

1 **Distinct functional responses of consumers and their**
2 **producers to climate drive mutualistic network**
3 **asymmetry**

4 **Gabriel Munoz¹, Paul Savary¹, W. Daniel Kissling², JP Lessard¹**

5 ¹Concordia University,
6 ²University of Amsterdam,

Corresponding author: Gabriel Munoz, gabrielmunoz1891@gmail.com

Abstract

Aim: Functional traits are often used to infer the ecological processes that determine the composition of species assemblages. However, most trait-based approaches to infer community assembly processes focus on a single trophic level. Owing to the matching of traits facilitating interactions between resource and consumer assemblages, the functional trait diversity of different trophic levels is expected to covary in space. However, differential response of consumers and producers to environmental gradients can cause a decoupling of functional diversity between trophic levels, which we coin functional trophic asymmetry. Here, we develop a metric to quantify functional trophic asymmetry (FTA) and use it to infer the processes underpinning multitrophic community assembly, and explore the role of these processes in shaping the topology of ecological networks.

Location: Neotropics.

Time period: Present.

Major taxa: Mammalian frugivores and palms.

Methods: We use digitally available data on the functional traits, pairwise mutualistic interactions, and geographic distributions of consumers (mammalian frugivores) and their producers (palms) to quantify functional trophic asymmetry for species occurring in the Neotropics. To cover major data gaps between species-level trait and interaction data, we train machine learning models to generate synthetic network data. We then use linear regression models to relate functional asymmetry to variation in climate, and to assess the influence of functional asymmetry on network specialization.

Results: Our approach generated probabilistic networks across 1,072 grid cells in the Neotropics, revealing networks with a clearly defined modular structure and substantial differences in their functional richness across trophic levels. Functional trophic asymmetry increases from regions of the Neotropics with low precipitation seasonality to regions with high precipitation seasonality. Along this same climatic gradient, network specialization is positively related to functional trophic asymmetry.

Main conclusions: Our results further suggest that mutualistic interactions between palms and mammals are mediated by matching traits and taxonomic overlap as a key assembly process at the regional scale. We conclude that increased warming and seasonal shifts in precipitation caused by global climate change could disproportionately impact specialist species while increasing functional trophic asymmetry in ecological networks.

1 Introduction

Ecologists often examine patterns of functional trait diversity to investigate community assembly processes (Ackerly, 2003; Kraft et al., 2015). To date, however, trait-based approaches in ecology often focus on a single trophic level, whereas approaches that consider multiple trophic levels remain rare (Lavorel et al., 2013; Seibold et al., 2018). An approach that considers processes operating within and between trophic levels is necessary to better understand the assembly of multitrophic communities (Allesina et al., 2008; Marjakangas et al., 2022; Saravia et al., 2022). Moreover, considering trophic interactions while studying community assembly could shed new light on processes underpinning ecological networks (Allesina et al., 2008).

Classical approaches to study community assembly rely on the concept of environmental filtering, sorting or selection, where density independent conditions constrain the functional richness of species assemblages (HilleRisLambers et al., 2012; Kraft et al., 2015; Laliberté & Legendre, 2010; Villéger et al., 2008). Functional richness

refers to the variability and relative frequency of different functional traits observed in a community. It is often used to estimate the strength of selection imposed by the environment (Kraft et al., 2008, 2015; Kraft & Ackerly, 2010). High functional richness can indicate weak environmental selection whereas low functional richness can indicate strong selection (Halpern & Floeter, 2008; Kraft et al., 2008; Paine et al., 2011). In a multitrophic context, the effects of environmental selection can cascade across trophic levels such that selection on consumer traits can shape the functional richness of their resources, modulated by their degree of reciprocal dependency or co-evolution (Guzman et al., 2019; Lavorel et al., 2013). Moreover, the same environmental gradient could exert selective pressures of different strength on communities at distinct trophic levels (Marjakangas et al., 2022). Differences in the strength of selective pressure among trophic levels could then possibly constrain the structure or topologies of trophic networks (Blüthgen et al., 2007; Dehling et al., 2020; Schleuning et al., 2012).

Inferring the relative strength of environmental selection between trophic levels requires using high-dimensional approaches that are able to deal with sparse observations for a large number of species (Rohr et al., 2010; Strydom et al., 2022). We introduce the concept of functional trophic asymmetry (FTA), which allows inferring the relative influence of environmental selection and trait matching on the composition of multitrophic assemblages (Figure 1). FTA is the difference in the richness of interaction-relevant traits between trophic levels in a multitrophic network. FTA can occur because traits mediating species interactions (i.e., interaction niches) across trophic levels can also mediate the responses of species to their abiotic environment (i.e. environmental niches) (Dehling et al., 2020; McCain & King, 2014; Moretti & Legg, 2009; Nagy et al., 2018). As an example, plant seed size determine the outcome of animal-mediated seed dispersal (Donoso et al., 2017, 2020) as well as physiological limits, such as tolerances of plant seedlings to desiccation (Hoekstra et al., 2001). High FTA could indicate differences in the strength of environmental selection over the interaction niches of distinct trophic levels within a multitrophic species assemblage. Alternatively, low FTA could indicate that the strength of the environment selection shaping interaction niches is similar between trophic levels, e.g. equally weak or equally strong (Marjakangas et al., 2022). When interactions between producers and consumers are mutualistic, low FTA could also emerge under strong trait matching and therefore indicate the influence of trait-coevolution during multitrophic community assembly (Albrecht et al., 2018; Dehling et al., 2014). By studying spatial variation in functional trophic asymmetry along environmental gradients, we could possibly identify the conditions promoting environmentally versus cross-trophic interaction- driven community assembly (Bello et al., 2023; Schleuning et al., 2020).

