Forest (Silva et al., 2002), investigating temporal changes in a species-level metric and two network metrics, between present and the future climate scenarios. The original interaction matrix has 76 bird species and 150 plant species before the correction and consolidation of names with current and valid synonyms, and was subsetted to include 67 bird species and 121 plant species. We used only a subset of the species because many of them did not have the minimum number of occurrences required for modelling. Therefore, we had to exclude them and their interactions from the interactions matrix, also excluding species that become non-interactive after that. First, we obtained occurrence records for these species (Global Biodiversity Information Facility- GBIF: http://www.gbif.org) and combined them with bioclimatic variables (Fick and Hijmans, 2017) to predict their current (1970–2000) and future (2050) potential distributions using the MaxEnt algorithm (Phillips et al., 2006, Phillips et al., 2017), through the ENMWizard R package (Heming et al., 2018). This process generated two sets of multilayer SpatRaster objects, where each layer represents a binary map of climatically suitable areas for the species in the present and future under an optimistic scenario for greenhouse gas emissions, projected across the Atlantic Forest (67 layers for birds and 121 for plants). We used these SpatRaster objects along with an interaction matrix, where the rows represent plant species and the columns represent bird species. In this matrix, observed interactions between species pairs (i.e., plant-bird interactions) are indicated by the number 1. To calculate Species Strength—a species-level metric—we employed the function specieslevel.spat() with the index argument set to “species strength.” This allowed us to highlight bird species with notable variation across space (Fig. 1a and b for current climatic conditions and Fig. 2a and b for a projected network, on future climatic conditions). Then, we computed the spatial variation of network-level metrics, such as Connectance and Nestedness, using the function networklevel.spat(), setting the index argument to “connectance” and then to “nestedness.” These metrics revealed higher values in the eastern region of the Central Corridor of the Atlantic Forest, particularly in the south of the state of Bahia and along the border with the Cerrado in central Brazil, both in the present (Fig. 1c and d) and in the future scenario (Fig. 2c and d).

5. Criticisms

Predicting the structure of ecological networks in a spatial context is a methodological challenge (Strydom et al., 2021). Predicting species interactions based solely on spatial co-occurrence can be problematic, particularly because ecological networks are influenced by a range of factors beyond mere co-occurrence, such as abundance, behaviour, and morphology (Blanchet et al., 2020; Stang et al., 2007; Vásquez et al., 2007; Vizentin-Bugoni et al., 2021). The net.raster package addresses this limitation by incorporating known interaction networks, which allows for the inclusion of some important drivers of network structure. Abundance data, for instance, can drive variation in species roles within networks (Vásquez et al., 2007, Vizentin-Bugoni et al., 2021). However, abundance data is often unavailable in macroecological studies (Howard et al., 2014). There is evidence of a positive relationship between species abundance and the suitability derived from ecological niche models (de la Fuente et al., 2021; Weber et al., 2017), which suggests that moving toward the use of continuous suitability data, rather than the current binary approach of suitable and unsuitable areas, could improve the package by better reflecting ecological gradients. Moreover, the net.raster package is built upon species distribution modelling, which is a well-established and predictive approach (Phillips et al., 2006, Phillips et al., 2017; Thuiller et al., 2009, Thuiller et al., 2024). Given that ecological niche models typically rely on climate data, the package already accounts for some abiotic factors that may influence species interactions, providing a more comprehensive foundation for inference.

We also recognize that the package has not undergone extensive validation with real field data. Besides, an accurate projection based on the mapping of true interactions seems impractical, reinforcing the need for coordinated improvement in our interaction data collection (Poisot et al., 2021). However, by integrating known interaction networks, net.raster moves beyond purely co-occurrence-based predictions. This enables users to explore geographic variation in species interactions and gain insights into the underlying drivers of these patterns. Lastly, while predicting interactions based on spatial data remains a challenge, net.raster provides a valuable framework for comparing observed and projected networks. It highlights the need for more detailed data on species interactions, facilitating the exploration of how spatial and macroecological factors shape species interaction networks, and offering a starting point for deeper investigations into the drivers of network structure. For instance, if in the future there is spatialized information on these drivers of the species role on networks (such as layers of geographical variation of species abundance, morphology, and behaviour), the net.raster package can act as a null model of what would be expected based on known interactions. Thus, it would allow comparisons between values above or below that expectation and the values found when including these (potential) interaction driver layers, for different network metrics.

6. Conclusions and future directions

The net.raster R package is the first tool capable of calculating bipartite ecological network metrics by combining binary species distribution rasters and interaction matrices. The net.raster allows the spatial calculation and visualisation of bipartite interaction diversity metrics with efficient memory usage. It is based primarily on extrapolation (spatial or temporal) of actual records of interactions, using co-occurrence as a proxy for an interaction between species. Despite some criticism of this approach, co-occurrence analysis may reveal new patterns of spatial association between pairs of known species (Thurman et al., 2019) as well as open new questions about differences between actual and projected interactions. It opens up other questions in the macroecological and biogeographical study of networks, in addition to allowing new insights into the conservation of important ecological interactions for the maintenance of biodiversity and important ecosystem services, such as seed dispersal and pollination. As an accurate projection based on the mapping of true interactions seems currently impractical (Poisot et al., 2021), net.raster will help to access geographical variation in interaction networks, as well as to reveal differences between actual and projected interactions to refine our knowledge of the causes of macroecological patterns in species interaction networks. Advances in the spatialization of interactions and the expansion of field studies of interaction data around the world can provide new spatial information directly associated with interactions. Also, net.raster is flexible to use raster data that is not derived from SDMs, and we encourage researchers to collaborate with us for the improvement of this free and pioneering tool in the development of the research field of macroecology and biogeography of diversity of interactions.

CRediT authorship contribution statement

Cynthia Valéria Oliveira: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Data curation, Conceptualization. Gabriela Alves-Ferreira: Writing – review & editing, Visualization, Validation, Conceptualization. Flávio Mariano Machado Mota: Writing – review & editing, Visualization, Validation, Conceptualization. Daniela Custódio Talora: Writing – review & editing, Visualization, Validation, Supervision, Conceptualization. Neander Marcel Heming: Writing – review & editing, Visualization, Validation, Supervision, Software, Methodology, Data curation, Conceptualization.

Data availability

All data and codes used are available in the GitHub repository ("CynOliveira/net.raster") presented in the article

Figures

Box 1- Overview of how *net.raster* uses presence-absence species distribution rasters and interaction network matrices as input to calculate community and species level interaction network metrics. The *net.raster* package calculates known and potential bipartite interactions in a grid.

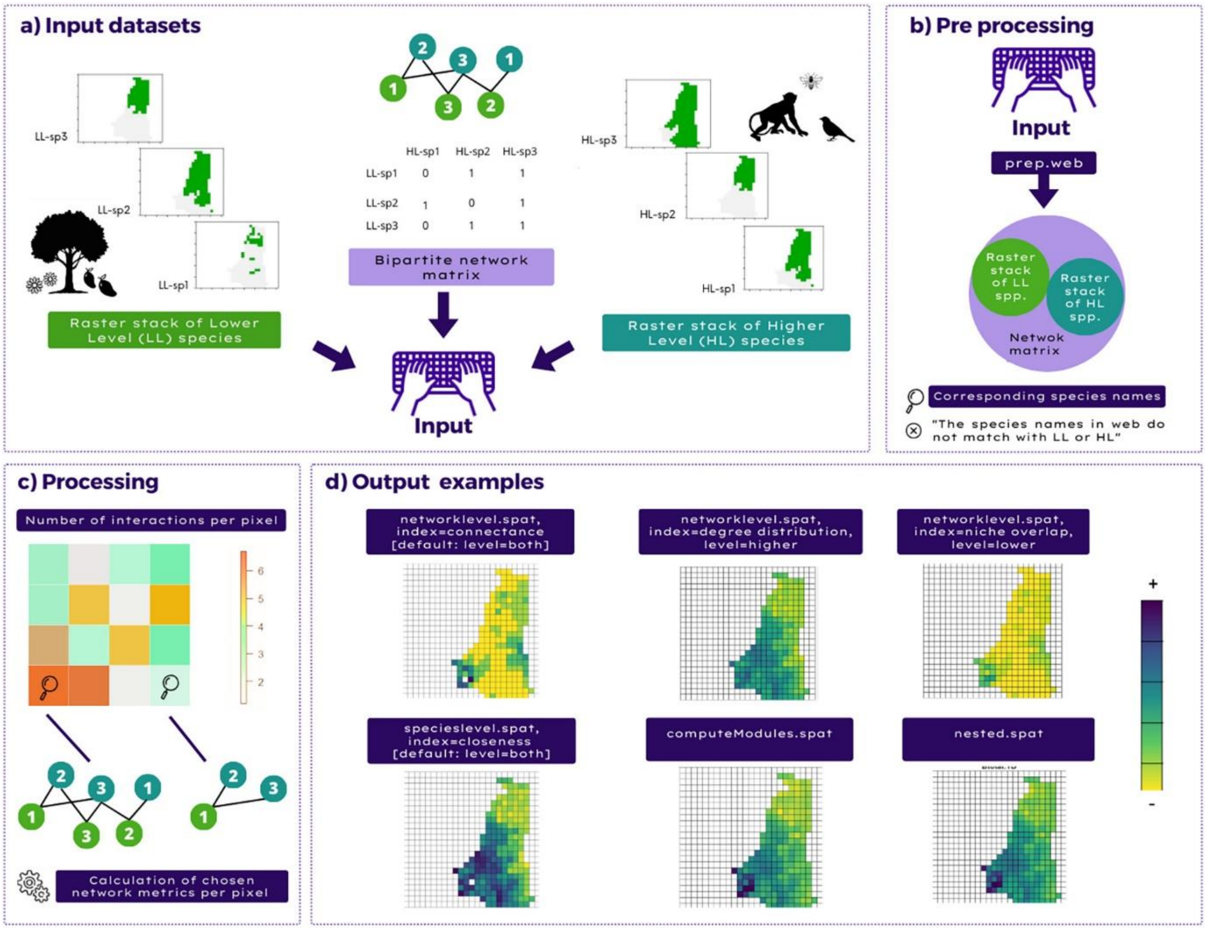


Fig. 1. Spatial variation of network-level and species-level metrics of a bird-plant network designed for the Atlantic Forest domain, in the present. We can see the difference in the Species Strength of *Trichothraupis melanops* (a), the strongest bird species, compared to *Euphonia violacea* (b), one of the species with the lowest values of this metric in this trophic level. In (c) we see the spatial variation of network Connectance and (c) Nestedness, in current climatic conditions . Example based on a real plant-frugivore network recorded in the Brazilian Atlantic Forest, with a subset of 67 bird species and 121 plant species (adapted from Silva et al., 2002).

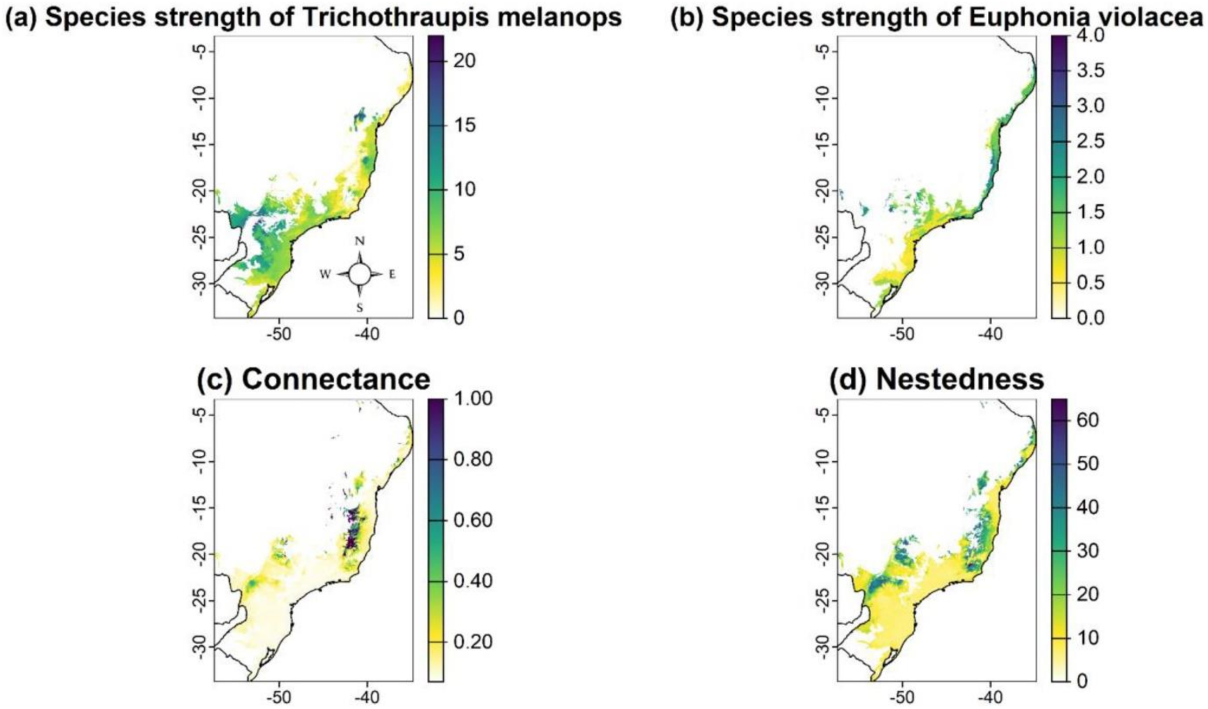
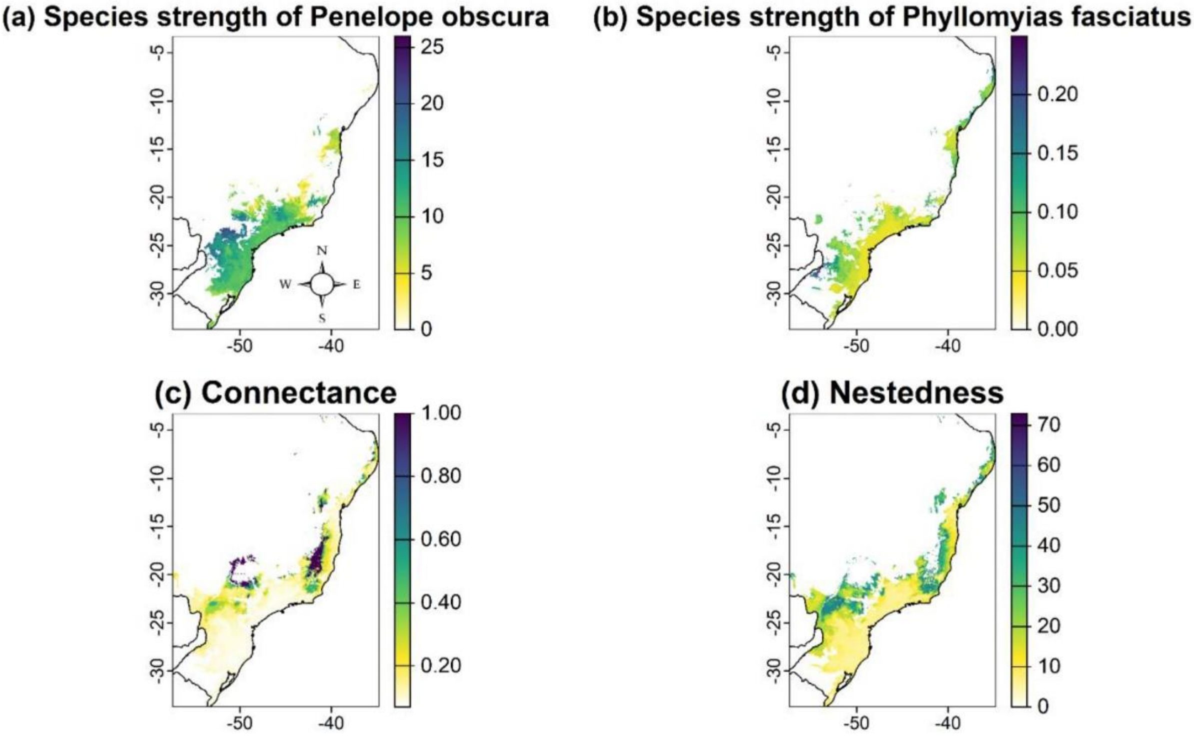


Fig. 2. Spatial variation of network-level and species-level metrics of a bird-plant network designed for the Atlantic Forest domain, for the future (2050 optimistic scenario). The image shows the difference in the Species Strength, for a future potential network, of *Penelope obscura* (a), the strongest bird species, compared to *Phyllomyias fasciatus* (b), one of the species with lowest values of this metric in this level. In (c) we see the spatial variation of network Connectance and (c) Nestedness, in the future climate scenario. Example based on a real plant-frugivore network recorded in the Brazilian Atlantic Forest, with a subset of 67 bird species and 121 plant species (adapted from Silva et al., 2002).



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Capítulo 3. Trait-mediated restructuring of Brazilian Atlantic Forest frugivory metanetwork under climate change

Trait-mediated restructuring of Brazilian Atlantic Forest frugivory metanetwork under climate change

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Abstract

The Brazilian Atlantic Forest is a biodiversity hotspot where frugivorous birds play a critical role in seed dispersal, but climate change threatens to disrupt these mutualistic networks. This study integrates macroecological and network-based approaches to assess how climate change and bird functional traits shape the structure of a bird-plant frugivory metanetwork in the AF. Using spatially explicit models under current and future (2050) climate scenarios, we assess changes in network metrics of species richness, interaction rates, and partner diversity, while examining the stabilizing roles of morphological and ecological traits (body mass, beak width, degree of frugivory, a proxy for flight efficiency, and range size). Our results reveal pronounced north-south and coastal-interior gradients in network vulnerability, with historically stable southern regions exhibiting greater stability. Climate change is projected to simplify network structure, particularly in northern and coastal areas, driven by species loss and the reconfiguration of interactions. Trait-mediated responses were consistent across scenarios: larger, highly frugivorous birds reinforced network stability, while species with wider ranges contributed disproportionately to functional erosion. Notably, flight efficiency (Hand-Wing Index) shifted from a negative to a positive role under extreme climate stress, highlighting its adaptive potential. These results highlight the importance of historical climate stability and trait diversity in maintaining mutualistic interactions. Conservation strategies should prioritize the protection of key frugivores and the preservation of functional trait diversity to mitigate the cascading impacts of climate change on seed dispersal services in this fragmented biome.