Frameworks linking multitrophic functional diversity to network topology along broad-scale environmental gradients are crucial to understand the effects of global change on biodiversity and ecosystem function (Bello et al., 2023; Dehling, 2018; Schleuning et al., 2014, 2020, 2023). Functional responses of consumer and producer assemblages to climate influence functional richness at the level of the multitrophic community (García et al., 2018). Because some of these traits are involved in interactions across trophic levels, the filtering of traits along environmental gradients could constrain the number of unique interactions and therefore, network topology (Albrecht et al., 2018; Emer et al., 2020; Marjakangas et al., 2022). As an example, low multitrophic functional richness could influence emergent patterns in network structure such as the specialization of multispecies interactions by limiting the relative availability of interaction partners across trophic levels (Blüthgen et al., 2006, 2007). While high levels of network specialization represent networks predominantly made of “one-to-one” interactions, low levels of network specialization represent networks with species showing predominantly “one-to-many” interactions (Blüthgen et

al., 2006; Blüthgen & Klein, 2011) (Figure 1B). One highly expected outcome is that when functional trophic asymmetry is high, networks will have low specialization. For example, take a plant community exhibiting a low richness of flower displays and which is associated with a bee community (pollinators) exhibiting a wide variety of proboscis lengths. These plants are unlikely to form “one-to-one” interactions with only a subset of bee species that have matching proboscis length. Otherwise, non-matching pollinators would have no food resource and be extirpated. By partitioning deviations from expected FTA and network specialization relationships with null models, one can separate the relative influences of processes operating between trophic levels (e.g. trait matching) and those within trophic levels (e.g. environmental selection) in network assembly (Marjakangas et al., 2022). However, the relationship between network specialization and functional trophic asymmetry has not been fully explored.

Preserving mutualistic interactions between palms and their mammalian frugivores is important to sustain biodiversity and ecosystem function in the tropics (Bogoni et al., 2020; Marques Dracxler & Kissling, 2022). Mammalian frugivores facilitate the dispersal of palm fruits, which helps to prevent local extinctions amid disturbance and to maintain biodiversity in these ecological networks (Acevedo-Quintero, Saldaña-Vázquez, et al., 2020; Dehling, 2018; Messeder et al., 2020). Exploring patterns of co-variation in the functional richness of palm and frugivore assemblages along environmental gradients is a first step in this direction. Here, we ask (1) which climatic variable(s) best explains variation in the functional richness of palms vs mammal frugivores, (2) whether differences in these relationships lead to functional trophic asymmetry, (3) where does functional asymmetry peaks in the Neotropics and (4) whether asymmetry relates to network specialization.

2 Methods

In this study, we investigated the variation of functional trophic asymmetry and network specialization along climatic gradients by gathering species-level information on traits, interactions, and distributions from literature, museum specimens, and field collections. The collected data were then processed to create synthetic networks across gridded regions of the Neotropics and to calculate functional trophic asymmetry and network specialization variables, followed by using climate data to explain the variation in these variables across the Neotropics (Figure S1).

2.1 Study system

We focused on multitrophic communities of Neotropical palms and their mutualistic, seed dispersing, mammalian frugivores. Palms (Plantae:Arecaceae), being a keystone plant family in tropical regions (Kissling et al., 2012; Onstein et al., 2017), provide fruit resources to a wide variety of vertebrate frugivores, including birds and mammals (Muñoz et al., 2019; Zona & Henderson, 1989). Frugivore mammals (Animalia:Mammalia) are among the most important palm-seed dispersers, particularly over long distances. Most frugivore mammals feeding on palms are seed eaters and pulp eaters, dispersing palm seeds mostly via ectozoochory dispersal (Messeder et al., 2020). Importantly, frugivory-related traits have notably underlain palm diversification and played a key role in the evolution of palm traits (Onstein et al., 2014, 2017).

2.2 Data collection

2.2.1 Species level geographic distribution data

We obtained binary species distribution data (present/absent) on palms from the geographic range maps of (Bjorholm et al., 2005) and on mammals from the IUCN (International Union for the Conservation of Nature) data portal. To generate local gridded multitrophic species assemblages across the Neotropics, we intersected the species-level range maps with a spatial grid where each grid cell represented every 1 by 1 degree latitude and longitude change along the extent of the entire Neotropics.

We then listed all palm and mammal frugivore species co-occurring in each grid-cell as our grid-cell level multitrophic assemblage.

2.2.2 Species level trait data

We collected species-level multitrophic trait data related to the physiological tolerance of palms and frugivorous mammals to the abiotic environment and to their mutualistic interactions. For palms, we extracted data from the PalmTraits 1.0 dataset (Kissling et al., 2019). We collected data on growth form, maximum stem height, and average fruit length. For frugivorous mammals, we obtained trait data from the EltonTraits 1.0 database (Wilman et al., 2014). We selected data on body mass, diet, and daily activities. Diet data from the EltonTraits 1.0 database is coded as percentage use distribution across ten diet categories. We excluded from our analysis species without fruit in their diet. Activity was coded as a dummy variable with three categories (Diurnal, Crepuscular, Nocturnal). Finally, body mass was coded as a numerical variable in kg. We excluded bats from the analysis as almost no Neotropical bat species is feeding on palm fruits (Messeder et al., 2020). In total, we subset from this dataset the species with available distribution range map, that is 494 palm species and 737 mammal frugivores.

2.2.3 Pairwise species level interaction data

We used data on seed dispersal interactions between palms and mammals for the Neotropics, originating from recollections of seed dispersal records found in the published literature and interaction records are recorded at the species level (Muñoz et al., 2019). Each pairwise species interaction record reflects where an article mentions the fruit or the seed of a palm being dispersed, carried or defecated by a frugivorous mammal. Interaction records collected in this database were previously vetted to reflect effective seed dispersal interactions, while avoiding those that reflect mere seed consumption (vetting criteria found in: (Muñoz et al., 2019)). In total, we gathered a total of 581 interaction records between 69 palms and 111 frugivore mammals.

2.2.4 Grid-cell level environmental data

We used bioclimatic variables from WorldClim (Fick & Hijmans, 2017) to represent large-scale spatial and temporal variation of climate in the Neotropics. Specifically, we used mean annual temperature (BIO01), total annual precipitation (BIO12), temperature seasonality (BIO04) and precipitation seasonality (BIO15). Using a moving window, we compute simple averages for every set of bioclimatic records at each grid cell, thereby re-scaling the spatial resolution of bioclimatic variables to 1 by 1 degree grid resolution from their original resolution (1 by 1 km²) to match the spatial resolution of our grid cell species-level data.

2.2.5 Continental level biogeographical data

The Neotropics is a region with a rich evolutionary history which significantly influenced patterns of species colonization and extinction across neotropical plant and animal species (Antonelli & Sanmartín, 2011; Whiteman-Jennings, 2015). The biogeographic regionalization patterns of (Morrone, 2014) distinguish seven major biogeographic regions (i.e., biogeographic dominions), we use them to delineate the spatial extent of species pools when simulating network assembly processes.