Keywords: frugivory networks, functional traits, climate change, Atlantic Forest, seed dispersal

1. Introduction

Over 80% of tropical forest plant species depend on frugivores for seed dispersal (Jordano 2000), but in tropical regions, this service is especially threatened by habitat fragmentation, hunting, and climate change, which can synergistically disrupt plant-frugivore networks (Bomfim et al. 2018; Bovo et al. 2018; Emer et al. 2018). Indeed, habitat fragmentation and defaunation have led to the decline of large frugivores and shade-tolerant plants, while favoring small frugivores and pioneer species (Galetti et al. 2013; Bello et al. 2015; Bomfim et al. 2018). Such shifts reduce species diversity and disrupt interactions, destabilizing mutualistic networks (Tylianakis et al. 2007; Emer et al. 2020).

Nearly 80% of frugivory network research focuses on the Neotropics, with 59% concentrated in Brazil, primarily on bird-plant interactions in the Atlantic Forest (AF; Baldiviezo et al. 2019; Escribano-Avila et al. 2018). This biodiversity hotspot, now reduced to a mosaic of small, fragmented patches (Joly et al. 2014; Myers et al. 2000; Ribeiro et al. 2009), relies heavily on birds for seed dispersal, especially in defaunated areas where large mammals are absent (Galetti et al. 2013). Habitat loss has severely disrupted plant-frugivore interactions on that biome, reducing interaction frequencies and shifting dominance to smaller, generalist species, a trend that risks long-term functional homogenization (Emer et al. 2020; Pinto et al. 2021; Bonfim et al. 2022).

From a macroecological perspective, the AF presents current north-south climatic heterogeneity, which shapes the distribution of species through physiological constraints and resource availability (Oliveira-Filho & Fontes, 2000, Carnaval et al. 2014, Leite et al. 2016). Historically stable areas, such as past climatic refugia, harbor higher endemism due to vicariance and genetic divergence (Carnaval et al. 2014; Costa et al. 2017). These regions exhibit minimal vegetational change over time, having been less impacted by interglacial shifts (Carnaval et al. 2014; Costa et al. 2017). This heterogeneity is also mirrored in the evolutionary history of AF passerine birds, whose endemism patterns reveal a historical split between a northern cluster (Pernambuco refugy) and a southern cluster (two refugies of Bahia and the one of Serra do Mar), suggesting divergent trajectories of diversification and forest connectivity across regions (Cardoso da Silva et al. 2004). Similarly, the east-west gradient is associated with coastal proximity, corresponding to climatically stable areas supporting higher biodiversity (Carnaval et al. 2014; Costa et al. 2017).

Climatic and spatial gradients not only shape species distributions but can also influence the functional traits of frugivorous communities and the bird-fruit trait matching (McFadden et al. 2022, Huang et al. 2025, Zhang et al. 2025). For instance, trait matching between frugivorous birds and palms is shaped both by local species richness and by broad-scale climatic and biogeographic factors, with stronger trait matching observed in tropical regions (McFadden et al. 2022). However, there is opposite evidence from recent global studies, showing that avian frugivore-plant trait matching decreases towards the tropics (Huang et al. 2025, Zhang et al. 2025). This highlights the need to better understand the connections between functional trait composition of frugivore communities, their trophic interactions, and abiotic and historical processes. Thus, understanding how these traits can affect frugivory networks is essential to comprehend patterns and the potential consequences for seed dispersal dynamics across extensive regions such as the Atlantic Forest.

Regarding frugivory interactions, frugivores often display overlapping resource use, with generalist species tending to dominate interaction networks (Correa et al. 2016, Malanotte et al. 2019). This pattern has been linked to morphological traits, such as gape size, which allows some species to consume a broader range of fruit sizes and consequently have more interactions in networks (Malanotte et al. 2019). These dominant species often play critical roles in network cohesion and seed dispersal, raising concerns about functional homogenization when such key species are lost (Emer et al. 2020). As a result, understanding the functional roles of frugivores becomes essential, particularly to assess whether species losses lead to the decline of unique ecological functions rather than being compensated by redundant interactions.

Moreover, the persistence and robustness of frugivory networks appear to depend not only on the number of interactions but also on the compatibility between interacting species, particularly regarding their morphology (Dehling et al. 2016; Morán-Lopez et al. 2019). Beyond morphological features like body size, beak width, and wing shape, other ecological traits—such as dietary specialization (e.g., degree of frugivory), foraging strata, and geographic range size—may also shape interaction patterns and the effectiveness of seed dispersal (Ramos-Robles et al. 2018; Malanotte et al. 2019; Sebastián-González et al. 2017; Carreira et al. 2020; Pizo et al. 2021; Vizentin-Bugoni et al. 2021). Investigating how these traits influence the structure and cohesion of ecological networks is crucial to understanding how communities respond to environmental change and which attributes confer stability or vulnerability in altered landscapes and regions.

Given this context, adopting a macroecological perspective based on network theory and functional traits allows the integration of species and local interaction data into a broader regional framework. By aggregating local frugivory networks, it is possible to construct a metanetwork that reflects the regional pool of species and their potential interactions across time and space (Araújo et al. 2018; Poisot et al. 2014; Moulatlet et al. 2023). This approach, based on the occurrence of interactions in at least one local assemblage (Poisot et al. 2014), is particularly valuable for conservation planning, as it captures regional patterns and highlights the vulnerability of seed dispersal services under anthropogenic pressures (Li et al. 2020; Santini et al. 2021). Moreover, because network structure is known to vary across spatial scales and it scales with area increasing (Galiana et al. 2019, Galiana et al. 2022. , Moulatlet et al. 2023), regional analyses are critical to understanding the mechanisms that sustain mutualistic systems and to guide management actions in fragmented tropical landscapes (Li et al. 2020). This approach also responds to broader efforts to integrate macroecological and network-based perspectives, especially by coupling species distribution models with interaction data to predict functional consequences of climate-driven range shifts (Kissling & Schleuning, 2014; Oliveira et al. 2025). Also, advancing trait-based models that bridge local and regional scales is essential to understand how multispecies interactions reorganize under environmental change (Kissling & Schleuning, 2014).

Considering the influence of climate and functional traits on frugivory networks, we address three central questions: (1) How is the current structure of the frugivory metanetwork shaped by contemporary climatic conditions?, (2) How might climate change alter the structure of that network in the future?, and (3) How do avian traits influence network properties across current and projected scenarios? We hypothesize that (i) current climatic stability promotes a complex and functionally diverse frugivory metanetwork, reflected in higher species richness of birds and plants, interaction rates (links per species), and partner diversity (generality/vulnerability), particularly in historically stable regions; (ii) climate change will lead to structural simplification of the AF frugivory metanetwork, reducing species richness, interaction rates and partner diversity disproportionately in historically climatically unstable regions, with trait-specific effects driving network simplification*;* and (iii) bird traits related to morphology, foraging behavior, and geographic range will significantly influence network metrics across scenarios, with generalist species (lower fugivory degree) and those with broader spatial niches contributing disproportionately to metanetwork structure under both current and future conditions.

2. Methods

2.1 Study area

The Atlantic Forest, a globally recognized biodiversity hotspot (Myers et al. 2000), originally spanned almost 1.5 million km², the oldest and richest South American forest (Joly et al. 2014). Today, only 12–28% of its native vegetation remains, predominantly in small, isolated fragments (<50 ha), which comprise over 80% of the remaining forest cover (Rezende et al. 2018; MapBiomas, 2023). In the remaining fragments of this biome, avian frugivores have become the dominant seed dispersers, compensating for the local extinction of large mammals caused by anthropogenic pressures (Galetti et al. 2013; Emer et al. 2020). This extreme fragmentation has led to significant defaunation, particularly affecting large-bodied frugivores, with 56% of avian seed-disperser species declining (Pires et al. 2014). Notably, fragments smaller than 100 ha retain just 10–40% of their original frugivorous bird diversity, with pronounced losses among understory specialists such as cotingas and toucans (Bovo et al. 2018).

2.2 Data collection

a) Network data

Bonfim et al. (2022) originally compiled the dataset on local plant-frugivore networks, however, we provide a concise overview here as it forms the basis of our analysis.

These authors extracted data from the ATLANTIC FRUGIVORY database (Bello et al. 2017), which contains over 8,000 interactions between 331 vertebrates and 788 plants from 166 studies. Their selection criteria focused exclusively on bird-plant network studies reporting complete interaction matrices, yielding an initial set of 12 studies. To expand geographic coverage, the authors supplemented these data through systematic searches in Web of Science and Scopus using the query: ("ecological network" OR "mutualistic network" OR "frugivor") AND ("bird") AND ("Atlantic Forest"). They incorporated 13 additional studies that provided georeferenced sampling locations, included complete interaction matrices, and explicitly documented network methodologies. The authors also provided us with a network that they compiled but did not include in their work, as they did not find information on sampling effort. For our purposes, it could be included, as it had geographic information in addition to the interaction matrix. Thus, the resulting dataset comprised 26 bird-plant networks (1994–2019) from fragmented Atlantic Forest sites (Supplementary Figure 1), combining phytocentric records (plant-focused observations) and zoocentric records (fecal analyses). Then, we conducted taxonomic harmonization and corrections. For plant taxa, we verified all species through SiBBr and excluded 9 records unidentifiable at the family level. For avian taxa, we standardized nomenclature using AVONET (Tobias et al. 2022), adopted current taxonomy (e.g., *Aburria jacutinga* per SiBBr), and retained 11 Psittacidae species based on emerging evidence of their dispersal role (Tella et al. 2019; Blanco et al. 2016). These adjustments required the removal of *Dysithamnus mentalis* from a network after plant exclusions nullified its interactions.

b) Bird species traits

We assembled a comprehensive dataset of morphological and ecological attributes associated with frugivory to investigate how avian traits shape species' functional roles within the Atlantic Forest seed-dispersal metanetwork. Specifically, we focused on five traits: beak width, body mass, frugivory degree, hand-wing index (HWI), and range size (see Supplementary Table 1 for trait definitions). We tested the correlation between all the ecological and morphological traits (Supplementary Table 2) and then excluded two categorical traits previously tested (degree of dependence on forests and forest stratum generalism/specialization). These traits were selected for their ecological relevance and empirical links to dispersal effectiveness and interaction patterns (Dehling et al. 2016), commonly studied in plant-frugivore networks, including across large geographical areas (e.g., Bender et al 2018, Moulatlet et al. 2023). Trait-based frameworks are fundamental in network ecology, as interspecific variation in morphology and behavior often predicts both niche differentiation and interaction probabilities (Dehling et al. 2016; Morán-López et al. 2019). These trait-mediated processes underpin the architecture of mutualistic networks (Rezende et al. 2007; Albrecht et al. 2018), ultimately influencing the persistence of species within them (Moulatlet et al. 2023).

Among our predictors, beak width is related to the limit of fruit size that birds can effectively consume, thus impacting the preferences of fruits chosen, and, therefore, partners in the network (Dehling et al. 2016; Sebastián-González et al. 2017). Body mass is broadly linked to gut passage effectiveness and dispersal distances, well-known as an important trait for many taxa (e.g., Mello et al. 2015; Correa et al. 2016; Malanotte et al. 2019; Carreira et al. 2020). Similarly, the frugivory degree, a proxy for dietary specialization, has been repeatedly associated with the emergence of keystone roles in seed dispersal systems (Mello et al. 2015; Vizentin-Bugoni et al. 2021). HWI serves as a proxy for flight performance and mobility (Sheard et al. 2020; Arango et al. 2022), while large geographic ranges may reflect ecological generalism, commonly observed among dominant frugivores in the AF (Pinto et al. 2021; Fuzessy et al. 2022). Trait data were primarily sourced from AVONET (Tobias et al. 2022) and EltonTraits (Wilman et al. 2014), ensuring comprehensive coverage of species.

Aiming for greater data adequacy and following previous work (Sebastián-González et al. 2017, Oliveira et al. manuscript in preparation), we transformed the geographic range size by means of a square root and used a log of body mass. Despite a low raw correlation between body mass and frugivory degree ($r = 0.18$), we detected severe collinearity in model structures (Variance Inflation Factor - VIF > 100), likely due to interactions with other traits. To preserve the ecological relevance of both variables, we adopted a residualization approach. Thus, frugivory degree was regressed on log-transformed body mass at the species level, and residuals were used as predictors in all network models. The same strategy was used for HWI, also regressed on log-transformed body mass. This method enables us to isolate the unique effect of the other traits beyond body mass, thereby improving interpretability in frugivory networks, where body mass, dietary breadth, and mobility can interact but reflect distinct ecological axes.

c) Climate data

We downloaded 19 bioclimatic variables for the baseline and future (2050) scenarios from the WorldClim v2.1 database (Fick & Hijmans, 2017) with a spatial resolution of 2.5 arc minutes. The bioclimatic variables are derived from monthly temperature and precipitation values and are widely used in species distribution modeling. The baseline scenario (‘current period’) is defined from 1950 to 2000 (worldclim.com). For each species, we chose variables with a correlation below 0.7 using the “select_vars” function of the “ENMwizard” package (Heming et al. 2019) to avoid collinearity. In the case of birds, we selected 19 available bioclimatic variables to test them (Mota et al. 2022). For plants, we pre-selected climate data according to available ecological knowledge about the species and expert opinions, performing the final selection based on correlation (Williams et al. 2009, Gardner et al. 2019, Zangiabadi et al. 2021). The pre-selected variables for plants were: BIO1 = Annual Mean Temperature, BIO4 = Temperature Seasonality (standard deviation ×100), BIO10 = Mean Temperature of the Warmest Quarter, BIO12 = Annual Precipitation, BIO15 = Precipitation Seasonality (Coefficient of Variation), BIO17 = Precipitation of the Driest Quarter, BIO18 = Precipitation of the Warmest Quarter.

2.3 Ecological niche models

We modelled the ecological niche of each frugivorous bird and plant species using MaxEnt (Phillips et al. 2006), an algorithm that performs comparably to others, basing only on occurrence data (Elith et al. 2006; Kaky et al. 2020). The “ENMwizard” package defined the calibration area for each species by creating a minimum convex polygon around all occurrences plus a 1.5° buffer (i.e., ~165 km2). To improve the predictive accuracy of ecological niche models (ENM), we delimited buffers around occurrence points to define the accessible area for each species, thus enhancing environmental heterogeneity and leading to more ecologically realistic niche estimations (Anderson & Raza, 2010; Barve et al. 2011). We then applied a spatial thinning procedure using the “spThin” R package (Aiello-Lammens et al. 2015), retaining only occurrences at least 10 km apart to reduce spatial sampling bias and improve model reliability (Boria et al. 2014). Only species with a minimum of ten spatially filtered records were retained for modeling, a criterion for robust predictions (Wisz et al. 2008).

For each species, we then calibrated MaxEnt models using the “ENMeval” package (Muscarella et al. 2014), testing all combinations of ten regularization multipliers (ranging from 0.5 to 5.0, in 0.5 increments) and three feature classes (linear, quadratic, and product, each one alone and their combinations). We excluded the hinge and threshold features based on their limited biological interpretability (Mertens et al. 2021). Spatial cross-validation followed a “block” data partitioning approach, which increases transferability across space and time (Hijmans, 2012; Veloz, 2009). For species with fewer than 15 occurrence points, we used jackknife partitioning, which is more appropriate for small sample sizes (Shcheglovitova & Anderson, 2013). For each species, we selected the top 10% performing models based on the lowest omission rate (OR) and the highest average AUC values, and used these to construct a consensus prediction (Boria et al. 2017). To project future distributions, we used climate data from three General Circulation Models (IPSL-CM6A-LR, MIROC6, and MRI-ESM2-0), selected for their strong performance and relevance to the South American region (Cannon, 2020). These were combined into a weighted ensemble forecast for the year 2050 under two Shared Socioeconomic Pathways: SSP245 (a mitigation scenario, “optmistic”) and SSP585 (a high-emission scenario, “pessimistic”). Final suitability maps were converted into binary habitat maps (suitable/unsuitable) using the “10 percentile training presence” threshold, which is recommended for presence-only datasets and helps reduce uncertainty from aggregated occurrence sources (Anderson et al. 2016). To mitigate overprediction in SDM, we applied a spatial filtering procedure based on the mean distance between bird and plant occurrences. For each taxonomic group, we combined all species occurrence records and calculated pairwise geographic distances between points, for each species. These mean distance values were used to create species-specific buffers around known occurrences. For each species and scenario (present and future), we overlaid the occurrence-based buffers on binary presence-absence rasters. Thus, pixels that fell outside the buffer area were zeroed out, restricting predictions to ecologically plausible regions around the observed records. All ecological niche models were done in R v. 4.3.0 (R Core Team 2023).

2.4 Metanetwork and its descriptors

To construct the metanetwork, we combined data from the 26 plant-frugivore networks into a single weighted adjacency matrix (A^{mn}), where m represents plant species (rows), n represents bird species (columns), and each cell contains the number of recorded interactions between a given bird-plant pair (edges) (Moulatlet et al. 2023). In this matrix, interaction frequency was determined by summing the occurrences of each unique bird-plant interaction across all networks. Consequently, the matrix weights interactions based on the number of studies in which each bird-plant pair was observed. However, we do not use weighted data in the spatial calculations, since using binary interaction networks offers a practical and robust alternative for large-scale ecological analyses, as they maximize geographical coverage and are less sensitive to local ecological variables such as species abundance or phenology, usually no available (Corso et al. 2015; Oliveira et al.2025, Huang et al. 2025). Moreover, weighted calculations are not currently available on the “net.raster” package (Oliveira et al. 2025), which we use to calculate spatialized network metrics. The package allows computing ecological network metrics by integrating binary species distribution rasters and bipartite interaction matrices as inputs, generating spatially explicit outputs for each metric. Built on SpatRaster objects (via the *terra* package; Hijmans, 2022), this tool enables the direct calculation of bipartite network indices across spatial grids, transforming theoretical interactions into mappable layers. It assumes co-occurrence as a proxy for potential interactions, leveraging known species associations to infer connectivity and map key descriptors of bipartite networks. Pixels lacking sufficient species to compute network metrics (e.g., no plant-frugivore pairs) were automatically excluded during raster calculations, and each raster cell was individually processed.

After all adjustments to the meta-network to retain only interactive species and the minimum number of records for niche modelling, it was possible to model 192 bird species and 320 plant species from the original compiled species set. Our finalized metanetwork matrix reflects these curation steps, and, given the AF history, likely aggregates many local networks of disturbed areas, which may have already lost their largest frugivorous birds. We then estimated the following metrics: number of species at each trophic level (higher and lower), links per species (combined), generality (birds), and vulnerability (specific for plants). In bipartite ecological networks, these key metrics provide insights into structure and functioning. The number of species at each trophic level (higher/lower) reflects network size and potential redundancy, while links per species (sometimes called linkage density) measure interaction diversity and reflect the network complexity (Montoya et al. 2006). Generality (average interactions per higher-level species) and vulnerability (average interactions per lower-level species) quantify asymmetry in specialization (Tylianakis et al. 2007). Also, the trait-mediated persistence of even simple interaction metrics across climate scenarios can provide insight into the structural stability of frugivory networks under environmental change. Thus, future reductions in species number at either trophic level may indicate loss of functional diversity and network simplification; declines in links per species may signal rarer interactions or more fragile systems; and changes in partner diversity metrics (generality and vulnerability) may suggest specialization and generalizations, besides reduced functional redundancy and potential loss of fruit resources.