2.3 Statistical analyses

2.3.1 A probabilistic continental metaweb

Here, we fitted latent variable models that vary in their assumptions to estimate interaction probabilities from observed binary data on species interactions. Specifically: the stochastic block model (SBM), the connectance model, the trait-matching model, and the matching-centrality model (Terry & Lewis, 2020). The SBM assumes that ecological networks are modular, with species interacting more within their groups, and outputs an two incidence matrix for palm and mammal species group affiliations, and a squared matrix (Theta matrix) for interaction probabili-

ties. The connectance model posits that interactions of specialist species are subsets of those of generalist species, optimizing connectivity scores to recreate observed network patterns. The trait-matching model assumes non-random species interactions determined by trait differences, optimizing parameters along latent-trait axes. The matching-centrality model combines connectivity scores and latent-trait axes (Terry & Lewis, 2020). We fitted these models to our available interaction data and selected the model that best predicted the observed continental pattern of seed dispersal interactions. Using Youden’s J as a metric that balanced model sensitivity and specificity (Poisot, 2023), we find that SBM was the best supported model (Figure S2 A-C). Additional details about the model assumptions are explained in *Supplementary Text S1*.

2.3.2 Downscaling the continental metaweb to generate grid-cell level networks

The digitally availability of primary biodiversity data on palms and their mammalian frugivores was imbalanced, with well covered data in terms of distribution ranges, followed by well covered data on species traits, to a limited number of interaction records. Therefore, to downscale our initial metaweb to include interactions between every potentially co-occurring palms and mammal frugivore at every gridcell of the Neotropics, we use a two fold approach. First, we employed multinomial logistic regression models that aimed to predict the species level SBM model results (i.e. group affiliations) from species-level trait data. We justify the choice of multinomial logistic regression models as these can handle the prediction of non-binary outcomes, that is in our case, the labeling of SBM groupings per species. We fitted separate multinomial models for palms and mammal frugivores using a label backpropagation algorithm and a neural network engine, with 75% of the data allocated for training and the 25% remaining for testing. We used neural networks because they are useful when dealing with multicollinearity, as they can learn complex and non-linear relationships and interactions among predictor variables. This allowed us to separate the relative importance of distinct matching traits on SBM group affiliations. We extracted variable importance scores based on the combinations of the absolute values of the best fit model weights (Gevrey et al., 2003). Second, we considered as local pairwise species interaction probabilities as the product of the values from the Theta matrix from the SBM model that represent the latent interaction probabilities between species pairs within and between groups multiplied by their probability of co-occurrence (POC) in a gridcell. To represent species’ co-occurrence probabilities, we used the reciprocal distance between the centroids of species pair ranges within the grid-cell, divided by the sum of its range areas within the grid-cell. This implied that within each grid cell, species with closer range centroids and larger cumulative areas are more likely to co-occur and interact. This approach allowed us to recreate synthetic probabilistic plant-mammal frugivore networks for each grid-cell across the Neotropics, while accounting for the heterogeneity of species ranges within each grid.

2.3.3 Measuring Functional Trophic Asymmetry (FTA) and Network Specialization (H2’)

We computed Functional Trophic Asymmetry (FTA) from the results of the SBM model fit. Specifically, from the matrices representing the incidence of palm or mammal frugivore species in one of the SBM groupings. Thus, as our measure of functional richness, we calculated the number of species of each taxon across SBM groups per grid. Because we had differences in the total number of palm and mammal species across grids, we normalized species counts within gridcells. We then computed the absolute difference between trophic levels to obtain a measure of FTA for each combination of SBM groups. Because we had the potential for each palms and mammals species at each grid to become affiliated to any of 7 SBM groups, and to interact with any species of the opposite trophic level within and between groups,

we obtained a total of 49 independent FTA measures for each gridcell, one for each palm-mammal group combination.

We measured network specialization at each grid cell using the metric H2'. H2' is a network-level index that describes the degree of specialization of interactions between species (Blüthgen et al., 2007). High values indicate networks that are more specialized, meaning that specialist species from one trophic level interact with specialist species from the opposite trophic level. Low H2' values indicate networks among generalists, meaning that there is a low specificity of interactions between species across trophic levels. Because inferred networks varied in their network size (i.e., number of unique interactions between palms and mammals), we rarefied the computation of H2' to networks of the same absolute size per gridcell, resampling networks to the same number of pairwise interactions (100) at each grid-cell 999 times (Terry & Lewis, 2020). We selected the median of this H2' distribution as our gridcell level measure of network specialization.

We assessed the deviance of 'observed' FTA and H2' from null models that simulated stochastic community assembly processes (Dormann et al., 2009). We created these null models by constructing networks of interactions between a randomized set of palms and mammals for each gridcell and computing expected values of FTA and H2'. To do this for a given gridcell, we identified their biogeographic domain (from (Morrone, 2014)) and randomly sampled 10 palm and mammal species, ensuring each species is selected only once. To this subsampled species set, we used the same procedures to calculate FTA and H2' and replicated the process 999 independent times to obtain a distribution of expected FTA and H2' values. Finally, we computed the deviance between observed and expected values with Z-scores.

2.3.4 Assessing the influence of climate in Functional Trophic Asymmetry

We fitted linear regression models to investigate the influence of climate to Functional Trophic Asymmetry. We used FTA z-scores as response variables and the four climatic predictor variables: Mean Annual Temperature (Temp), Total Annual Precipitation (Prec), Temperature Seasonality (TS), and Precipitation Seasonality (PS) as predictor variables. In addition, we included the identity of the SBM palm-mammal group combination as an interaction term. Prior to fitting the models, we scale-transformed the climatic variables such that they all share the same mean but only differ in their standard deviation.

2.3.5 Assessing the influence of Functional Trophic Asymmetry in Network Specialization

We fitted linear regression models to investigate the effects of Functional Trophic Asymmetry in Network specialization. We used the average (mean) and standard deviation (sd) of FTA across all gridcells and SBM combinations as our predictor variables. By including both as predictors, the model accounts for not only the overall asymmetry but also its distribution among SBM groupings. We used the rarefied gridcell records of H2' as our response variable. To assess model significance, we compared the estimates of this model to a distribution of expected model coefficients from fitting the same linear model for each of the null network assembly replicates.