2.5 Data analyses and model selection

We analyzed spatial patterns of meta-network change by comparing current conditions with projections for 2050 under two climate scenarios (RCP 4.5 and RCP 8.5), focusing on five network metrics. We conducted a spatially stratified descriptive analysis, emphasizing geographic gradients (north–south, east–west). We used pre-processed raster layers at a 2.5 arc-minute resolution, representing each metric for the present and future scenarios. Percentage change was calculated per pixel as ((future − present) / present) × 100, with divisions by zero set to NA. Spatial analyses were conducted in R using the packages *terra*, *tidyverse* (Wickham 2019), *tidyterra* (Hernangómez 2023), and *viridis* (Garnier e al. 2024). We computed summary statistics (mean, median, standard deviation, quartiles, and range) across all valid pixels, as well as regional means after spatial stratification by median latitude (North vs. South) and longitude (West vs. East). Outputs included difference rasters for each network metric, tabular summaries, and visualization maps generated using *ggplot2* (Wickham 2016) with a diverging Viridis color scale constrained to ±100%.

This approach allowed us to capture both global and region-specific patterns of network change across the Atlantic Forest.

To investigate the effects of avian traits on network structure, we implemented generalized linear mixed models (GLMMs) using the “glmmTMB” function of “glmmTMB” package (Brooks et al. 2017), fitted by maximum likelihood. First, we evaluated the distribution of each network metric through visual inspection of their histograms for all scenarios (Supplementary Figure 2), which revealed non-normality (e.g., zero-inflation in links per species, right-skewness in vulnerability). Unlike our previous study (Oliveira et al., manuscript in preparation), which employed automated model selection via “MuMIn”, here we adopted a full-model testing approach based on a priori trait selection. This decision was motivated by two main considerations. First, the current analysis involved 18 models in total (five network metrics across three scenarios, plus the two components of the two-part model for links per species), making manual specification more computationally efficient by avoiding the combinatorial explosion of automated selection. Second, our spatially explicit framework, which generated one frugivory network per pixel using “net.raster”, involved trait values averaged per pixel. This design inherently accounted for spatial structure and rendered the inclusion of random effects unnecessary, as we can assume that spatial autocorrelation was addressed through prior raster aggregation. Moreover, unlike single-metanetwork studies, our spatially explicit approach (one network per pixel) required full-model testing to prioritize ecological hypotheses over exploratory selection.

We specified two types of models depending on the network metric. For vulnerability, generality, and species richness (of both birds and plants), we applied hierarchical GLMMs with appropriate error structures: Gaussian distributions for generality and vulnerability (validated through residual diagnostics), and negative binomial (nbinom2) for species richness (for plants and birds) to account for overdispersion. To model the zero-inflated nature of the links per species metric, we applied a two-part modeling approach (Welsh et al. 1996; Martin et al. 2005). This involved fitting a binomial model to capture the presence or absence of links, followed by a Gamma model with log link for the positive values, implemented separately to capture the distinct processes governing link occurrence and intensity. Finally, we calculated models standardized beta according to the number of observations (pixels without NA) of each scenario (present = 62394, optimistic = 63981, pessimistic = 64013; Bring, 1994). Models were compared using Akaike's Information Criterion (AIC), where lower values indicate better trade-offs between model fit and complexity (Akaike 1974). When ΔAIC < 2 between competing models, we considered them equally plausible. We report model AIC and log-likelihood values as indicators of model performance, since marginal R^2 could not be reliably estimated for some families (e.g., log-linked Gamma, negative binomial) and random effects were not included due to spatial aggregation of trait data at the pixel level. Therefore, conditional R^2 was not applicable. This approach is consistent with ecological modeling studies focused on inference and in which the estimation of standard R^2 is limited by distributional or structural constraints.All analyses were run in R v. 4.4.1 (R Core Team 2024).

3. Results

Projections of the Brazilian Atlantic Forest (AF) bird-plant frugivory metanetwork reveal complex spatial and trait-mediated responses to climate change. Based on projections for the present and 2050 climate scenarios (SSP245 and SSP585), we expect a notable difference in network metric responses between the northern and southern regions of the biome and between its coastal (eastern) area and interior (western) regions (Figures 1 and 2). Our main results revealed: (1) greater species loss in northern vs. southern regions, particularly for birds (-23.97% vs -14.96% in the pessimistic projection; Table 1); (2) coastal areas showed 1.5-3.7× steeper declines in interaction metrics (links per species, generality and vulnerability) than interior forests; (3) amplified differences for all metrics and across the biome in the pessimistic scenario; (4) trait-mediated reorganization where body mass ($\beta = +0.25$ to $+0.42$) and frugivory degree ($\beta = +0.45$ to $+0.49$) stabilized interactions, while range size ($\beta = –0.27$ to $–0.14$) consistently reduced network richness, interaction rates and partner diversity; and (5) climate scenario-dependent effects of flight efficiency (HWI as proxy) (Table 2 for summary effects and complete model coefficients in Supplementary Table 3). All beta values presented are from the pessimistic scenario, considering the minimum and maximum among all network metrics.

Geographical patterns exhibited north–south and east–west asymmetries, with more consistent patterns and absolute declines in the north-south gradient for all metrics (Supplementary Table 3 presents complete statistics). The number of plant species also presented a greater loss in northern vs. southern regions (-26.37% vs -13.21%). Northern regions showed 1.8–2.5× greater median declines in interaction metrics than southern areas (e.g., –27% vs –9.28% for generality and vulnerability, and -23.34% vs -8.57% for links per species). East–west gradients were also evident: coastal areas experienced steeper declines than inland areas (e.g., "–16.10% vs –15.75% for links per species). Generality and vulnerability**,** however, exhibited minimal east–west contrast, suggesting a more homogeneous response (e.g., –18.45% in east vs –17.76% in west).

Trait effects diverged by climate scenario (see effect plots in Supplementary Figure 3). For higher trophic level (birds), body mass increased bird species richness in the metanetwork (β = +0.25 to +0.33, optmistic and pessimistic projections, respectivley), while beak width reduced it (β = –0.30 to –0.47, optmistic and pessimistic), despite their moderate correlation (r = 0.63). Frugivory degree also rised avian species (β = +0.51 to +0.05, optmistic and pessimistic), while range size reduced bird richness in the metanetwork (β = +0.21 to +0.23, optmistic and pessimistic). For the plants level, the effect direction patterns of each trait were similar (Supplementary Table 4). The residualized Hand-Wing Index (HWI) was the only trait with scenario-dependent effects: negative in present (β = +0.13 to +0.05) and optimistic (β = +0.12 to 0.02) projections, and positive in the pessimistic scenario (β = +0.05 to 0.18), for all network metrics (minimum and maximum beta values among them). The only traits that showed any non-significant effect were only for plant richness in the metanetwork: beak width in the present scenario and HWI in the pessimistic future.

Network architecture responded non-uniformly across metrics and regions. Greater reductions are projected for northern areas pessimistic scenario, where all metrics are expect to decrease above 23.37%, reaching 27% in partner diversity. The most conservative (optimistic) projection in the region with the least predicted change, the south of the AF, still estimates a 7-8% reduction in interaction rates and partner diversity and around 11% loss in species richness at both trophic levels. Generality and vulnerability, given their similar natures, presented showed steepest reductions in areas where plant diversity also declined, especially in the northern region (–27%), with body mass (β = +0.48 to +0.37, optmistic and pessimistic) and frugivory degree (β = +0.48 to +0.45) exerting a consistent buffering effect .

The two-part model revealed that all traits only affected interaction frequency (the positive component), not interaction occurrence probability (the binary component). Table 2 summarizes trait effects across all metrics (see Supplementary Table 5 for full model diagnostics). Residualization of HWI and frugivory degree, both by body mass, isolated independent effects, and VIFs < 2.35 confirme minimal collinearity (Supplementary Table 6).

Table 1 - Expected percentage of change in each metric across the north-south and east-west gradients for each future scenario, based on current climatic conditions. N = number of; spp = species.

Metanetwork metric	**Optimistic**				**Pessimistic**			
	North	South	West	East	North	South	West	East
N. plant spp.	-21.30	-11.37	-15.54	-17.07	-26.37	-13.22	-18.09	-21.41
N. bird spp.	-17.06	-11.53	-15.46	-13.10	-23.99	-14.96	-19.49	-19.40
Links per spp.	-17.99	-7.08	-11.05	-13.94	-23.36	-8.58	-13.08	-18.75
Generality	-21.35	-7.95	-12.67	-16.53	-27.02	-9.29	-14.82	-21.36
Vulnerability	-21.35	-7.95	-12.67	-16.53	-27.02	-9.29	-14.82	-21.36

Table 2 - Directions of the effects of avian traits on metanetwork metrics across scenarios. For each metric, we show the effect of present → optimistic → pessimistic scenarios. If the trait had a stable effect across all scenarios for that metric, there is only one signal indicated. Positive (+) and negative (-) signals indicate the direction of the trait's effect on the metric, ns = not significant, spp = species, N= number of. Traits values consider transformations performed: logarithm of body mass, square root of range size, residualizations of frugivory degree and HWI by body mass.

Trait	**Links per spp.**	**Generality**	**Vulnerability**	**N. plant spp.**	**N. bird spp.**
Body mass	+	+	+	+	+
Beak width	–	–	–	ns / – / –	–
Frugivory	+	+	+	+	+

HWI	– / – / +	– / – / +	– / – / +	– / – / ns	– / – / +
Range size	–	–	–	–	–

4. Discussion

We evidenced that current climatic stability shapes a more complex and functionally diverse plant-frugivore metanetwork than what is expected under climate change in the Brazilian Atlantic Forest (AF). The predicted simplification of the metanetwork is even greater in the pessimistic scenario and varies across the biome, exhibiting north-south and east-west gradients. The restructuring of AF metanetwork under climate change is trait-mediated through consistent yet nuanced patterns, highlighting body mass and frugivory degree as the main bird species traits stabilizing network richness, interaction rates, and partner diversity across all climate scenarios.

Spatially, our results mirror biogeographic discontinuities across the Atlantic Forest. Particularly in the historically stable southern AF, a region that consistently exhibited higher bird richness, links per species, and partner diversity, which supports our first hypothesis and reinforces the idea that climatic history influences both species diversity and network architecture (Carnaval et al. 2014; Poisot et. 2017). The Doce River is an important region where a recent subdivision of the Atlantic Forest took place, dividing the biome into two bioclimatic domains (Carnaval et al. 2014). Indeed, network metrics declines were pronounced north of the Doce River, a known contact zone for multiple lineages, also presenting limited overlap in floristic and faunal assemblages and greater climatic exposure (Costa & Leite, 2012, Leite et al. 2016), conditions that may contribute to the reduced interaction metrics observed. In contrast, southern interior regions, which were more exposed during glacial periods and exhibit demographic continuity and stability (Leite et al. 2016), showed greater trait-mediated resistance in network structure.

Interestingly, this north–south divergence in network responses parallels historical patterns of avian endemism areas: analysis of endemism identified a basal dichotomy between Pernambuco as a northern cluster and Coastal Bahia, Central Bahia, and Serra do Mar as a southern cluster for passerine birds (Cardoso da Silva et al. 2004). These southern areas, which showed greater interaction retention in our projections, have been historically more connected in terms of passerine diversification, possibly due to shared topographic complexity and forest continuity (Oliveira-Filho & Fontes, 2000, Cardoso da Silva et al. 2004). In contrast, Pernambuco represents an evolutionarily distinct region for birds (Cardoso da Silva et al. 2004), where isolation and climatic stress may have jointly shaped the lower network stability we observed. Similar spatial asymmetries have also been identified in climate-based projections for the same biome, where forest frugivorous bird richness is expected to decline more sharply in the west and southwest due to warming and reduced forest cover (Mota et al. 2022).

These spatial patterns in network structure also echo historical shifts in floristic composition. The marked floristic differentiation between the north and south of the biome is due to the distinct temperature and precipitation regimes, related to the topographic gradient: the mountain ranges are lower in altitude and progressively further away from the coast north of the Rio Doce (Oliveira-Filho & Fontes, 2000). Historically, cold-adapted assemblages persisted through the Last Glacial Maximum across highland plateaus, while warmer and more seasonal communities fluctuated in the Holocene, creating a mosaic of plant communities (Arruda et al. 2017; Wilson et al. 2021). Such legacy effects likely contribute to present-day patterns. Moreover, differential climatic tolerance among plant species may also contribute to the north–south asymmetry observed in network stability. In the Atlantic Forest, tree species from colder or drier environments tend to exhibit broader climatic niches, whereas those from warmer and wetter regions, such as the northern coastal forests, have narrower tolerances and may be more vulnerable to warming and precipitation shifts (Klipel et al. 2022). These differences may partly explain the steeper declines in mutualistic interactions and frugivore persistence projected for northern regions. These findings underscore the importance of moving beyond biome-wide generalizations when modeling ecological responses or planning conservation. They also align with broader calls to treat refugia not as static zones but as dynamic components of conservation planning that reflect ecological and evolutionary processes across scales (Leite et al. 2016, Rossetto & Kooyman 2021). Thus, areas functioning as microrefugia or enabling species reassembly under future climates should be prioritized in adaptive management strategies.

Consistent with our second hypothesis, future scenarios projected structural simplification across the frugivory networks, particularly in historically climatically unstable regions. We observed marked declines in frugivore richness, links per species, and interaction diversity (for both trophic levels) under optimistic and pessimistic projections, suggesting that functional erosion may precede taxonomic loss (Emer et al. 2020). Our results align with previous evidence that interspecific interactions can capture variations that are not apparent when only the occurrence of species is observed across environmental and climatic gradients (Poisot et al. 2017). Importantly, our spatially explicit estimates allow the detection of climate-driven changes in network structure at scales relevant for conservation planning and action. This spatially integrated approach enhances the ecological application of network metrics and provides a reproducible framework for assessing interaction stability under environmental change (Oliveira et al. 2025).

Although our approach does not directly model climatic refugia, the consistent spatial gradients in network structure, particularly the stability observed in southern and interior regions, suggest that these areas historically acted as microrefugia for frugivory interactions. Paleoecological evidence from the southern Atlantic Forest, however, reveals substantial shifts in species composition over past climate oscillations, with the early Holocene generating novel assemblages not found today (Wilson et al. 2021; Arruda et al. 2017). Once driven by natural variability, these transformations may now be exceeded in magnitude and speed by anthropogenic climate change, risking seed dispersal services in extense areas of the biome. Indeed, modelling studies suggest that projected shifts in distribution and community turnover over the coming decades could surpass those seen since the Last Glacial Maximum, particularly in highland areas of southern Paraná and Santa Catarina, where cold-adapted plant species are likely to decline severely (Wilson et al. 2021).

Trait-based effects, aligned with our third hypothesis, revealed consistent yet nuanced patterns. Generalist traits such as broader body mass and higher frugivory degree indeed promoted interaction diversity, reflecting their role in stabilizing links across variable environments by enhancing dietary flexibility and resilience to partner loss (Mello et al. 2015, Correa et al. 2016, Carreira et al. 2020).This is presumably due to the greater ingestion of fruits for energy supply by both large and frugivorous birds. In addition, larger birds may have greater movement and dispersal potential on a medium scale. Obligate frugivores, well known as functional specialists, are also essential for the functional cohesion of networks (Sazima et al. 2010, Mello et al. 2015, Malanotte et al. 2019). Since the effect is positive even after the residualization of body mass, this trait captures an independent functional axis, probably linked to trophic fidelity and dispersal efficiency. Thus, larger and more frugivorous dispersers act as stable keystone species in the AF frugivory metanetwork, with robust contribution even under climate change. However, the less frugivorous and small-bodied bird species were the more important at small spatial scales in fragmented areas of the same biome in another study wearing metanetwork approach (Emer et al. 2018), highlighting the difference responses we can infer from various scales, even when.

Contrary to our expectation based on the literature regarding the fruit handling capacity and size selectivity (Sebastián-González et al. 2017), beak width had a negative effect on the metrics in all scenarios (except to plant richness on the current metanetwork - non-significant). This is probably due to climate-driven resource scarcity, since future scenarios may favor smaller, generalist birds as fruit size distributions shift. Importantly, this is a two-way relationship, as demonstrated by the diagnosis of the rapid reduction in seed size of Euterpe edulis, a threatened palm tree in the Atlantic Forest, due to the absence of its large native seed dispersers (toucans, cracids, and greater cotingas; Galetti et al., 2013). Regarding birds, understanding the mechanistic links between body size and environmental heterogeneity due to climate change still requires further studies, as there are few studies with few avian species that investigate whether the trend is in fact declining body size (Gardner et al. 2011).

The Hand-Wing Index (HWI) showed scenario-dependent effects: positive in present and optimistic projections, but negative in the pessimist scenario, which may suggest that flight efficiency matters most under extreme climate stress.This highlights the importance of conserving the diversity of frugivore assemblages at a local scale, since species with a greater potential capacity to traverse larger areas across the biome appear to provide a small part of the seed dispersal service (Morán-Lopez et al. 2019). In the pessimistic scenario, however, they gain importance, possibly due to their greater ability to track habitats adequately, maintaining functional interactions in a more hostile environment. Therefore, HWI may become an important adaptive axis under climate stress, favoring more mobile birds in the future. Similarly, species with wide distribution tend to have a peripheral functional role in the metanetwork over time, in terms of their effect on species richness, interaction rates and partner diversity. Despite being present in more areas, they may be ecological generalists, with less structuring interactions. This indicates that species with more restricted distribution contribute more to the cohesion of the metnetwork, and that the loss of endemic or limited-distribution species may represent a disproportionate functional loss - which is even more worrying when considering the high endemism of the biome (Cardoso et al. 2004, Carnaval et al 2014). This result differs from previous studies that evaluated the effect of range size on the centrality of bird species in the same biome (Emer et al. 2018, Pinto et al. 2021, Fuzessy et al. 2022, Oliveira et al. manuscript in preparation). This highlights the need for caution when discussing the implications of the effect of different ecological and morphological attributes on metrics at the species or network level and at different scales.