3 Results

3.1 The structure of mutualistic networks between palms and their mammalian frugivores across the Neotropics

The SBM model organized the continental set of palm and mammal species into a matrix sorting species into seven SBM groups and an accompanying matrix that quantified interaction probabilities between and within groups. In our model, there was a 1.74 fold increase in the likelihood of interactions between species within SBM groups rather than between SBM groups (Figure 2A). For palms, important trait

variables that predicted SBM group affiliation were palm fruit length, maximum stem height, and palm growth form (*Acaulescent* or *Erect*) (Figure S3-A). For mammals, important trait variables to predict species group affiliations were mammal activity, the logarithm of the *body mass*, and percentage of frugivory on diet as predictor variables (Figure S3-B). These analysis revealed that SBM group assortments represent communities of palms (Figure S4) and mammal frugivores (Figure S5) with unique trait combinations within the high-dimensional multitrophic spectrum of interaction-relevant traits. Our approach to downscale a continental metaweb was able to generate probabilistic networks between palms and mammalian frugivores for 1,072 grid cells across the Neotropics. Each network had in average nine interaction partners per species ($sd = 5.62$), 27 mammals per grid cell ($sd = 14.97$), and 11 palms per grid cell ($sd = 11.42$).

3.2 Differences in trait-climate relationships across trophic levels lead to Functional Trophic Asymmetry

FTA z-scores (Figure 2B) indicate that in average FTA was less than the FTA expected in a null model. Out of the 49 SBM group combinations, those with less than expected asymmetries are generally between palms in groups 1, 2, and 5 and mammals in groups 6 and 3. Conversely, combinations with significantly greater than expected asymmetries are generally found between palms in SBM groups 6 and 4 and mammals in SBM groups 1, 2, and 5. FTA peaks in tropical and mountainous regions while being lower in more temperate areas of the Neotropics, and remains stable throughout tropical and humid regions (Figure 2A). The results of our linear model shows significant differences in FTA among SBM groups. In addition, it shows a relationship between the spatial variation of climate and FTA. However, the significance and direction of effects vary as a function of the SBM group combinations (Figure 2B, Table 1). While the overall fixed model estimates do not show significant effects of climatic variation in FTA across all SBM group combinations [Temp (Mean annual temperature) ($\beta = 0.0051$, $p = 0.859$), Prec (Total annual precipitation) ($\beta = -0.0364$, $p = 0.384$), TS (Temperature Seasonality) ($\beta = -0.0180$, $p = 0.746$), and PS (Precipitation Seasonality) ($\beta = -0.0507$, $p = 0.250$)]; for specific group combinations, FTA is significantly predicted by climate, particularly by changes in Precipitation Seasonality (Figure S6). Approximately 59% of the variability in the FTA z-score is explained by the linear model with our climate predictors as fixed effects and SBM group identity as interaction terms (adjusted R-squared = 0.59).

On one hand, group combinations exhibiting a positive relationship between FTA and precipitation seasonality are characterized by a relatively stable functional richness of mammals across gradients of precipitation seasonality, while the functional richness of palms increases under these conditions (Figures S6, S7). A significant portion of this pattern can be attributed to turnover within the palm community of SBM group 6, which predominantly consists of small to medium-sized drupes or berries. These palms, which belong to genera such as *Acrocomia*, *Allagoptera*, and *Astrocaryum* are typically of tropical origin and display diverse growth forms, including both erect and acaulescent. Conversely, group combinations showing a negative association between FTA and precipitation seasonality are primarily driven by patterns in the palm community of SBM group 5 (Figures S6, S7). In this scenario, while the functional richness of mammals remains stable, the functional richness of these palms, generally characterized by species with erect growth forms and large fruits, increases in regions with low precipitation seasonality.

3.3 Functional Trophic Asymmetry increases Network Specialization

We found overall, palm-mammalian frugivore networks had low specialization, H2' ranged from 0.12 to 0.25. In addition, there was a significant relationship between aggregated gridcell records of Functional Trophic Asymmetry and H2' metric. Specifically, FTA z-scores increased H2' by 3.28 units per mean unit increase across all

SBM groups. Additionally, the standard deviation of FTA z-scores decreased H2' by 1.01 units per unit increase across all SBM groups (SD FTA). While this linear model explained only around 8.7% of the total spatial variability in H2' (adjusted R-squared = 0.087), the results of our simulations show that the intercept and slope estimates are statistically significant from null assembly models (Figure S7).

4 Discussion

Our approach unveils novel insights into the assembly of mutualistic networks by making use of digitally available primary biodiversity data at broad scales. By identifying species of palms and mammals with similar interaction patterns, we can offer a more nuanced understanding of network assembly dynamics within these multitrophic communities. The observed Functional Trophic Asymmetry (FTA) across different climatic regions of the Neotropics underscores the importance of contemporary climate change in shaping interaction niches across species' distributional ranges. Precipitation seasonality emerging as a key predictor of FTA in certain SBM palm and mammal group combinations, where higher FTA increase overall network specialization.

The delineation of interactions into distinct groups indicates that, at a continental scale, the network of seed dispersal interactions is highly compartmentalized. This finding aligns with previous work reporting significant modularity in palm seed dispersal interactions across the Neotropical continent. Muñoz et al. (2019) In our study, we extend this understanding by identifying palm growth form and mammal foraging activity periods as key palm and animal traits driving this broad scale modularity through changes in functional richness. While our analysis revealed a higher probability of pairwise species interactions occurring within Stochastic Block Model (SBM) groups, interactions between SBM groups are not at all improbable. The observed distribution of interaction probabilities within and between SBM groups highlights multitrophic assemblages being central to the entire metaweb, notably the palm and mammal species in SBM groups 5 and 6, which are those with extensive distributional ranges and more generalist diets. Conversely, it also identifies peripheral groups, such as species in SBM groups 1-3, which exhibit narrower interaction niches. These peripheral species assemblages which may correspond to those species with restricted ranges or specialized diets. Indeed, SBM groups 5-6 include larger, nocturnal mammals that feed on palms with varying fruit sizes and growth forms, ranging from erect to acaulescent, whereas SBM groups 1-3 predominantly consist of smaller, diurnal mammals that consume small fruits from erect palms.

Communities of similarly interacting species obtained from SBM models have been shown to reflect ecological factors, such as the spatio-temporal segregation of species assemblages and the differentiation of interaction niches Durand-Bessart et al. (2023). Our linear model highlights Precipitation Seasonality as a key factor influencing Functional Trophic Asymmetry (FTA) across SBM groupings. This suggests that spatial variation in interaction niches emerges from the differences in the strength of environmental selection between trophic levels. Such uneven pressures result in multitrophic assemblages where not all trait combinations align optimally with the global preferences of their co-occurring interaction partners, thus contributing to promote structural diversity in seed dispersal networks across Neotropical sites. For example, mammalian frugivores, which can exhibit a broad tolerance for varying levels of precipitation seasonality, may predominantly consume small-fruited palms in regions with high precipitation seasonality. This is likely because palms with smaller fruits are better adapted to thrive under conditions of variable water availability. Consequently, this ecological scenario is expected to result in increased FTA, driven by the restricted functional richness of available resources for consumers. Similarly, palms with larger fruit sizes and predominantly erect growth forms consumed by large sized frugivores might reflect adaptations to attract high

quality animal seed disperses in environments where consistent water availability promotes higher habitat complexity and plant competition. Consequently, this ecological scenario is expected to result in increased FTA, driven by the restricted functional richness of available consumers relative to producers. In both cases, FTA imposes limits over trait matching between partners of distinct trophic levels and the partitioning of interaction niches within species of the same trophic level.

Having a low degree of specialization in palm-mammal frugivore seed dispersal networks is not entirely unexpected given the historical ecological shifts that these species have experienced in the Neotropics. Unlike other major tropical regions, such as the Afrotropics and South-East Asia, the Neotropics had significant post-Pleistocene extinctions, which heavily altered mammalian communities. These extinctions, which impacted disproportionately to mammal megafauna, likely exacerbate competition and extinction rates among their large-fruited palm partners, particularly in those regions with high mammal diversity and endemism. Webb (2006); Whiteman-Jennings (2015) Concurrently, the radiation of small-fruited palm taxa Onstein et al. (2014); Onstein et al. (2017) further contributed to the decoupling of trait diversity between palms and mammals and the re-structuring of seed dispersal networks across trophic levels in the Neotropics. Without this trait decoupling due the co-evolutionary dynamics between palms and mammal frugivores may have remained unaltered, fostering otherwise more specialized networks.

The positive estimate for mean FTA suggests a strong positive influence of FTA on $H2'$, thus promoting network specialization. In contrast, the negative estimate for FTA standard deviation (SD) indicates that a large variation in FTA within SBM group combinations significantly reduces $H2'$, implying more generalist interactions. This suggest, that while overall higher FTA promotes network specialization, an inconsistent FTA across SBM groups can disrupt this pattern, making network structure less predictable from multitrophic trait patterns. Previous research in insular regions where trophic communities are often subject to asymmetric filtering strengths have shown that the specialization of mutualistic networks can indeed be resilient to shifts in the degree of ecological filters between trophic levels. Particularly, if the networks are well supported by generalist species (Schleuning et al., 2012; Schleuning et al., 2016). It is therefore critical to consider changes in the underlying network structure when evaluating potential effects that climate-driven species or species trait losses have in ecosystem function Classen et al. (2020)

We validated the statistic significance of the model parameters through null simulations of network assembly,. However, it is noteworthy that our null models are limited to presence/absence permutations. Therefore, the potential influence of varying species relative abundances across sites was not considered in this study. It is well established that population-density dependent effects can modify interaction probabilities from trait matching and range co-occurrences [Peña et al. (2023), Donoso et al. (2017), McFadden et al. (2022)] Future studies should aim to incorporate species abundance estimates when defining interaction probabilities. However, despite ongoing efforts, such data is not readily available for multiple species at different trophic levels, and at broad spatial scales. Our results help elucidate mechanisms that contribute towards a broader theory of multitrophic community assembly. However, given the current limitation in obtaining reliable species abundance data, we advise caution when utilizing our data pipelines for making finer-scale spatial predictions of network assembly and interaction diversity. Similarly, the use biogeographic domains to delineate the species pools in the construction of our null models respects ecological theory and considers both historical and regional species pools [McFadden et al. (2022), Carstensen et al. (2013), Cornell & Harrison (2014)]. However, one critical assumption of this approach is that species within each biogeographic dominion are all equally likely to colonize a given community [Lessard et al. (2012)] While this assumption may simplify the computational complexity of our algorithms,

future work could penalize dispersal distances with landscape level variables such as the slope terrain [Préau et al. (2022); Schlägel et al. (2020)]. Finally, the clustering of interactions captured by the SBM may be also capturing reveal relatively unexplored drivers of interaction assembly, such as phylogenetic niche conservatism [Ackerly (2003); Wiens & Graham (2005); Pyron et al. (2015)], where closely related species retain similar ecological traits over evolutionary time, and/or the widespread extinctions of large mammals frugivores and the rapid trait speciation of small fruited palms (Donoso et al., 2020; Lim et al., 2020; Onstein et al., 2017) . Partitioning these aspects and their relative influences in delineating SBM group assignments can be future research avenues to better understand the underlying mechanisms behind mutualistic interaction patterns in space and time.

Unraveling the complexity of network assembly processes across broad spatial scales requires continous development and refining of statistical workflows and biodiversity data pipelines that integrate digitally available data from diverse sources (Kissling et al., 2012; Thuiller et al., 2024) Continued field collection, their open-release, and data standardization is crucial if we want to expand our capacity to training models capable of predicting ecological network structures at a global scale with a high degree of spatial and/or temporal resolution(Poisot et al., 2016, 2021). While many of these modelling approaches are in early development, their success hinges on the availability and reliability of foundational data. We have demonstrated that with sparse data across large scales, novel models can indeed be developed. Filling global data gaps and leveling data completeness across species ranges, traits, and interactions can certainly enhance predictive accuracy. While our case study has a history of digitally available natural history data on both palms and mammal frugivores, such comprehensive datasets are not available for many other tropical clades. We thus advocate for increased awareness, action, and funding for global biodiversity programs that collect and digitize natural records, thus enabling the continous development of large-scale spatially explicit predictive models that inform about mechanisms of network assembly, and their relationship to climate and ecosystem function.

5 Data Accessibility Statement

Data is available at...

6 References

7 Tables

Table 1: Linear regression analysis of the relationship between Bioclimatic Predictors (Mean Annual Temperature, Total Annual Precipitation, Precipitation Seasonality, Temperature Seasonality) and Functional Trophic Asymmetry within SBM groups (p1m1 - p7m7). Statistically significant effects ($p < 0.05$) are marked with (*). Beta correspond to the variable effect coefficient in the model and SE correspond to the standard error.