Body mass and degree of frugivory are the traits most robustly associated with network complexity and functionality, both in the present and in future climates. The effects of beak width and range size, on the other hand, highlight a potential vulnerable specialization, supported in future scenarios by changes in the distribution of fruit size, and the functional importance of species with restricted distributions in the biome. HWI may be indifferent in the present, but becomes functionally relevant in extreme scenarios (SSP 585), bringing a latent adaptive response and an emerging potential for future stability. Despite these trait-level influences, current climatic stability emerged as a stronger predictor of network structure across regions, consistent with macroecological expectations for mutualistic systems based on historical climate tendencies (Dalsgaard et al. 2013). Still, the persistence of trait effects across all scenarios indicates their consistent impact on the structural stability, even amid compositional turnover, except for the scenario-dependent effect of HWI. Our approach, though powerful in mapping broad-scale patterns, does not account for local interaction variability or fine-scale behavioral processes. Incorporating data on gut passage time, movement behavior, or intraspecific variation could refine trait–interaction links in future studies. Moreover, spatial network metrics derived from co-occurrence-based predictions may overestimate realized interactions, especially where environmental filtering or behavioral mismatches occur (Oliveira et al. 2025).

In summary, our study bridges macroecology and network theory by scaling local trait-based interactions to spatially explicit forecasts. This integration revealed that both historical climatic stability and ecological traits shape the architecture and cohesion of frugivory networks. As climate change accelerates, the species richness and interaction diversity are likely to erode disproportionately in unstable areas, driven by species losses and shifting trait compositions. Regions of historical stability may function as mutualistic refugia, harboring trait combinations that sustain interactions despite climatic perturbations. In our system, such homogenization threatens not only interaction richness but also the ecological roles underpinning seed dispersal. At a broader scale, the integration of trait-informed ecological networks with macroecological data is crucial to understanding biodiversity responses to global change. While ecological networks remain underrepresented in biogeography due to data limitations (Kissling et al. 2011), their spatial and functional structure can provide mechanistic insights that complement species-level approaches (Windsor et al. 2022). Our study reinforces the idea that interaction patterns themselves carry biogeographical signals and should be incorporated into distribution models, restoration efforts, and conservation prioritization.

5. Concluding remarks

By integrating local interaction data with SDM-predicted co-occurrences, our trait-based metanetwork framework scaled local frugivory patterns to regional predictions, a critical step for fragmented tropical systems (Poisot et al. 2014; Li et al. 2020). Climate change poses escalating risks to tropical seed-dispersal systems, especially in biodiversity hotspots such as the Atlantic Forest (AF), where frugivorous birds are key dispersal agents in increasingly fragmented landscapes (Galetti et al. 2013; Pires et al. 2014). In our projections, large-bodied frugivores maintained richer interactions, underscoring their pivotal role in seed dispersal, yet their vulnerability to anthropogenic pressures creates a size–persistence paradox (Galetti et al. 2013), where keystone mutualists face disproportionate declines.

Climate-driven disruption of frugivory networks in the Atlantic Forest is not spatially uniform. Trait-mediated responses vary across regions, metrics, and scenarios, revealing complex interactions between morphology, ecological roles, and environmental stress. The projected erosion of interaction diversity mirrors ongoing defaunation and habitat loss in the biome (Emer et al. 2018; Pinto et al. 2021), and suggests that even generalist-dominated networks may face collapse under extreme climate scenarios, especially in northern and coastal regions. Functional homogenization will likely intensify in northern/coastal regions, while southern interior forests, with higher climatic stability, may buffer network collapse (Carnaval et al. 2014). Protecting old-growth forest remnants, restoring connectivity, and guiding restoration by functional trait composition are urgent strategies to mitigate these declines. This is especially important to ensure the permanence and circulation of large birds, which, although they support richer networks, may have less effective seed dispersal and even carbon storage due to limited movement across the landscape (Bello et al. 2024). Our projections assume niche conservatism; future work should test how trait plasticity or adaptive shifts might alter outcomes. Safeguarding these species is essential not only for frugivory networks but for the long-term persistence of one of the world’s most threatened tropical ecosystems (Banks-Leite et al. 2014; Tobias et al. 2013; Fuzessy et al. 2022).

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Figures

Figure 1 - Maps of the differences between current (baseline) and optimistic future scenarios, for each metric: a) number of bird species, b) number of plant species, c) links per species, d) generality, e) vulnerability.

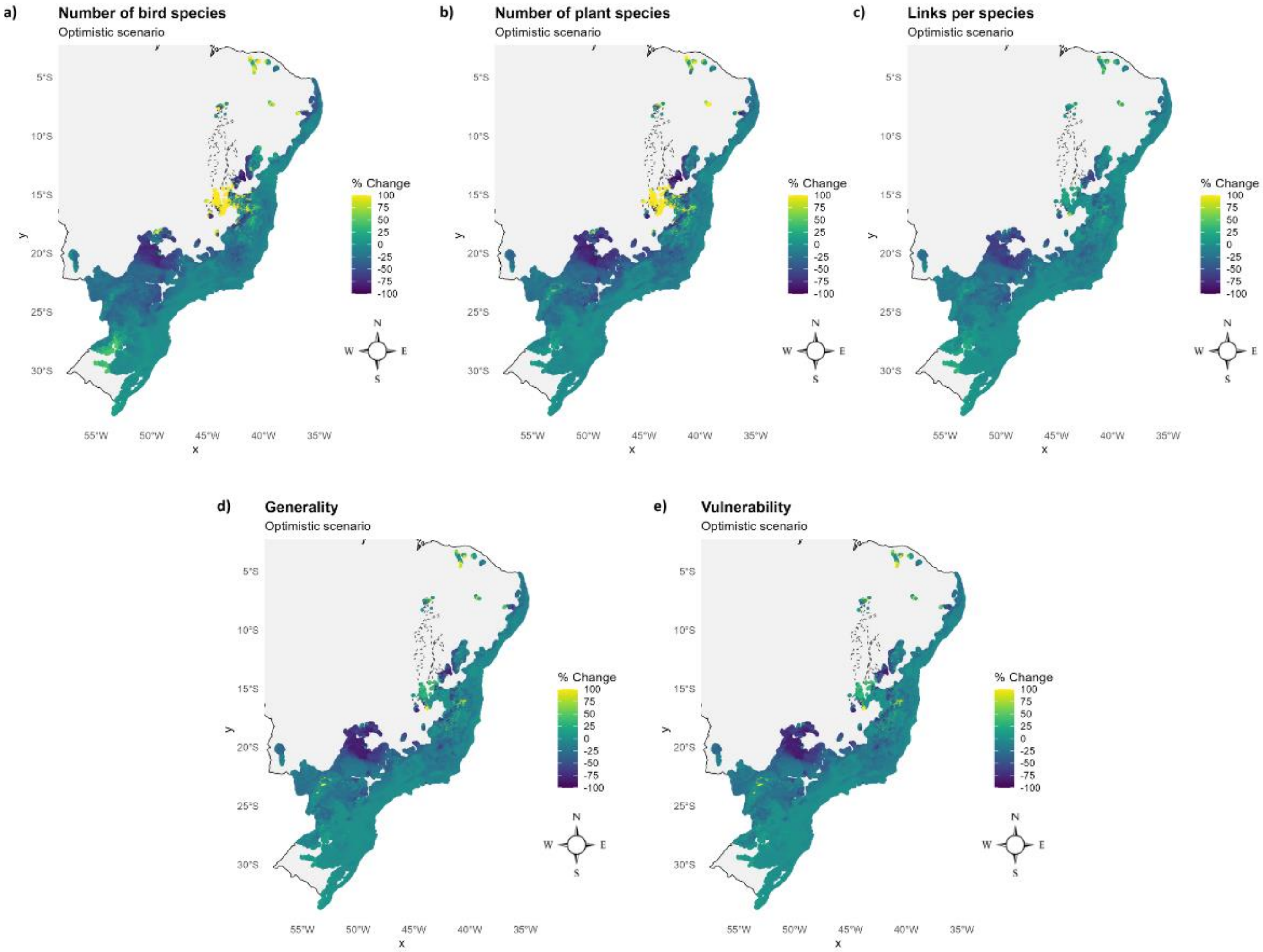
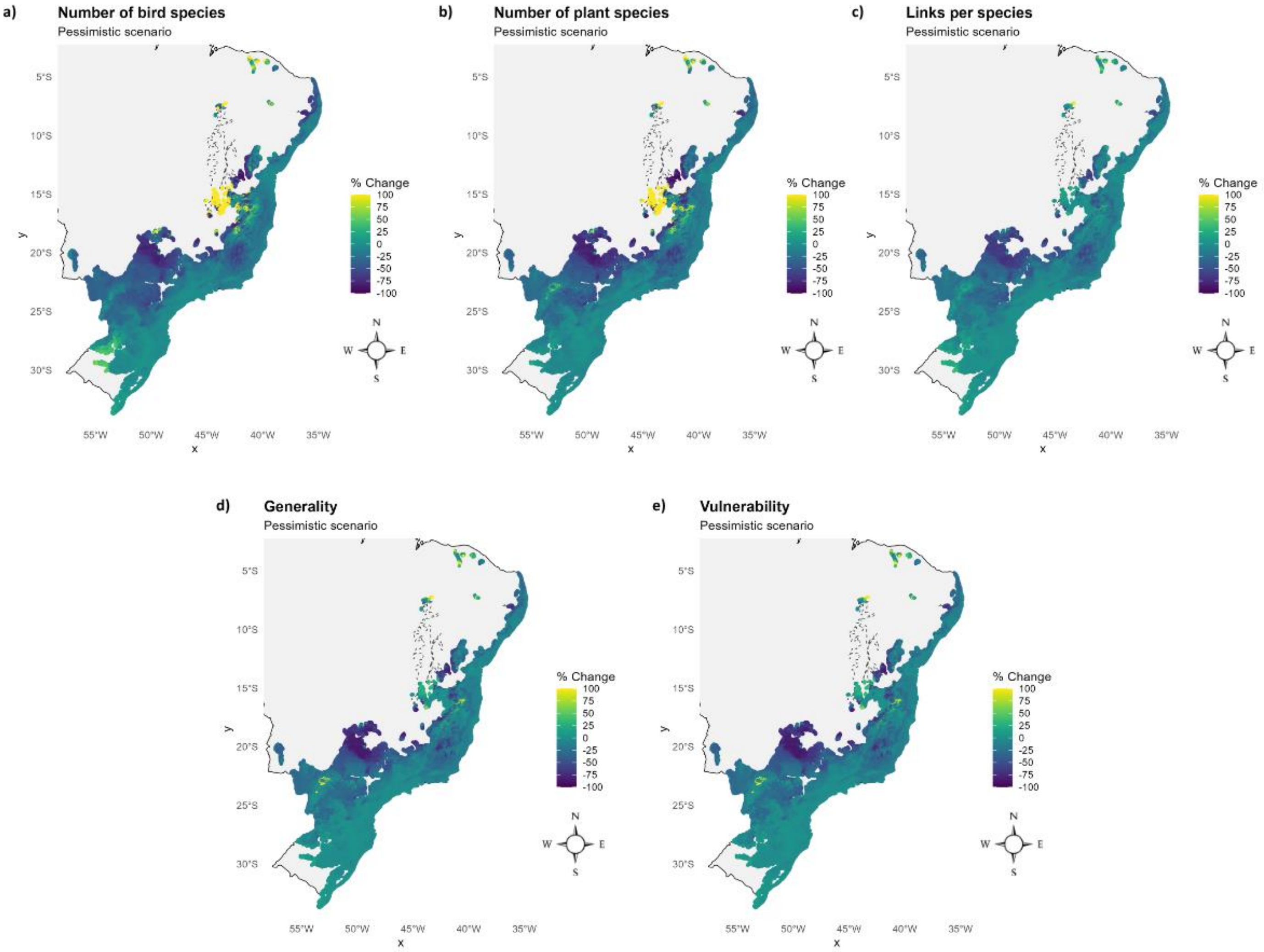
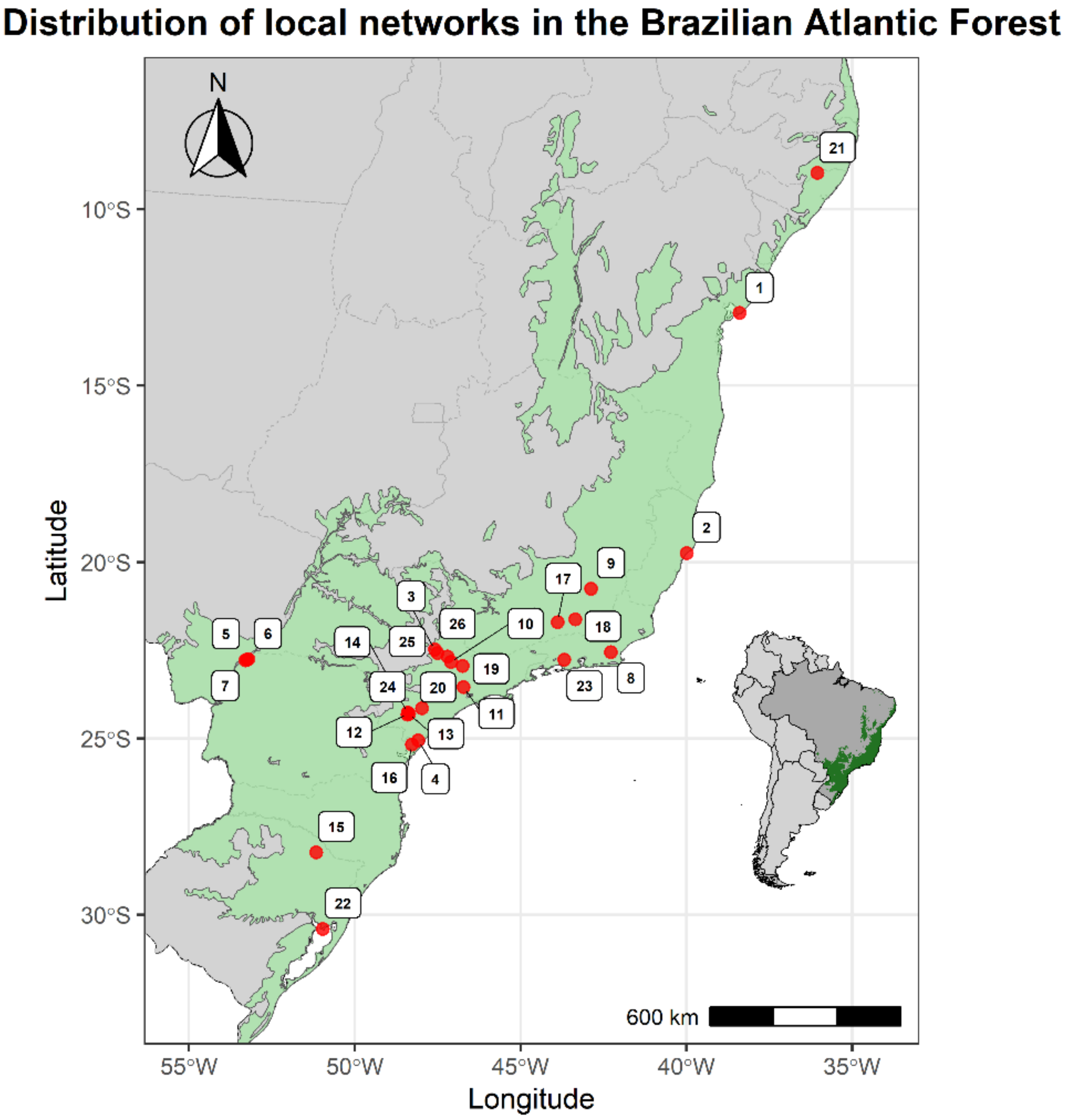


Figure 2 - Maps of the differences between current (baseline) and pessimistic future scenarios, for each metric: a) number of bird species, b) number of plant species, c) links per species, d) generality, e) vulnerability.



Supplementary material

Supplementary Figure 1 - Distribution of the 26 plant-frugivore networks in the Brazilian Atlantic Forest, based on studies carried out from 1994 to 2019.



Supplementary Table 1 - Definitions of ecological and morphological traits of bird species.

Bird trait	**Definition**
Beak width	Morphological beak measurement, sometimes called beak size (Rezende et al. 2007).
Body mass	Morphological measurement of the entire body of birds, measured in grams.
Frugivory degree	Ecological metric based on the degree of dependence on fruit in the overall diet (Fuzessy et al. 2022), expressed as a percentage (Wilman et al. 2014). We classified each bird species as occasional frugivorous, if it consumes less than 80% fruit in its diet, or obligate frugivorous, those that feed heavily on fruit and whose diet comprises equal to or greater than 80% fruit, following Wilman et al. (2014).
Hand-wing index (HWI)	A metric of bird wing shape and the most commonly used morphological proxy for dispersal (Arango et al. 2022).
Range size of spatial distribution	Geographic range of bird species distribution (Lester et al. 2007).