Characteristic	Beta ¹	SE ²
Mean Annual Temperature	0.01	0.029
SBM group		
p1m1	—	—
p1m2	-0.65***	0.035
p1m3	-0.50***	0.035
p1m4	0.00	0.035
p1m5	-1.5***	0.035
p1m6	0.57***	0.035
p1m7	0.00	0.035
p2m2	0.77***	0.035

p2m3	0.42***	0.035
p2m5	-2.0***	0.035
p2m6	0.84***	0.035
p3m1	-1.4***	0.035
p3m2	-1.7***	0.035
p3m3	-1.5***	0.035
p3m4	-1.4***	0.035
p3m5	-0.22***	0.035
p3m6	-1.8***	0.035
p3m7	-1.4***	0.035
p4m1	0.15***	0.035
p4m2	-0.12***	0.035
p4m3	-0.59***	0.035
p4m4	0.15***	0.035
p4m5	-1.8***	0.035
p4m6	0.47***	0.035
p4m7	0.15***	0.035
p5m2	0.77***	0.035
p5m3	0.42***	0.035
p5m5	-2.0***	0.035
p5m6	0.84***	0.035
p6m1	1.5***	0.035
p6m2	0.03	0.035
p6m3	0.02	0.035
p6m4	1.5***	0.035
p6m5	-2.7***	0.035
p6m6	-0.01	0.035
p6m7	1.5***	0.035
p7m1	0.37***	0.035
p7m2	-0.45***	0.035
p7m3	-0.22***	0.035
p7m4	0.37***	0.035
p7m5	-1.9***	0.035
p7m6	0.43***	0.035
p7m7	0.37***	0.035
Total Annual Precipitation	-0.04	0.042
Temperature Seasonality	-0.02	0.056
Precipitation Seasonality	-0.05	0.044
Mean Annual Temperature * SBM group		
Mean Annual Temperature * p1m2	0.01	0.040
Mean Annual Temperature * p1m3	-0.01	0.040
Mean Annual Temperature * p1m4	0.00	0.040
Mean Annual Temperature * p1m5	-0.01	0.040
Mean Annual Temperature * p1m6	0.04	0.040
Mean Annual Temperature * p1m7	0.00	0.040
Mean Annual Temperature * p2m2	0.02	0.040
Mean Annual Temperature * p2m3	-0.06	0.040
Mean Annual Temperature * p2m5	-0.01	0.040
Mean Annual Temperature * p2m6	0.02	0.040
Mean Annual Temperature * p3m1	0.05	0.040
Mean Annual Temperature * p3m2	0.04	0.040
Mean Annual Temperature * p3m3	0.06	0.040
Mean Annual Temperature * p3m4	0.05	0.040
Mean Annual Temperature * p3m5	0.05	0.040
Mean Annual Temperature * p3m6	0.06	0.040

Mean Annual Temperature * p3m7	0.05	0.040
Mean Annual Temperature * p4m1	-0.05	0.040
Mean Annual Temperature * p4m2	0.08	0.040
Mean Annual Temperature * p4m3	0.00	0.040
Mean Annual Temperature * p4m4	-0.05	0.040
Mean Annual Temperature * p4m5	0.01	0.040
Mean Annual Temperature * p4m6	0.05	0.040
Mean Annual Temperature * p4m7	-0.05	0.040
Mean Annual Temperature * p5m2	0.02	0.040
Mean Annual Temperature * p5m3	-0.06	0.040
Mean Annual Temperature * p5m5	-0.01	0.040
Mean Annual Temperature * p5m6	0.02	0.040
Mean Annual Temperature * p6m1	-0.05	0.040
Mean Annual Temperature * p6m2	0.06	0.040
Mean Annual Temperature * p6m3	0.03	0.040
Mean Annual Temperature * p6m4	-0.05	0.040
Mean Annual Temperature * p6m5	0.01	0.040
Mean Annual Temperature * p6m6	0.05	0.040
Mean Annual Temperature * p6m7	-0.05	0.040
Mean Annual Temperature * p7m1	-0.03	0.040
Mean Annual Temperature * p7m2	0.08*	0.040
Mean Annual Temperature * p7m3	0.01	0.040
Mean Annual Temperature * p7m4	-0.03	0.040
Mean Annual Temperature * p7m5	0.00	0.040
Mean Annual Temperature * p7m6	0.04	0.040
Mean Annual Temperature * p7m7	-0.03	0.040
SBM group * Total Annual Precipitation		
p1m2 * Total Annual Precipitation	0.01	0.059
p1m3 * Total Annual Precipitation	-0.05	0.059
p1m4 * Total Annual Precipitation	0.00	0.059
p1m5 * Total Annual Precipitation	0.10	0.059
p1m6 * Total Annual Precipitation	-0.08	0.059
p1m7 * Total Annual Precipitation	0.00	0.059
p2m2 * Total Annual Precipitation	0.04	0.059
p2m3 * Total Annual Precipitation	0.10	0.059
p2m5 * Total Annual Precipitation	0.10	0.059
p2m6 * Total Annual Precipitation	-0.06	0.059
p3m1 * Total Annual Precipitation	0.04	0.059
p3m2 * Total Annual Precipitation	0.04	0.059
p3m3 * Total Annual Precipitation	0.02	0.059
p3m4 * Total Annual Precipitation	0.04	0.059
p3m5 * Total Annual Precipitation	-0.11	0.059
p3m6 * Total Annual Precipitation	0.05	0.059
p3m7 * Total Annual Precipitation	0.04	0.059
p4m1 * Total Annual Precipitation	0.03	0.059
p4m2 * Total Annual Precipitation	0.00	0.059
p4m3 * Total Annual Precipitation	-0.06	0.059
p4m4 * Total Annual Precipitation	0.03	0.059
p4m5 * Total Annual Precipitation	0.10	0.059
p4m6 * Total Annual Precipitation	-0.06	0.059
p4m7 * Total Annual Precipitation	0.03	0.059
p5m2 * Total Annual Precipitation	0.04	0.059
p5m3 * Total Annual Precipitation	0.10	0.059
p5m5 * Total Annual Precipitation	0.10	0.059
p5m6 * Total Annual Precipitation	-0.06	0.059