Supplementary Table 2 - Associations among bird traits in the Brazilian Atlantic Forest plant-frugivore metanetwork. a) Correlation matrix for quantitative traits; b) Contingency table for qualitative traits, “strata generalism” and “habitat preference”; c) Results of association tests between qualitative traits; d) Significant ANOVA results: qualitative vs. quantitative traits. HWI = Hand-wing índex; log = logarithm; sqrt = square root.

a)

Trait Pair	r
log(Body mass) x beak width	0.63
log(Body_mass) x HWI	0.18
log(Body_mass) x sqrt(Range size)	0.001
log(Body_mass) x Frugivory degree	0.18
Beak width x sqrt(Range size)	0.03
Beak width x Frugivory degree	0.15
HWI x sqrt(Range size)	0.04
HWI x Frugivory degree	0.09
sqrt(Range size) x Frugivory degree	-0.3

b)

c)

	Forest	Grassland	Human modified	Shrubland	Wetland	Woodland
Strata generalist	105	6	6	14	0	6
Strata specialist	41	2	4	10	1	1

Test	Results
Chi-squared Test	$X^2 = 6.3724$, df = 6, $p = 0.3828$
Fisher's Exact Test	$p = 0.3974$

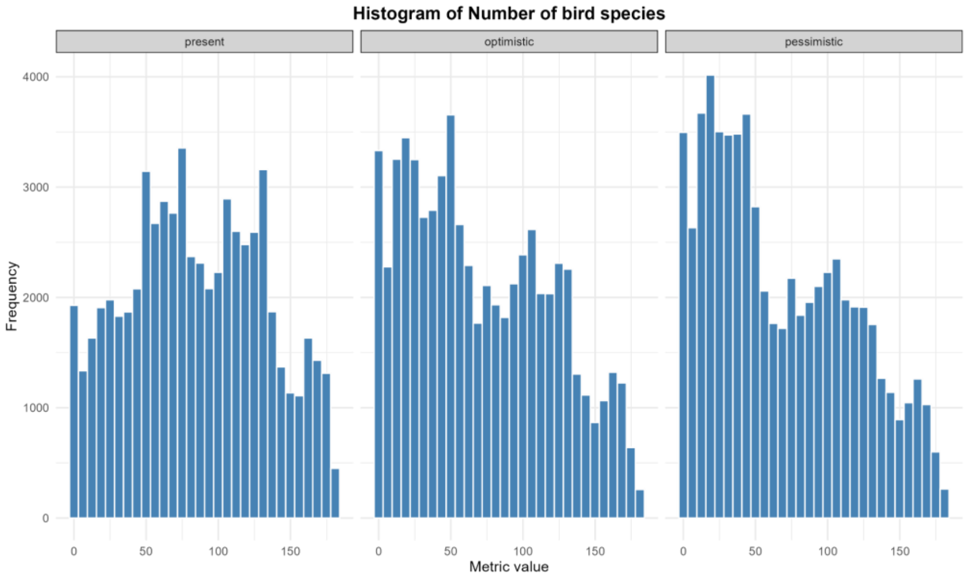
d)

Qualitative Trait	Quantitative Trait	p value	p adjusted
Forest dependence degree	Range size	3.08E-05	0.000154
Forest dependence degree	Frugivory degree	2.91E-05	0.000154
Strata generalism	Frugivory degree	0.000366	0.00122
Strata generalism	Range size	0.0112	0.028
Strata generalism	Body mass	0.0222	0.0444

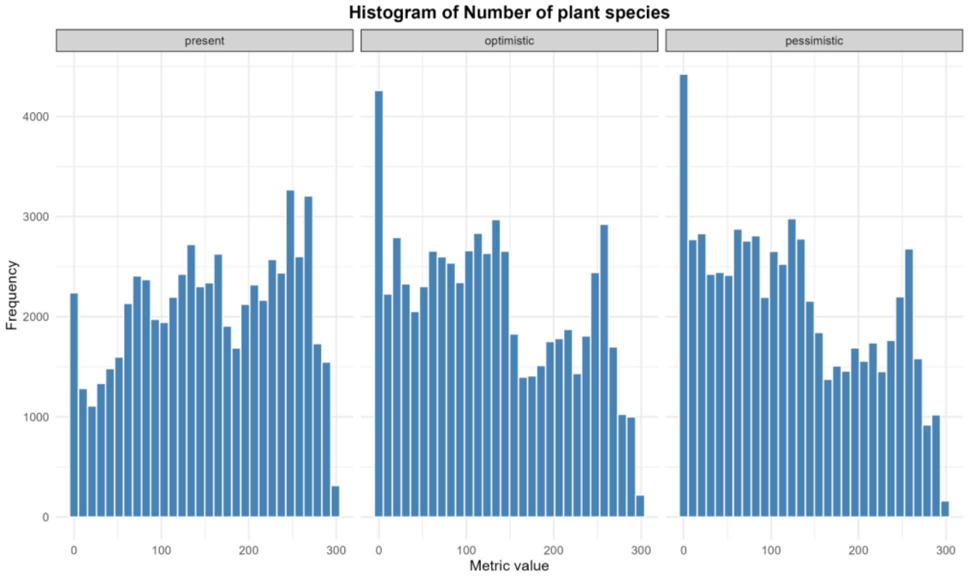
Supplementary Figure 2 - Histograms of metanetwork metric distributions by scenario.

a) number of bird species, b) number of plant species, c) links per species, d) generality, e) vulnerability.

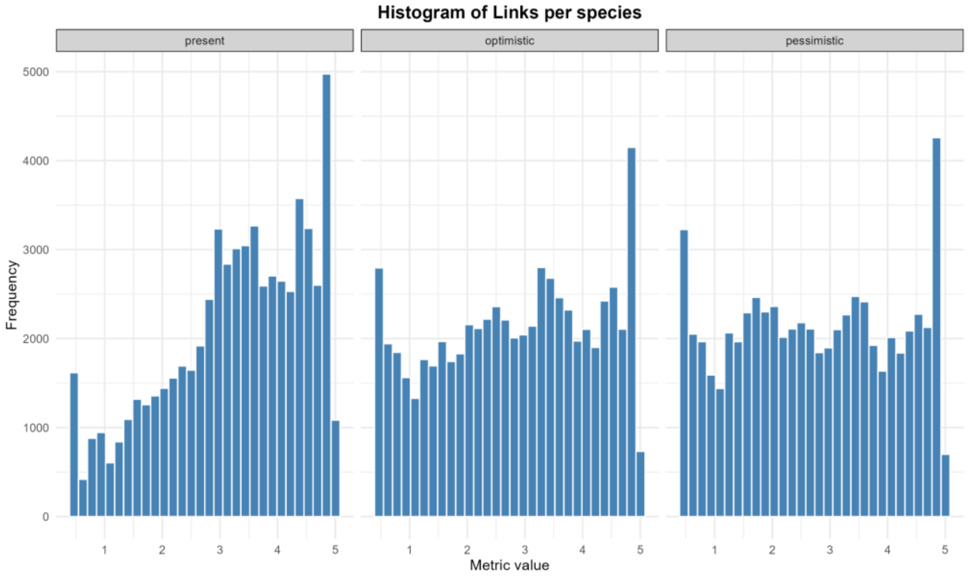
a)



b)

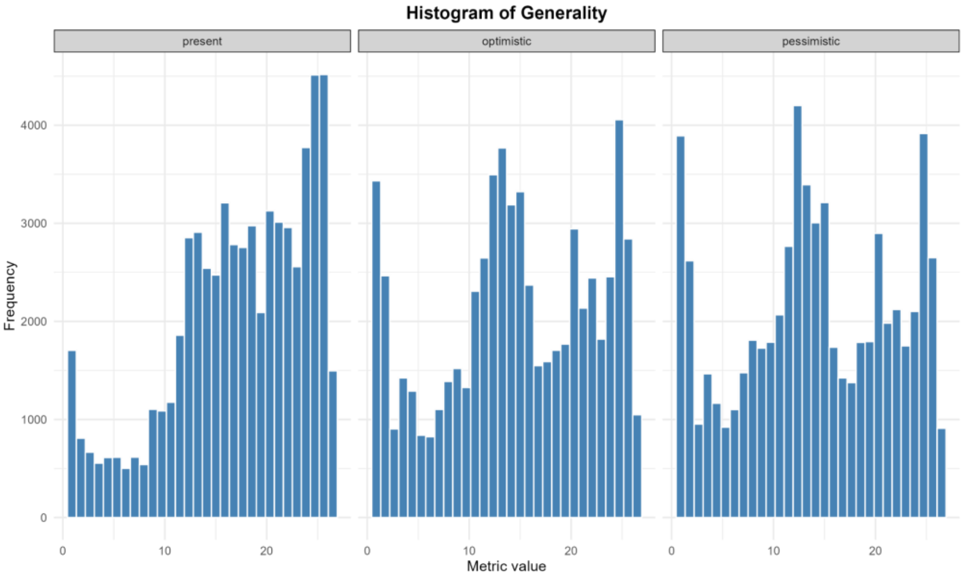


c)

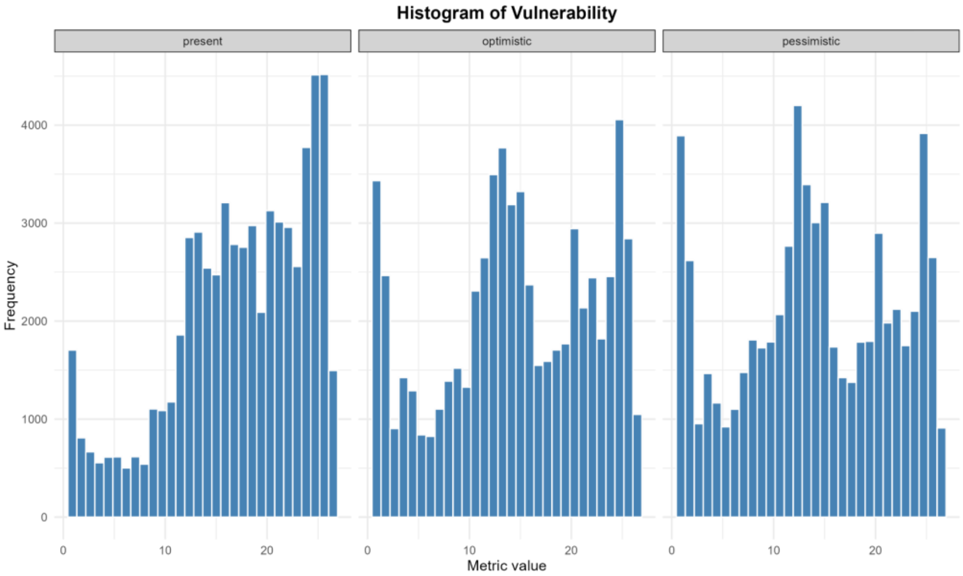


Supplementary Figure 2 - Histograms of metanetwork metric distributions by scenario. a) number of bird species, b) number of plant species, c) links per species, d) generality, e) vulnerability (cont.)

d)



e)



Supplementary Table 3 - Statistical summary of the variation of metanetwork metrics across regional gradients (north-south, east-west) in the two future climate scenarios for 2050 (Opt = Optimistic, Pes = Pessimistic). The number of pixels with valid values was 62153 for the optimistic scenario and 62157 for the pessimistic.

Metric	**2050**	**Median**	**Mean**	**Sd**	**Min**	**Max**	**Q25**	**Q75**	**North**	**South**	**East**	**West**
Number of bird species	Opt	-13.25	-14.27	32.64	-96.55	1100	-28.20	-2.92	-17.04	-11.52	-10.12	-18.44
Number of bird species	Pes	-18.75	-19.45	33.67	-97.44	700	-37.5	-5	-23.97	-14.96	-16.04	-22.86
Number of plant species	Opt	-13.22	-16.31	28.56	-97.78	700	-28.95	-3.74	-21.30	-11.35	-14.32	-18.31
Number of plant species	Pes	-17.20	-19.76	31.35	-97.87	700	-34.23	-5.49	-26.37	-13.19	-18.40	-21.12
Links per species	Opt	-8.55	-12.50	17.08	-79.08	100	-20.67	-0.75	-17.97	-7.08	-11.52	-13.49
Links per species	Pes	-11.71	-15.93	18.84	-80.77	100	-26.77	-1.53	-23.34	-8.57	-16.10	-15.75
Generality	Opt	-10.08	-14.61	21.22	-90.78	200.7	-23.12	-1.60	-21.33	-7.94	-13.74	-15.49
Generality	Pes	-13.17	-18.10	22.81	-91.82	180.8	-29.21	-2.55	-26.99	-9.28	-18.45	-17.76
Vulnerability	Opt	-10.08	-14.61	21.22	-90.78	200.7	-23.12	-1.60	-21.33	-7.94	-13.74	-15.49
Vulnerability	Pes	-13.17	-18.10	22.81	-91.82	180.8	-29.21	-2.55	-26.99	-9.28	-18.45	-17.76

Supplementary Table 4 - Full model outputs (GLMM estimates) for all network metrics across scenarios. The intercept represents the expected response value when all predictor variables are at their mean. All terms presented are the mean value of traits; body mass was logarithmized, range size is presented as its square root; frugivory degree and HWI were residualized by body mass. Fixed effect and conditional component for all models. Results presented for each climate scenario: a) Present; b) Optimistic; c) Pessimistic. *** p<0.001, ** p<0.01, * p<0.05, ns= "not significant", Est = "Estimate", Std.e = "Standard error", Stat = "Statistic", Sign = "Significance", M = million, N. = "number of", spp = "species", Links p. spp-B = "links per species - binary model", Links p. spp-P = "links per species - positive model".

a) Present

Model	**Term**	**Est**	**Std.e**	**Stat**	**p.value**	**Conf.low**	**Conf.high**	**Sign**
N. bird spp.	(Intercept)	6.90	0.10	68.86	0	6.70	7.09	***
N. bird spp.	body mass	2.34	0.09	25.59	2.03E-144	2.16	2.52	***
N. bird spp.	beak width	-0.16	0.00	-35.18	3.77E-271	-0.17	-0.15	***
N. bird spp.	frugivory	0.13	0.00	218.38	0	0.13	0.13	***
N. bird spp.	HWI	-0.13	0.00	-33.33	1.44E-243	-0.13	-0.12	***
N. bird spp.	range size	-0.08	0.00	-69.20	0	-0.08	-0.08	***
N. plant spp.	(Intercept)	0.87	0.11	8.10	5.63E-16	0.66	1.07	***
N. plant spp.	body mass	6.43	0.10	66.85	0	6.24	6.62	***
N. plant spp.	beak width	0.00	0.00	-1.00	0.317808	-0.01	0.00	ns
N. plant spp.	frugivory	0.14	0.00	233.02	0	0.14	0.15	***
N. plant spp.	HWI	-0.12	0.00	-28.81	1.68E-182	-0.13	-0.11	***
N. plant spp.	range size	-0.07	0.00	-57.10	0	-0.07	-0.07	***
Links p. spp-B	(Intercept)	0.02	7073.58M	0.00	1	-13863.96M	13863.96M	ns
Links p. spp-B	body mass	0.03	6271.66M	0.00	1	-12292.23M	12292.23M	ns
Links p. spp-B	beak width	0.15	363.30M	0.00	1	-712.06M	712.06M	ns
Links p. spp-B	frugivory	-0.12	73.21M	0.00	0.9999	-143.50M	143.50M	ns
Links p. spp-B	HWI	0.00	328.12M	0.00	1	-643.10M	643.10M	ns
Links p. spp-B	range size	0.98	107.83M	0.00	0.9999	-211.34M	211.34M	ns
Links p. spp-P	(Intercept)	1.44	0.06	23.73	1.81E-124	1.32	1.56	***
Links p. spp-P	body mass	2.32	0.05	42.34	0	2.22	2.43	***
Links p. spp-P	frugivory	0.08	0.00	266.63	0	0.08	0.08	***
Links p. spp-P	HWI	-0.03	0.00	-14.54	6.94E-48	-0.04	-0.03	***

a) (cont.)

Links p. spp-P	range size	-0.03	0.00	-50.36	0	-0.04	-0.03	***
Generality	(Intercept)	39.17	0.77	51.09	0	37.66	40.67	***
Generality	body mass	40.49	0.68	59.44	0	39.16	41.83	***
Generality	beak width	-0.74	0.03	-22.90	4.36E-116	-0.81	-0.68	***
Generality	frugivory	0.82	0.00	219.66	0	0.81	0.82	***
Generality	HWI	-0.33	0.03	-12.00	3.58E-33	-0.38	-0.28	***
Generality	range size	-1.33	0.01	-155.35	0	-1.34	-1.31	***
Vulnerability	(Intercept)	39.17	0.77	51.09	0	37.66	40.67	***
Vulnerability	body mass	40.49	0.68	59.44	0	39.16	41.83	***
Vulnerability	beak width	-0.74	0.03	-22.90	4.36E-116	-0.81	-0.68	***
Vulnerability	frugivory	0.82	0.00	219.66	0	0.81	0.82	***
Vulnerability	HWI	-0.33	0.03	-12.00	3.58E-33	-0.38	-0.28	***
Vulnerability	range size	-1.33	0.01	-155.35	0	-1.34	-1.31	***

b) Optimistic

Model	**Term**	**Est**	**Std.e**	**Stat**	**p.value**	**Conf.low**	**Conf.high**	**Sign**
N. bird spp.	(Intercept)	3.26	0.12	28.09	1.31E-173	3.04	3.49	***
N. bird spp.	body mass	7.65	0.09	82.51	0	7.47	7.83	***
N. bird spp.	beak width	-0.67	0	-142.01	0	-0.68	-0.67	***
N. bird spp.	frugivory	0.1	0	127.95	0	0.1	0.1	***
N. bird spp.	HWI	-0.1	0	-22.57	9.49E-113	-0.11	-0.09	***
N. bird spp.	range size	-0.07	0	-53.15	0	-0.07	-0.07	***
N. plant spp.	(Intercept)	-3.88	0.13	-29.12	1.88E-186	-4.15	-3.62	***
N. plant spp.	body mass	12.69	0.1	121.21	0	12.48	12.89	***
N. plant spp.	beak width	-0.55	0.01	-102.3	0	-0.56	-0.54	***
N. plant spp.	frugivory	0.11	0	131.53	0	0.11	0.11	***
N. plant spp.	HWI	-0.16	0.01	-31.74	4.74E-221	-0.17	-0.15	***

b) (cont.)

N. plant spp.	range size	-0.06	0	-40.43	0	-0.06	-0.06	***
Links p. spp-B	(Intercept)	0.02	3.45E+09	0	1	-6.8E+09	6.77E+09	ns
Links p. spp-B	body mass	0.03	3.38E+09	0	1	-6.6E+09	6.63E+09	ns
Links p. spp-B	beak width	0.16	1.74E+08	0	1	-3.4E+08	3.41E+08	ns
Links p. spp-B	frugivory	-0.12	22835652	0	1	-4.5E+07	44757056	ns
Links p. spp-B	HWI	0	1.23E+08	0	1	-2.4E+08	2.4E+08	ns
Links p. spp-B	range size	0.98	45270072	0	1	-8.9E+07	88727712	ns
Links p. spp-P	(Intercept)	-2.28	0.08	-30.28	1.83E-201	-2.43	-2.14	***
Links p. spp-P	body mass	6.51	0.06	109	0	6.39	6.62	***
Links p. spp-P	beak width	-0.48	0	-164.98	0	-0.48	-0.47	***
Links p. spp-P	frugivory	0.06	0	138.87	0	0.06	0.06	***
Links p. spp-P	HWI	-0.01	0	-4.24	2.20E-05	-0.02	-0.01	***
Links p. spp-P	range size	-0.02	0	-28.51	7.85E-179	-0.02	-0.02	***
Generality	(Intercept)	-24.66	0.92	-26.8	2.94E-158	-26.47	-22.86	***
Generality	body mass	90.21	0.74	121.45	0	88.75	91.66	***
Generality	beak width	-5.15	0.04	-142.44	0	-5.22	-5.08	***
Generality	frugivory	0.66	0.01	121.55	0	0.65	0.67	***
Generality	HWI	-0.71	0.03	-20.56	5.86E-94	-0.78	-0.65	***
Generality	range size	-0.69	0.01	-67.65	0	-0.71	-0.67	***
Vulnerability	(Intercept)	-24.66	0.92	-26.8	2.94E-158	-26.47	-22.86	***
Vulnerability	body mass	90.21	0.74	121.45	0	88.75	91.66	***
Vulnerability	beak width	-5.15	0.04	-142.44	0	-5.22	-5.08	***
Vulnerability	frugivory	0.66	0.01	121.55	0	0.65	0.67	***
Vulnerability	HWI	-0.71	0.03	-20.56	5.86E-94	-0.78	-0.65	***
Vulnerability	range size	-0.69	0.01	-67.65	0	-0.71	-0.67	***

c) Pessimistic

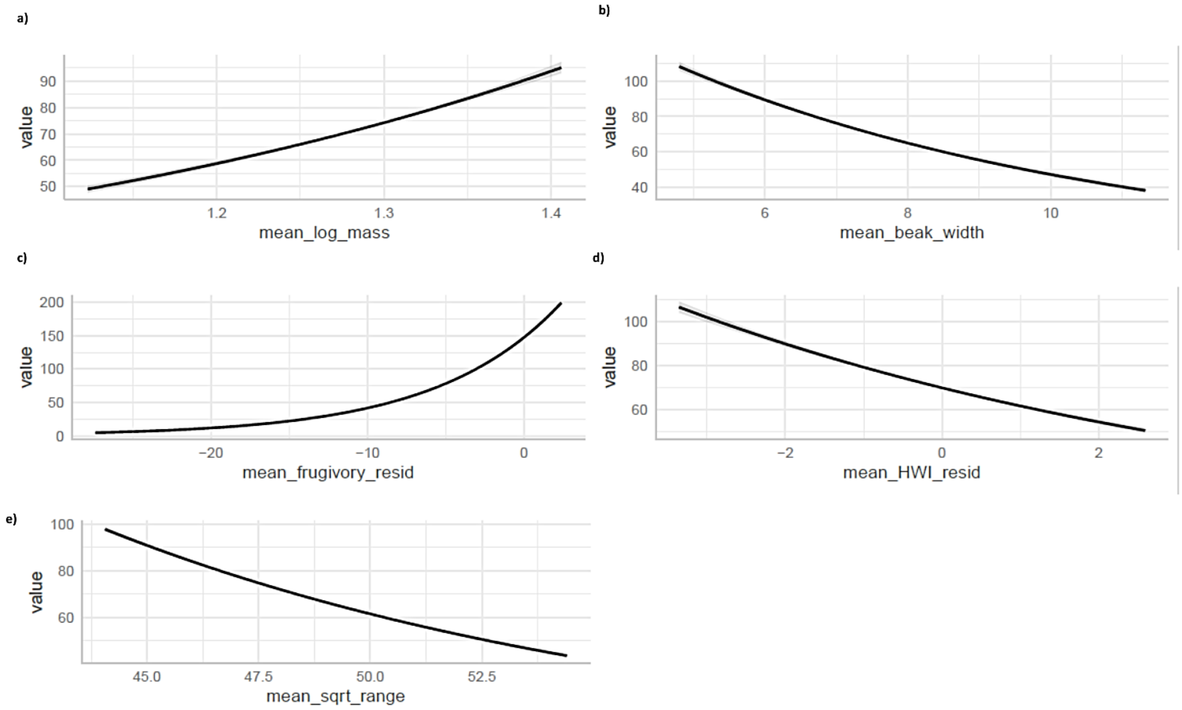
Model	**Term**	**Est**	**Std.e**	**Stat**	**p.value**	**Conf.low**	**Conf.high**	**Sign**
N. bird spp.	(Intercept)	5.77	0.12	49.77	0	5.55	6	***
N. bird spp.	body mass	5.98	0.09	64.28	0	5.8	6.16	***
N. bird spp.	beak width	-0.67	0	-150.97	0	-0.68	-0.66	***
N. bird spp.	frugivory	0.09	0	114.93	0	0.09	0.09	***
N. bird spp.	HWI	0.05	0	13.32	1.88E-40	0.05	0.06	***
N. bird spp.	range size	-0.08	0	-58.19	0	-0.08	-0.07	***
N. plant spp.	(Intercept)	-2.34	0.14	-17.32	3.11E-67	-2.61	-2.08	***
N. plant spp.	body mass	11.52	0.11	107.94	0	11.31	11.73	***
N. plant spp.	beak width	-0.59	0.01	-114.92	0	-0.6	-0.58	***
N. plant spp.	frugivory	0.11	0	124.3	0	0.11	0.12	***
N. plant spp.	HWI	-0.01	0	-1.21	0.225662	-0.01	0	ns
N. plant spp.	range size	-0.06	0	-35.86	1.12E-281	-0.06	-0.05	***
Links p. spp-B	(Intercept)	0.02	3.43E+09	0	1	-6.7E+09	6.72E+09	ns
Links p. spp-B	body mass	0.03	3.04E+09	0	1	-6E+09	5.96E+09	ns
Links p. spp-B	beak width	0.16	1.42E+08	0	1	-2.8E+08	2.78E+08	ns
Links p. spp-B	frugivory	-0.11	21144984	0	1	-4.1E+07	41443406	ns
Links p. spp-B	HWI	0	67455610	0	1	-1.3E+08	1.32E+08	ns
Links p. spp-B	range size	0.98	34437538	0	1	-6.7E+07	67496336	ns
Links p. spp-P	(Intercept)	-0.58	0.08	-7.6	2.98E-14	-0.73	-0.43	***
Links p. spp-P	body mass	5.26	0.06	86.83	0	5.14	5.38	***
Links p. spp-P	beak width	-0.44	0	-167.5	0	-0.45	-0.44	***
Links p. spp-P	frugivory	0.06	0	122.97	0	0.06	0.06	***
Links p. spp-P	HWI	0.11	0	45.97	0	0.1	0.11	***
Links p. spp-P	range size	-0.03	0	-37.53	0	-0.03	-0.03	***
Generality	(Intercept)	-2.43	0.95	-2.55	0.010794	-4.29	-0.56	*
Generality	body mass	71.37	0.75	94.6	0	69.89	72.85	***
Generality	beak width	-4.79	0.03	-137.08	0	-4.86	-4.72	***

c) (cont.)

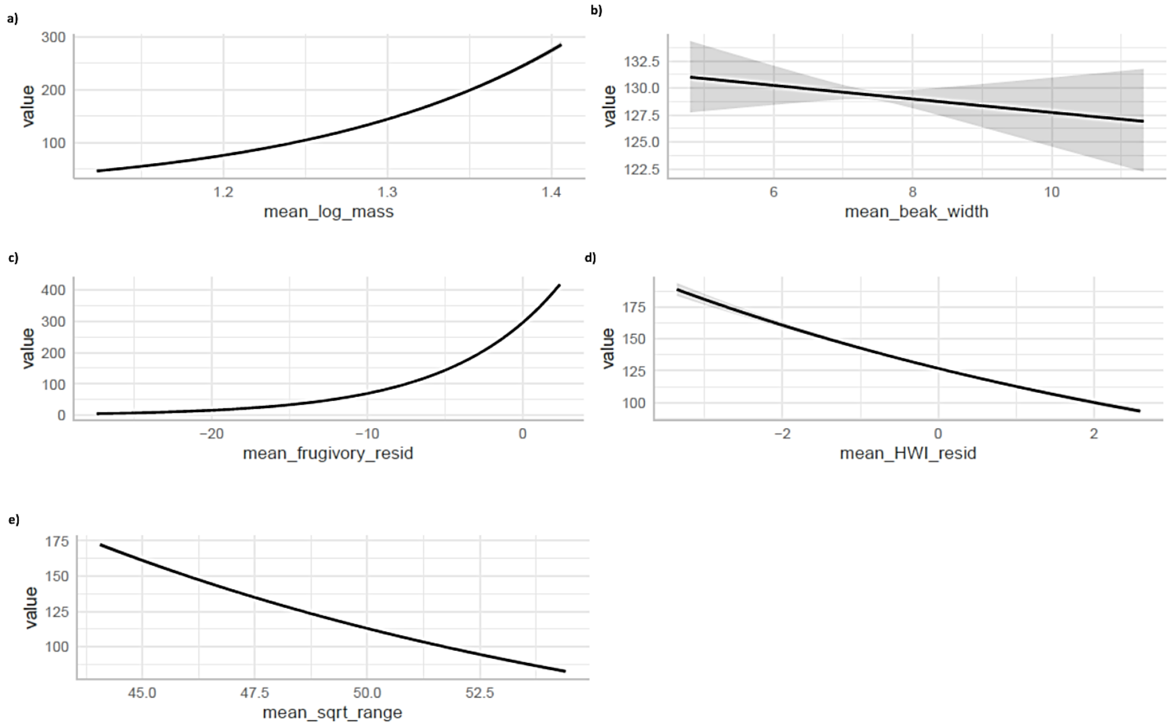
Generality	frugivory	0.65	0.01	113.24	0	0.64	0.67	***
Generality	HWI	0.88	0.03	27.96	5.47E-172	0.81	0.94	***
Generality	range size	-0.71	0.01	-67.74	0	-0.73	-0.69	***
Vulnerability	(Intercept)	-2.43	0.95	-2.55	0.010794	-4.29	-0.56	*
Vulnerability	body mass	71.37	0.75	94.6	0	69.89	72.85	***
Vulnerability	beak width	-4.79	0.03	-137.08	0	-4.86	-4.72	***
Vulnerability	frugivory	0.65	0.01	113.24	0	0.64	0.67	***
Vulnerability	HWI	0.88	0.03	27.96	5.47E-172	0.81	0.94	***
Vulnerability	range size	-0.71	0.01	-67.74	0	-0.73	-0.69	***

Supplementary Figure 3 – Effect plots for each bird species trait by climate scenario, for each metanetwork metric. Scenarios: A) present; B) optimistic; C) pessimistic. Metanetwork descriptors: 1) number of bird species; 2) number of plant species; 3) links per species (levels combined); 4) generality; 5) vulnerability. Traits: a) body mass (mean and logarithmized); b) mean beak width; c) frugivory degree (mean and residualized by body mass); d) Hand-wing index (HWI, mean and residualized by body mass); e) mean range size.