p6m1 * Total Annual Precipitation	0.11	0.059
p6m2 * Total Annual Precipitation	0.02	0.059
p6m3 * Total Annual Precipitation	0.07	0.059
p6m4 * Total Annual Precipitation	0.11	0.059
p6m5 * Total Annual Precipitation	0.06	0.059
p6m6 * Total Annual Precipitation	-0.10	0.059
p6m7 * Total Annual Precipitation	0.11	0.059
p7m1 * Total Annual Precipitation	0.02	0.059
p7m2 * Total Annual Precipitation	-0.03	0.059
p7m3 * Total Annual Precipitation	0.06	0.059
p7m4 * Total Annual Precipitation	0.02	0.059
p7m5 * Total Annual Precipitation	0.10	0.059
p7m6 * Total Annual Precipitation	-0.05	0.059
p7m7 * Total Annual Precipitation	0.02	0.059
SBM group * Temperature Seasonality		
p1m2 * Temperature Seasonality	0.01	0.079
p1m3 * Temperature Seasonality	0.13	0.079
p1m4 * Temperature Seasonality	0.00	0.079
p1m5 * Temperature Seasonality	0.02	0.079
p1m6 * Temperature Seasonality	0.16*	0.079
p1m7 * Temperature Seasonality	0.00	0.079
p2m2 * Temperature Seasonality	0.01	0.079
p2m3 * Temperature Seasonality	-0.10	0.079
p2m5 * Temperature Seasonality	0.01	0.079
p2m6 * Temperature Seasonality	0.10	0.079
p3m1 * Temperature Seasonality	0.03	0.079
p3m2 * Temperature Seasonality	0.04	0.079
p3m3 * Temperature Seasonality	0.08	0.079
p3m4 * Temperature Seasonality	0.03	0.079
p3m5 * Temperature Seasonality	0.17*	0.079
p3m6 * Temperature Seasonality	0.04	0.079
p3m7 * Temperature Seasonality	0.03	0.079
p4m1 * Temperature Seasonality	-0.02	0.079
p4m2 * Temperature Seasonality	-0.02	0.079
p4m3 * Temperature Seasonality	0.05	0.079
p4m4 * Temperature Seasonality	-0.02	0.079
p4m5 * Temperature Seasonality	0.02	0.079
p4m6 * Temperature Seasonality	0.12	0.079
p4m7 * Temperature Seasonality	-0.02	0.079
p5m2 * Temperature Seasonality	0.01	0.079
p5m3 * Temperature Seasonality	-0.10	0.079
p5m5 * Temperature Seasonality	0.01	0.079
p5m6 * Temperature Seasonality	0.10	0.079
p6m1 * Temperature Seasonality	0.09	0.079
p6m2 * Temperature Seasonality	0.10	0.079
p6m3 * Temperature Seasonality	0.14	0.079
p6m4 * Temperature Seasonality	0.09	0.079
p6m5 * Temperature Seasonality	-0.04	0.079
p6m6 * Temperature Seasonality	0.07	0.079
p6m7 * Temperature Seasonality	0.09	0.079
p7m1 * Temperature Seasonality	-0.01	0.079
p7m2 * Temperature Seasonality	0.06	0.079
p7m3 * Temperature Seasonality	0.03	0.079
p7m4 * Temperature Seasonality	-0.01	0.079
p7m5 * Temperature Seasonality	0.01	0.079

p7m6 * Temperature Seasonality	0.11	0.079
p7m7 * Temperature Seasonality	-0.01	0.079
SBM group * Precipitation Seasonality		
p1m2 * Precipitation Seasonality	-0.05	0.062
p1m3 * Precipitation Seasonality	0.12*	0.062
p1m4 * Precipitation Seasonality	0.00	0.062
p1m5 * Precipitation Seasonality	-0.06	0.062
p1m6 * Precipitation Seasonality	0.49***	0.062
p1m7 * Precipitation Seasonality	0.00	0.062
p2m2 * Precipitation Seasonality	-0.09	0.062
p2m3 * Precipitation Seasonality	-0.09	0.062
p2m5 * Precipitation Seasonality	-0.14*	0.062
p2m6 * Precipitation Seasonality	0.39***	0.062
p3m1 * Precipitation Seasonality	0.06	0.062
p3m2 * Precipitation Seasonality	0.11	0.062
p3m3 * Precipitation Seasonality	0.11	0.062
p3m4 * Precipitation Seasonality	0.06	0.062
p3m5 * Precipitation Seasonality	0.29***	0.062
p3m6 * Precipitation Seasonality	-0.04	0.062
p3m7 * Precipitation Seasonality	0.06	0.062
p4m1 * Precipitation Seasonality	0.00	0.062
p4m2 * Precipitation Seasonality	-0.09	0.062
p4m3 * Precipitation Seasonality	0.06	0.062
p4m4 * Precipitation Seasonality	0.00	0.062
p4m5 * Precipitation Seasonality	-0.09	0.062
p4m6 * Precipitation Seasonality	0.43***	0.062
p4m7 * Precipitation Seasonality	0.00	0.062
p5m2 * Precipitation Seasonality	-0.09	0.062
p5m3 * Precipitation Seasonality	-0.09	0.062
p5m5 * Precipitation Seasonality	-0.14*	0.062
p5m6 * Precipitation Seasonality	0.39***	0.062
p6m1 * Precipitation Seasonality	0.22***	0.062
p6m2 * Precipitation Seasonality	0.19**	0.062
p6m3 * Precipitation Seasonality	0.32***	0.062
p6m4 * Precipitation Seasonality	0.22***	0.062
p6m5 * Precipitation Seasonality	-0.20**	0.062
p6m6 * Precipitation Seasonality	0.29***	0.062
p6m7 * Precipitation Seasonality	0.22***	0.062
p7m1 * Precipitation Seasonality	0.02	0.062
p7m2 * Precipitation Seasonality	-0.03	0.062
p7m3 * Precipitation Seasonality	0.09	0.062
p7m4 * Precipitation Seasonality	0.02	0.062
p7m5 * Precipitation Seasonality	-0.10	0.062
p7m6 * Precipitation Seasonality	0.40***	0.062
p7m7 * Precipitation Seasonality	0.02	0.062

¹*p<0.05; **p<0.01; ***p<0.001

²SE = Standard Error

Source: [Article Notebook](#)

Table 2: Linear regression analysis of the relationship between Functional Trophic Asymmetry and Network Specialization. Statistically significant effects (p<0.05) are marked with (*). Beta correspond to the variable effect coefficient in the model and SE correspond to the standard error.