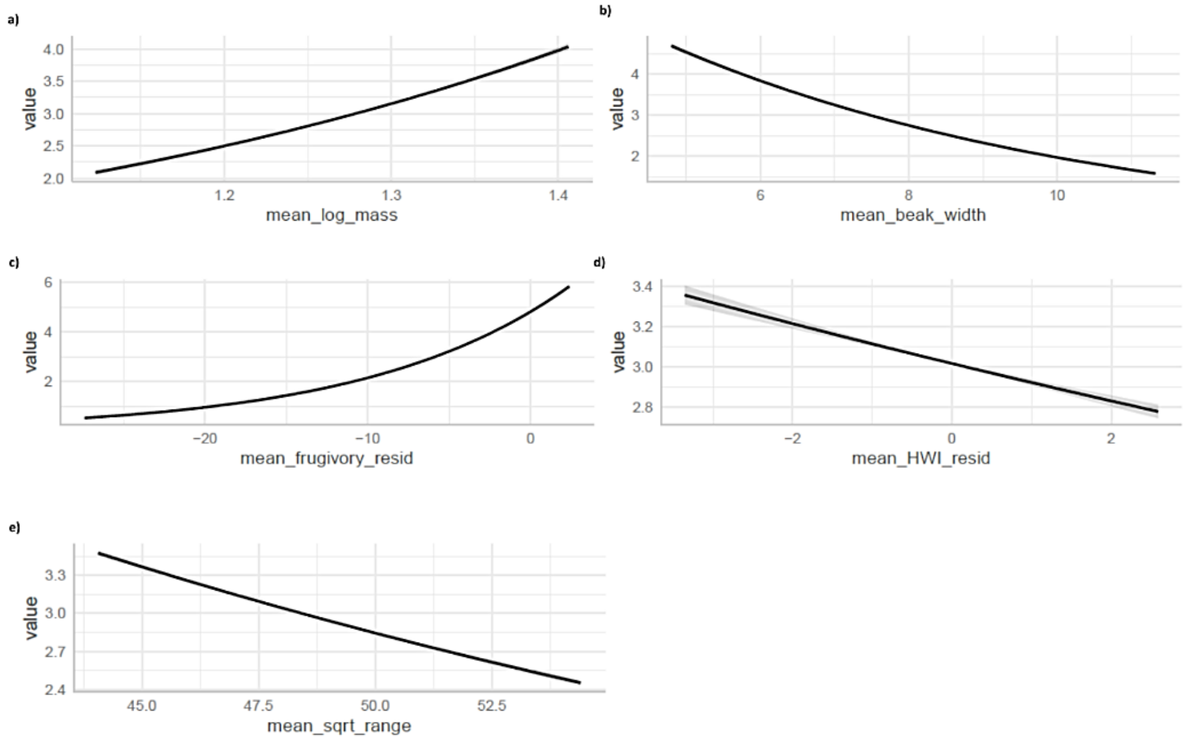
A.1) Present - Number of bird species



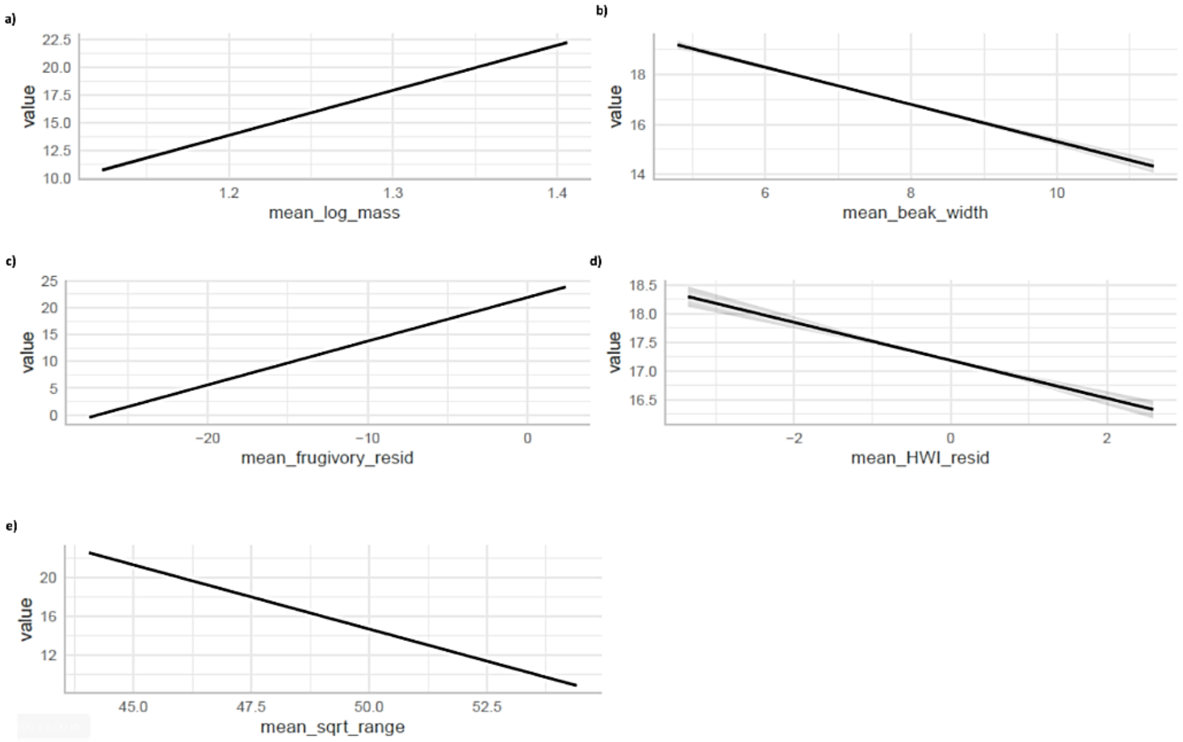
A.2) Present - Number of plant species



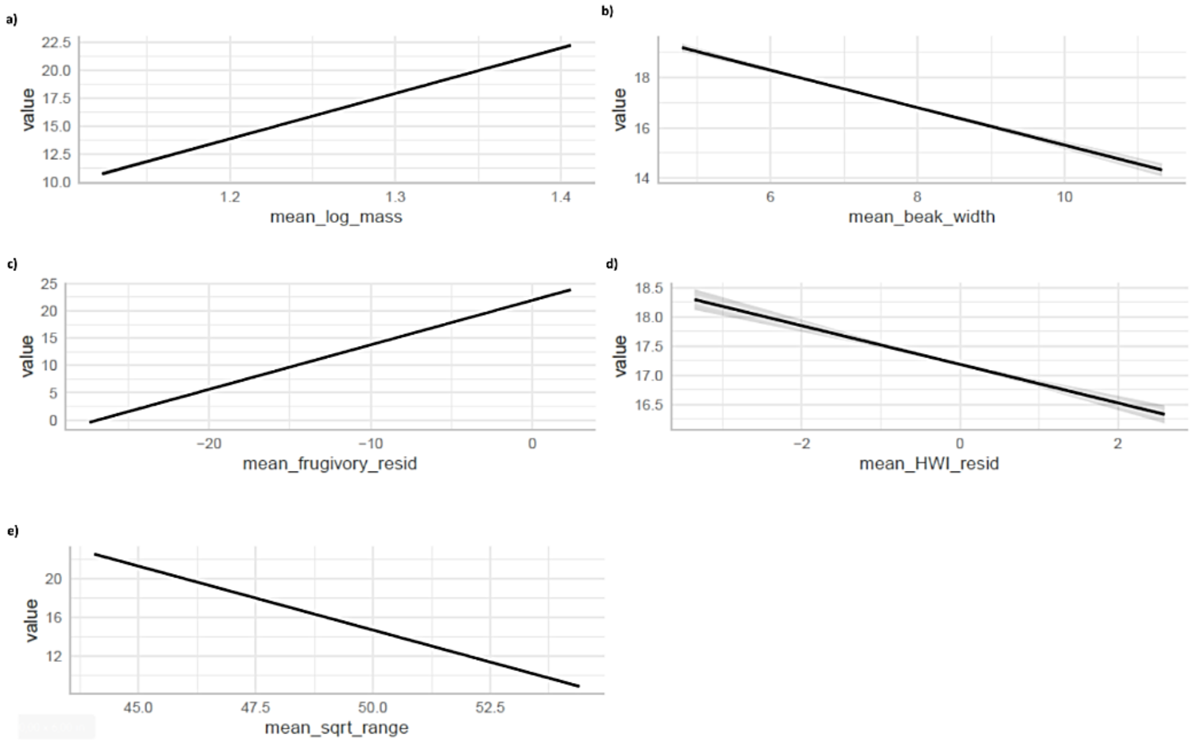
A.3) Present - Links per species



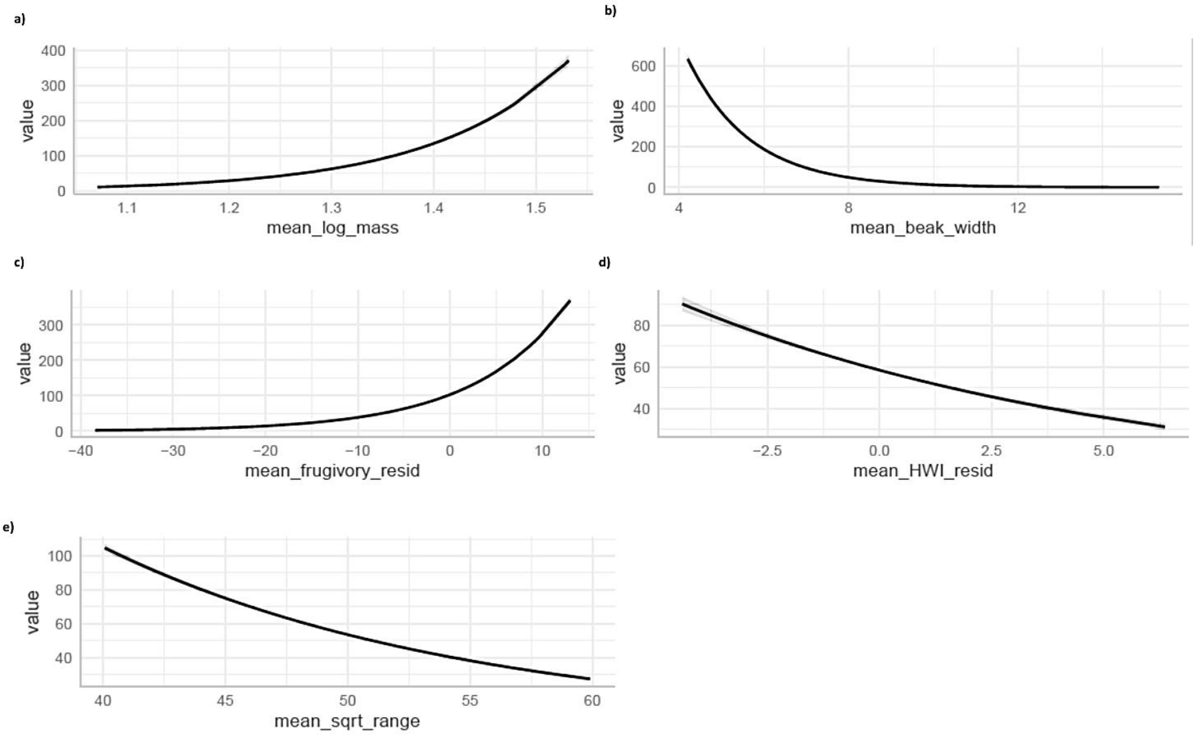
A.4) Present – Generality



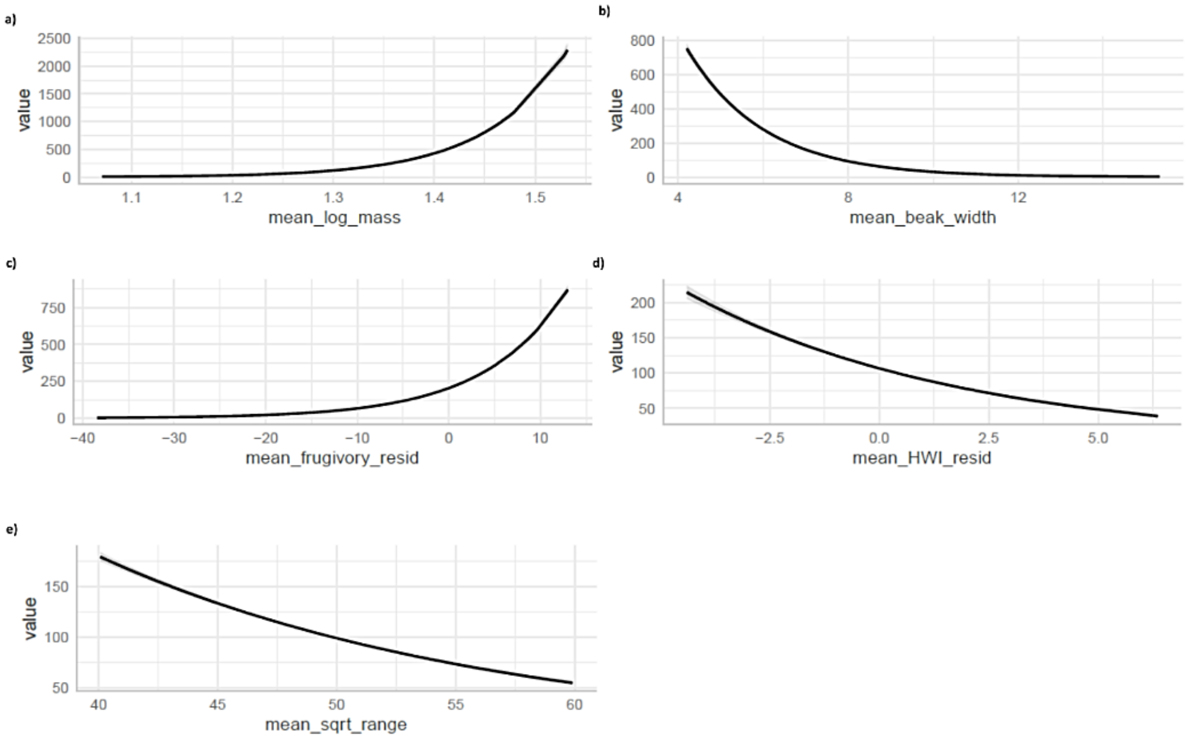
A.5) Present – Vulnerability



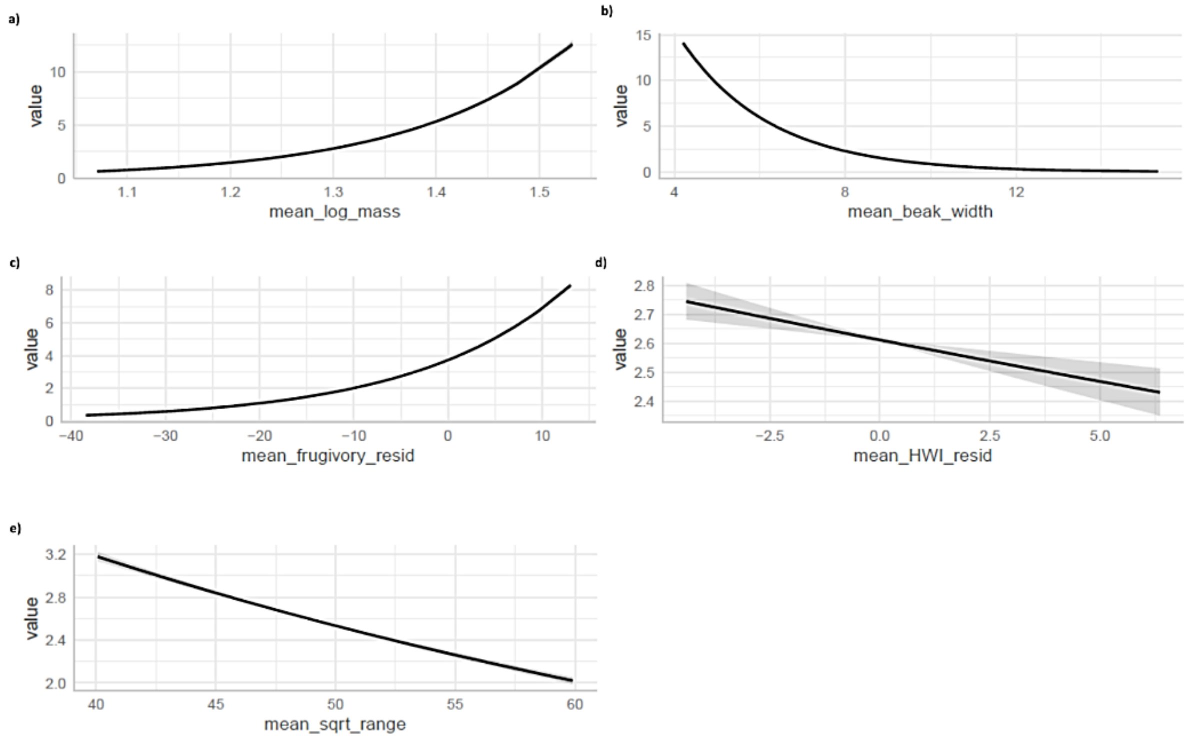
B.1) Optimistic – Number of bird species



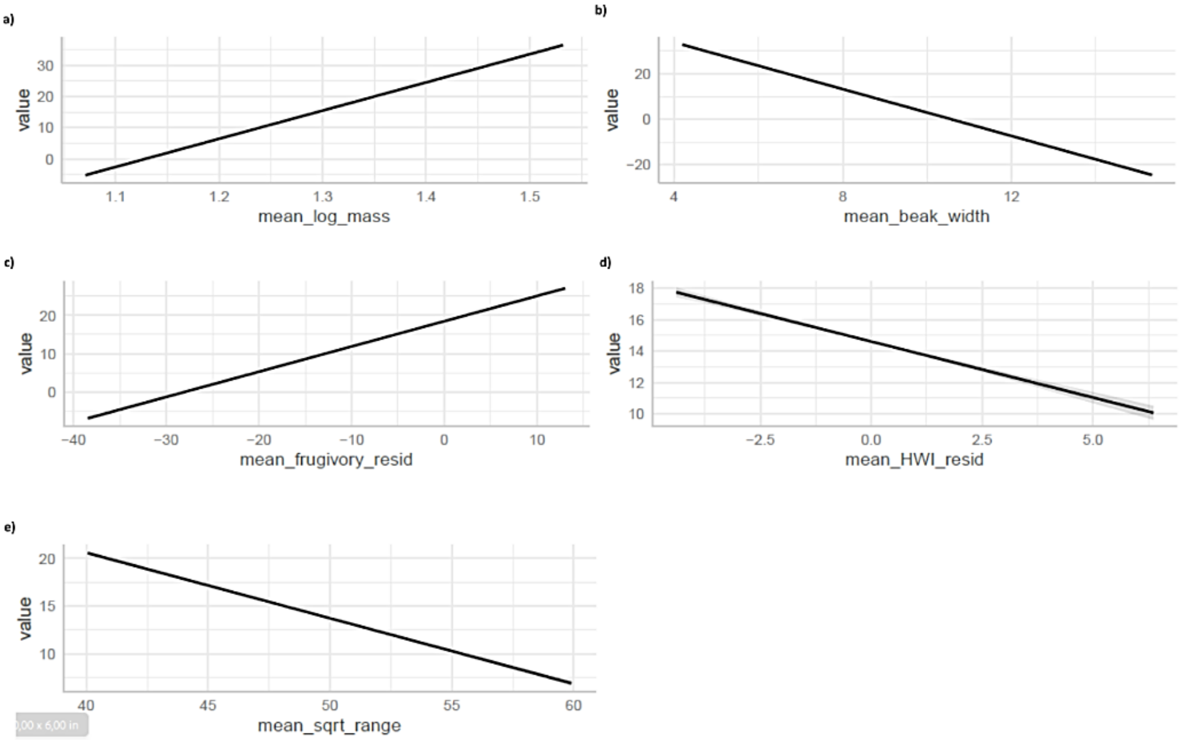
B.2) Optimistic – Number of plant species



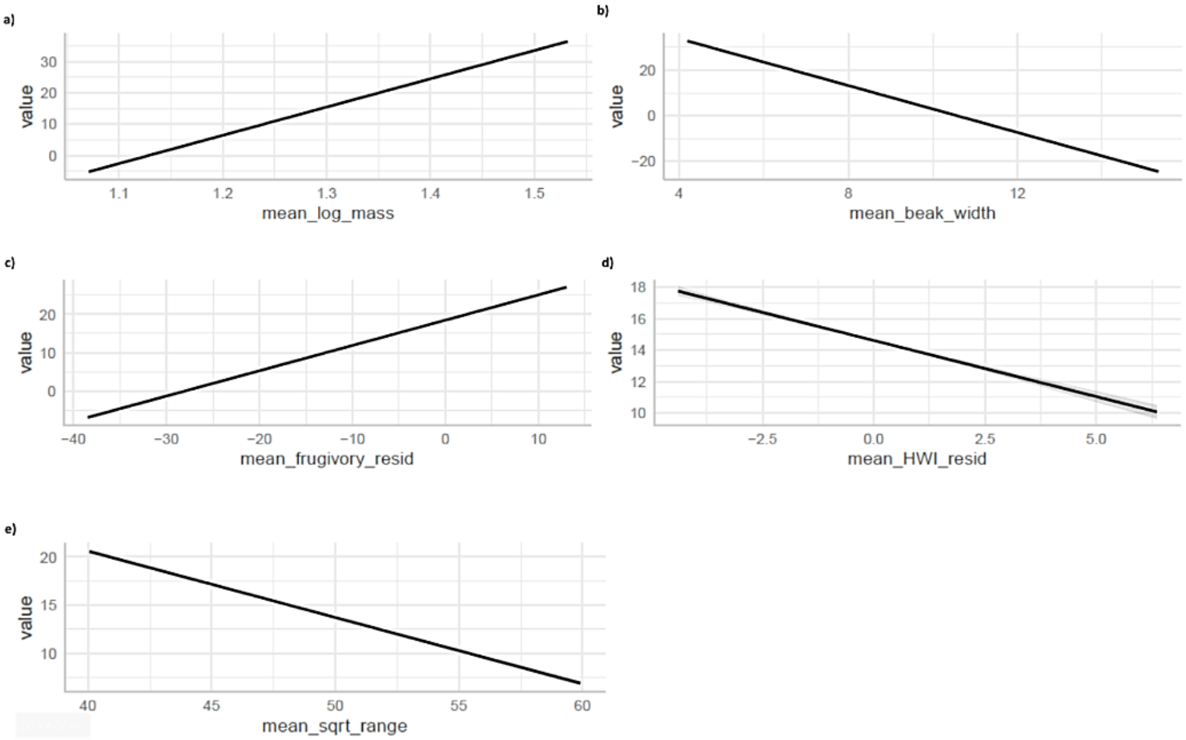
B.3) Optimistic – Links per species



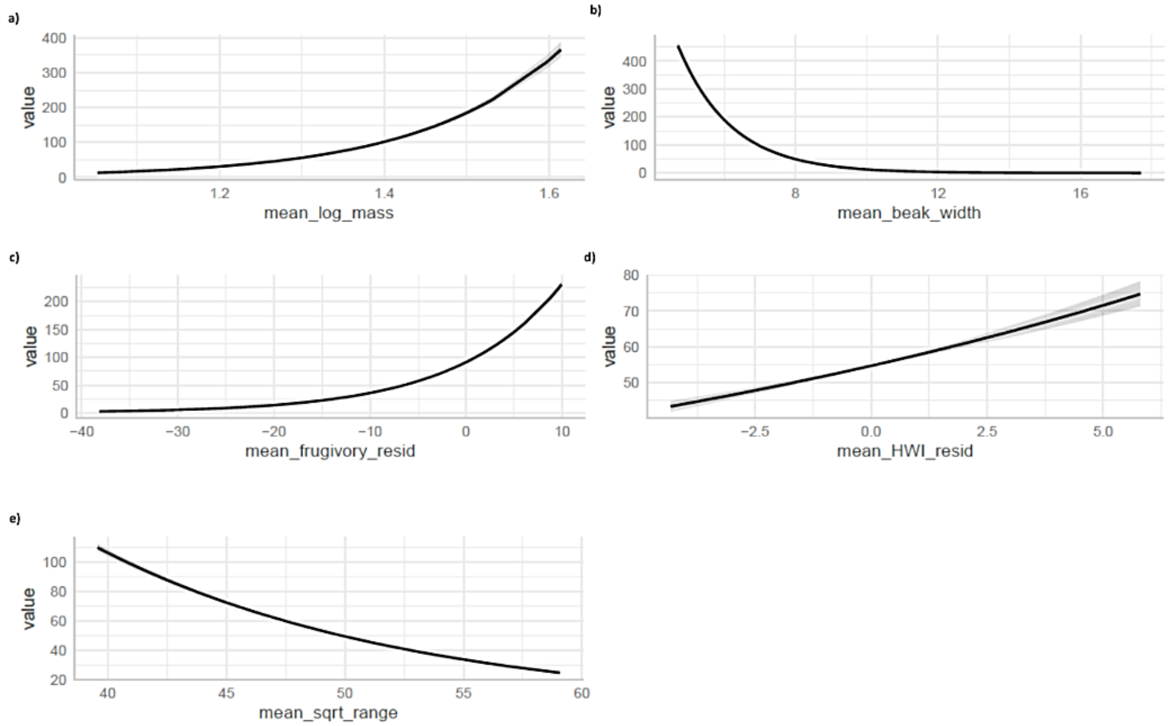
B.4) Optimistic – Generality



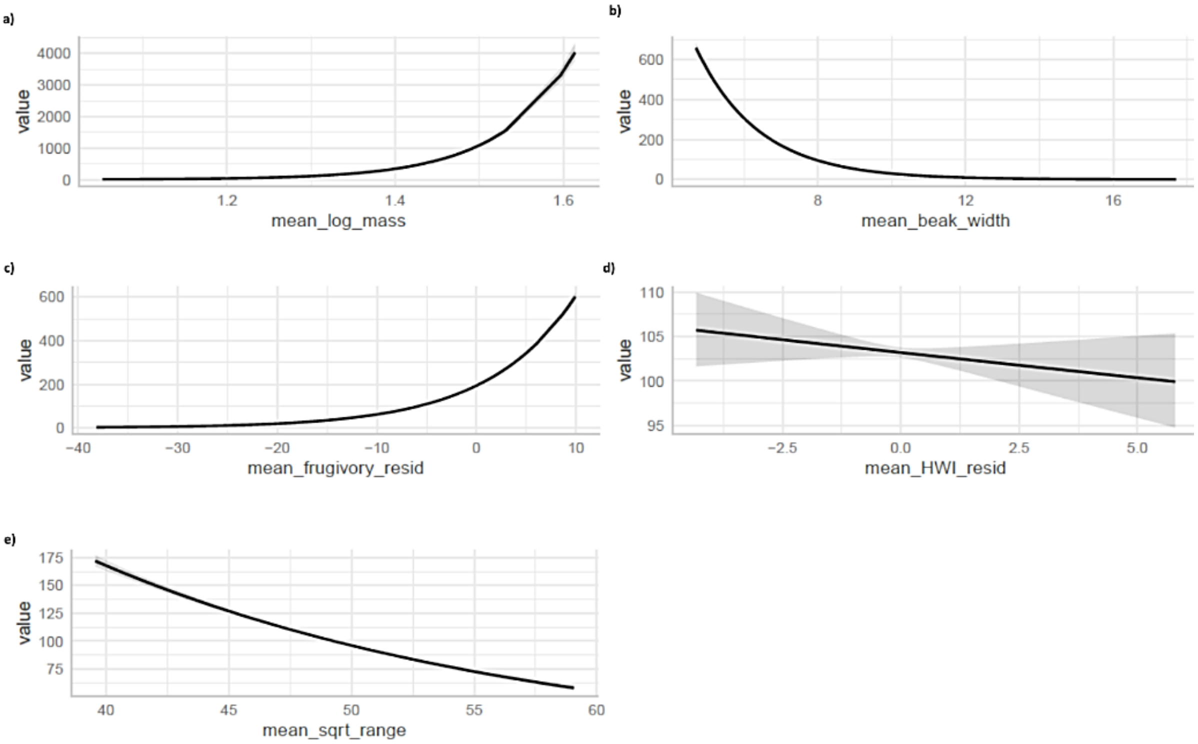
B.5) Optimistic – Vulnerability



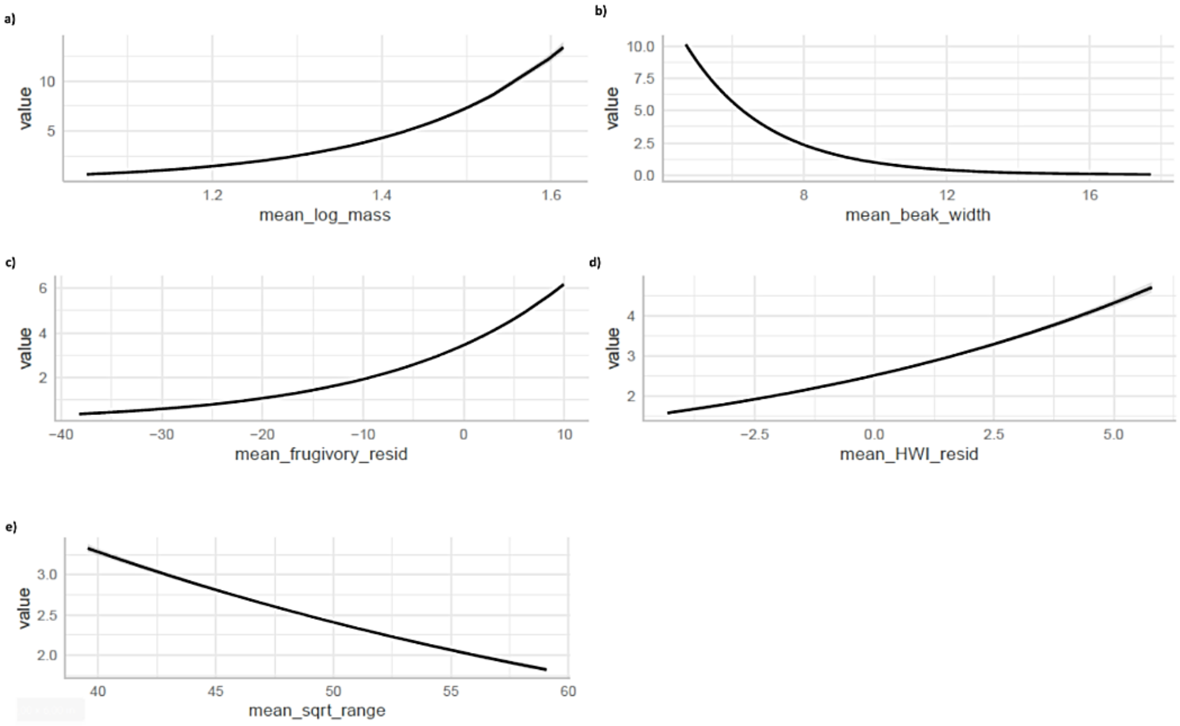
C.1) Pessimistic – Number of bird species



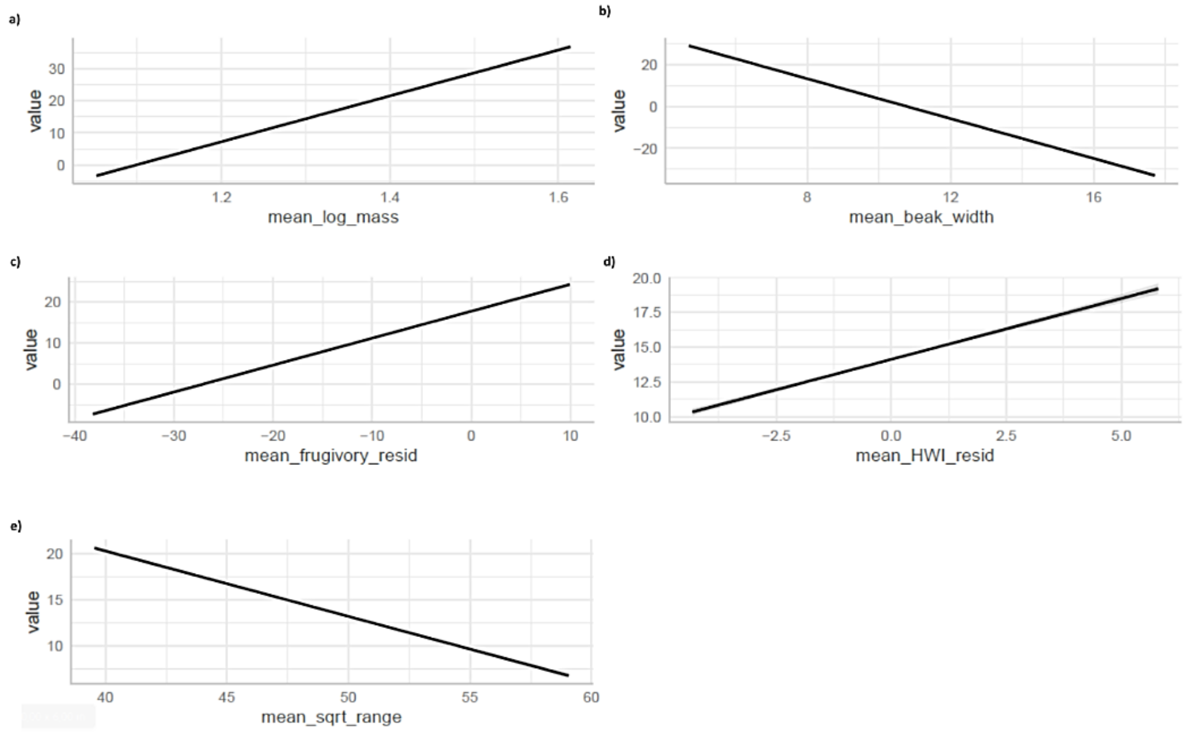
C.2) Pessimistic – Number of plant species



C.3) Pessimistic – Links per species

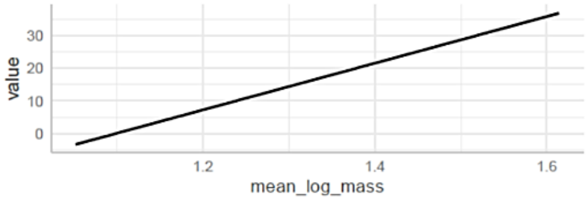


C.4) Pessimistic – Generality

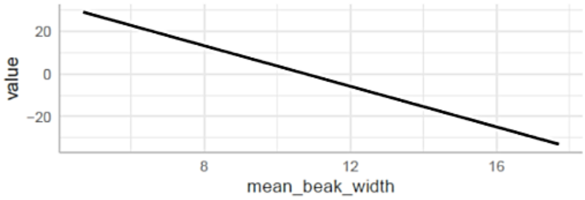


C.5) Pessimistic – Vulnerability

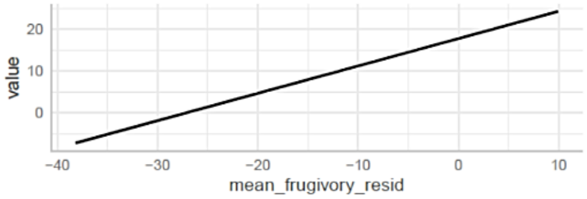
a)



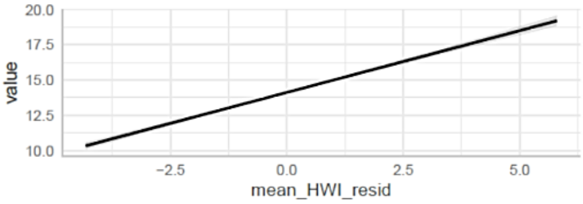
b)



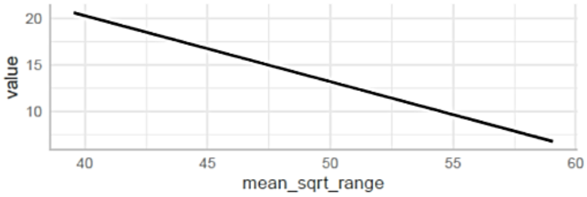
c)



d)



e)



Supplementary Table 5 – Complete model diagnostics. All models converged.

Scenario	**Model**	**AIC**	**logLik**	**Family**
Present	Number of bird species	589894.9	-294940	nbinom2
Present	Number of plant species	673730.2	-336858	nbinom2
Present	Links per species - binary	12	-2.73E-16	binomial
Present	Links per species - positive	136927.7	-68456.9	Gamma
Present	Generality	322908.7	-161447	gaussian
Present	Vulnerability	322908.7	-161447	gaussian
Optimistic	Number of bird species	620380	-310183	nbinom2
Optimistic	Number of plant species	709118.6	-354552	nbinom2
Optimistic	Links per species - binary	12	-4.27E-16	binomial
Optimistic	Links per species - positive	176834.2	-88410.1	Gamma
Optimistic	Generality	393526.9	-196756	gaussian
Optimistic	Vulnerability	393526.9	-196756	gaussian
Pessimistic	Number of bird species	614097.5	-307042	nbinom2
Pessimistic	Number of plant species	707580.6	-353783	nbinom2
Pessimistic	Links per species - binary	12	-4.78E-16	binomial
Pessimistic	Links per species - positive	175290.3	-87638.1	Gamma
Pessimistic	Generality	397580.8	-198783	gaussian
Pessimistic	Vulnerability	397580.8	-198783	gaussian

Supplementary Table 6 – Results of Variance Inflation Factor (VIF) analysis of generalized linear mixed models (GLMMs) GLMM for all network metrics across scenarios. All terms presented are the mean value of traits; body mass was logarithmized, range size is presented as its square root; frugivory degree and HWI were residualized by body mass.

Scenario	**Model**	**Term**	**Vif**
Present	Number of bird species	body mass	2.192458
Present	Number of bird species	beak width	2.351085
Present	Number of bird species	frugivory	1.818311
Present	Number of bird species	HWI	1.164103
Present	Number of bird species	range size	1.992426
Present	Number of plant species	body mass	2.192458
Present	Number of plant species	beak width	2.351085
Present	Number of plant species	frugivory	1.818311
Present	Number of plant species	HWI	1.164103
Present	Number of plant species	range size	1.992426
Present	Links per species - binary	body mass	2.192458
Present	Links per species - binary	beak width	2.351085
Present	Links per species - binary	frugivory	1.818311
Present	Links per species - binary	HWI	1.164103
Present	Links per species - binary	range size	1.992426
Present	Links per species - positive	body mass	2.192458
Present	Links per species - positive	beak width	2.351085
Present	Links per species - positive	frugivory	1.818311
Present	Links per species - positive	HWI	1.164103
Present	Links per species - positive	range size	1.992426
Present	Generality	body mass	2.192458
Present	Generality	beak width	2.351085
Present	Generality	frugivory	1.818311
Present	Generality	HWI	1.164103
Present	Generality	range size	1.992426
Present	Vulnerability	body mass	2.192458
Present	Vulnerability	beak width	2.351085
Present	Vulnerability	frugivory	1.818311
Present	Vulnerability	HWI	1.164103
Present	Vulnerability	range size	1.992426
Optimistic	Number of bird species	body mass	1.791797
Optimistic	Number of bird species	beak width	1.850053
Optimistic	Number of bird species	frugivory	1.354434
Optimistic	Number of bird species	HWI	1.103769
Optimistic	Number of bird species	range size	1.518266
Optimistic	Number of plant species	body mass	1.791797
Optimistic	Number of plant species	beak width	1.850053
Optimistic	Number of plant species	frugivory	1.354434

Scenario	**Model**	**Term**	**Vif**
Optimistic	Number of plant species	HWI	1.103769
Optimistic	Number of plant species	range size	1.518266
Optimistic	Links per species - binary	body mass	1.791797
Optimistic	Links per species - binary	beak width	1.850053
Optimistic	Links per species - binary	frugivory	1.354434
Optimistic	Links per species - binary	HWI	1.103769
Optimistic	Links per species - binary	range size	1.518266
Optimistic	Links per species - positive	body mass	1.791797
Optimistic	Links per species - positive	beak width	1.850053
Optimistic	Links per species - positive	frugivory	1.354434
Optimistic	Links per species - positive	HWI	1.103769
Optimistic	Links per species - positive	range size	1.518266
Optimistic	Generality	body mass	1.791797
Optimistic	Generality	beak width	1.850053
Optimistic	Generality	frugivory	1.354434
Optimistic	Generality	HWI	1.103769
Optimistic	Generality	range size	1.518266
Optimistic	Vulnerability	body mass	1.791797
Optimistic	Vulnerability	beak width	1.850053
Optimistic	Vulnerability	frugivory	1.354434
Optimistic	Vulnerability	HWI	1.103769
Optimistic	Vulnerability	range size	1.518266
Pessimistic	Number of bird species	body mass	1.928278
Pessimistic	Number of bird species	beak width	2.008676
Pessimistic	Number of bird species	frugivory	1.310236
Pessimistic	Number of bird species	HWI	1.208811
Pessimistic	Number of bird species	range size	1.510315
Pessimistic	Number of plant species	body mass	1.928278
Pessimistic	Number of plant species	beak width	2.008676
Pessimistic	Number of plant species	frugivory	1.310236
Pessimistic	Number of plant species	HWI	1.208811
Pessimistic	Number of plant species	range size	1.510315
Pessimistic	Links per species - binary_	body mass	1.928278
Pessimistic	Links per species - binary	beak width	2.008676
Pessimistic	Links per species - binary	frugivory	1.310236
Pessimistic	Links per species - binary	HWI	1.208811
Pessimistic	Links per species - binary	range size	1.510315

Scenario	Model	Term	Vif
Pessimistic	Links per species - positive	body mass	1.928278
Pessimistic	Links per species - positive	beak width	2.008676
Pessimistic	Links per species - positive	frugivory	1.310236
Pessimistic	Links per species - positive	HWI	1.208811
Pessimistic	Links per species - positive	range size	1.510315
Pessimistic	Generality	body mass	1.928278
Pessimistic	Generality	beak width	2.008676
Pessimistic	Generality	frugivory	1.310236
Pessimistic	Generality	HWI	1.208811
Pessimistic	Generality	range size	1.510315
Pessimistic	Vulnerability	body mass	1.928278
Pessimistic	Vulnerability	beak width	2.008676
Pessimistic	Vulnerability	frugivory	1.310236
Pessimistic	Vulnerability	HWI	1.208811
Pessimistic	Vulnerability	range size	1.510315

General Conclusions

This thesis explores how avian functional traits and climate conditions shape mutualistic interactions across spatial and temporal scales in the Atlantic Forest, combining network theory, trait-based ecology, and climate projections. By integrating species-level and network-level analyses, we show that avian traits are powerful predictors of both current and future patterns of frugivory, influencing key structural features of seed-dispersal networks.

In Chapter 1, we demonstrate that species strength and centrality metrics in the frugivory metanetwork are primarily shaped by frugivory degree, range size, and the dispersal-related trait HWI (hand-wing index). Strong seed dispersers tend to be highly frugivorous with lower HWI, suggesting lower dispersal capacity but stronger and more frequent interactions with fruiting plants. In contrast, species with large geographic ranges, often generalist and disturbance-tolerant, are central connectors in the metanetwork, bridging distant subnetworks and supporting cohesion at the biome scale. These findings highlight the complementary roles of specialist and generalist species in maintaining mutualistic networks under environmental heterogeneity.

Key frugivorous bird species, such as *Turdus rufiventris*, *Turdus albicollis*, *Chiroxiphia caudata*, and *Penelope obscura*, emerge as both central and strong partners, reinforcing their role as potential keystone seed dispersers in the Atlantic Forest. This aligns with global metanetwork findings (Moulatlet et al. 2023), where widespread Neotropical genera like *Turdus* and *Tangara* consistently show high centrality and interaction frequency, suggesting functional redundancy and stability across scales. These species often thrive in disturbed or fragmented habitats, making them essential for restoring and sustaining ecosystem processes like seed dispersal in defaunated landscapes (Galetti et al. 2013; Carreira et al. 2020; Fuzessy et al. 2022).

In Chapter 2, we developed a novel analytical framework to calculate spatially explicit network metrics using interaction records and species distribution models. This tool allowed us to investigate how climate variables interactively influence frugivory network structure in the Atlantic Forest. The integration of spatial data on species assemblages and climate, combined with trait distributions, opens new ways for biogeographic research on mutualistic interactions.

In Chapter 3, we applied this framework to evaluate how climate change and avian traits jointly shape future seed-dispersal networks. Our projections suggest important reductions in network complexity (number of species and interaction rates) and partner diversity by 2050, especially under pessimistic climate scenarios. However, regions in the southern Atlantic Forest appear as potential climatic refugia, harboring trait-diverse bird assemblages and more resilient network configurations. Importantly, we find that some traits that confer importance to bird species today, such as body mass, frugivory degree, and range size will likely shape their future contributions to network structure. This temporal consistency suggests that trait-based indicators can serve as robust predictors of mutualistic function, even under environmental change.

Surprisingly, morphological traits like body mass and beak width showed weak or no association with species centrality or strength, a pattern also observed in other Neotropical and global metanetworks (Emer et al. 2018; Moulatlet et al. 2023). This may reflect the historical defaunation of the Atlantic Forest, where large-bodied species have become rare or extinct in many fragments. In this context, small-bodied, generalist birds have become disproportionately important regarding species-level metrics, assuming roles once played by larger frugivores (Pinto et al. 2021; Galetti et al. 2013). While this shift may maintain short-term seed dispersal, it could compromise the long-term persistence of large-seeded plant species and affect forest regeneration dynamics (Neuschulz 2016; Fuzessy et al. 2022). However, these morphological characteristics can affect network-level properties, with body mass being one of the consistently positive factors.

Overall, our findings contribute to a more nuanced understanding of how ecological and morphological traits shape species’ roles and system properties in complex networks. By revealing the spatial and temporal dynamics of trait-mediated interactions, we offer a foundation for trait-based conservation planning and scenario modeling. Future efforts should aim to incorporate plant functional traits, more detailed interaction data, and multi-trophic perspectives, especially under global change scenarios. Moreover, advancing macroecological approaches to mutualistic networks will be essential to predict cascading effects on biodiversity and ecosystem functioning across biomes.

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