Characteristic	Beta ¹	SE ²
----------------	-------------------	-----------------

FTA (mean)	3.3***	0.327
FTA (sd)	-1.0***	0.137

¹*p<0.05; **p<0.01; ***p<0.001
²SE = Standard Error

Source: [Article Notebook](#)

8 Figure legends and embedded figures

8.1 Figure 1

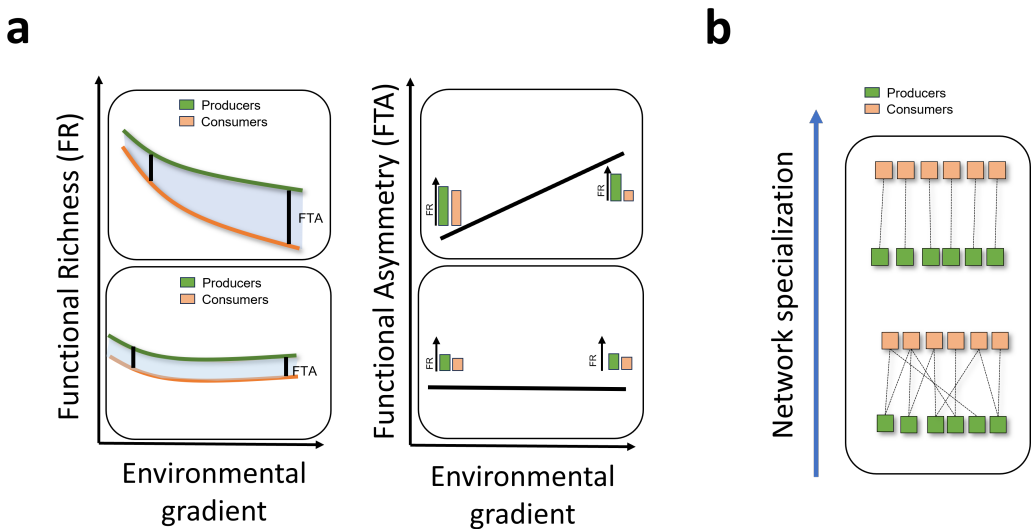


Figure 1: This conceptual model illustrates the dynamic relationship between functional diversity metrics—specifically Functional Richness (FR) and Functional Trait Asymmetry (FTA)—and environmental gradients within ecological networks. The left panel of **Figure A** visualizes the variation in FR for producers (depicted in green) and consumers (depicted in orange) along an environmental gradient. As the environmental gradient intensifies (e.g., through changes in temperature, precipitation, or habitat fragmentation), FR for both producers and consumers generally declines. However, this decline can occur at different rates, leading to two scenarios: (1) **Differential Decline in FR**: If consumer FR declines more sharply than producer FR, a substantial increase in Functional Trait Asymmetry (FTA) occurs. (2) **Parallel Decline in FR**: Alternatively, if both producer and consumer FRs decline at a similar rate, FTA remains relatively constant along the gradient. This scenario indicates a balanced impact of environmental changes across trophic levels, preserving the relative functional relationship between producers and consumers. **Figure B** shifts focus to the implications of changing FTA on network specialization—a measure of how distinct or generalized interactions are between producers and consumers within ecological networks. **Higher Specialization**: This scenario, shown on the left side of the gradient, involves more distinct producer-consumer interactions, where specific consumer species interact with particular producer species. This high specialization often correlates with low FTA, where the functional traits between interacting species are closely aligned. **Lower Specialization**: As environmental stress increases, leading to a higher FTA, the network may shift towards lower specialization. In this state, interactions become more generalized, with consumers utilizing a broader range of producers due to the loss of specific functional traits.

8.2 Figure 2

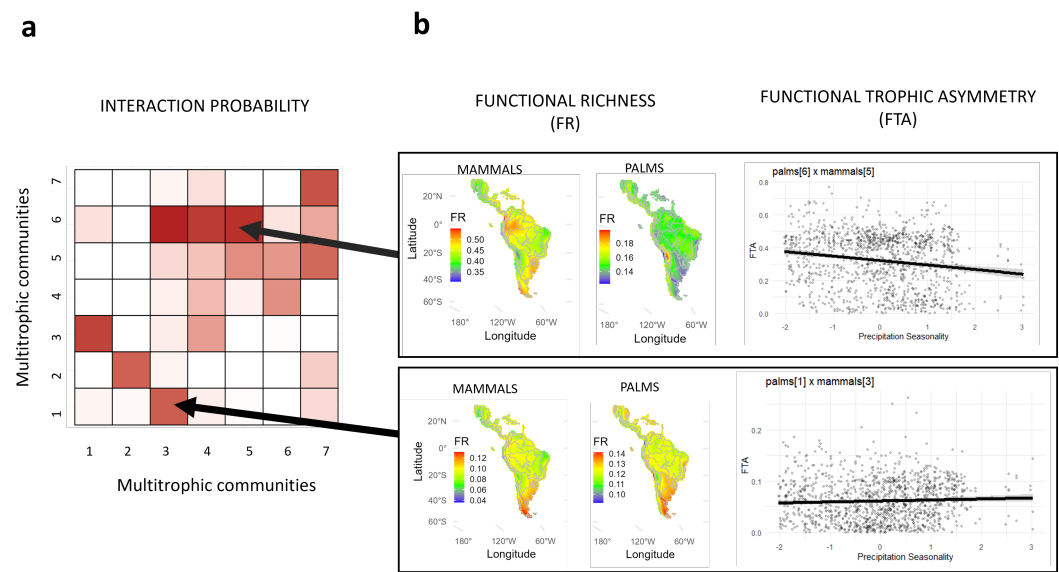


Figure 2: (A) Heatmap depicting the interaction probability among various multitrophic communities across different SBM (Stochastic block model) groups. The intensity of red shading correlates with the strength of these interactions, where darker shades signify higher probabilities of interaction between species within or between SBM groups. (B) The left panels present geographical maps illustrating the distribution of FR for both mammals and palms, identifying regions with distinct levels of functional diversity for a given multitrophic combination of species at one SBM group pair. The right panels illustrate the significant relationship observed between FTA and precipitation seasonality.

534

8.3 Figure 3

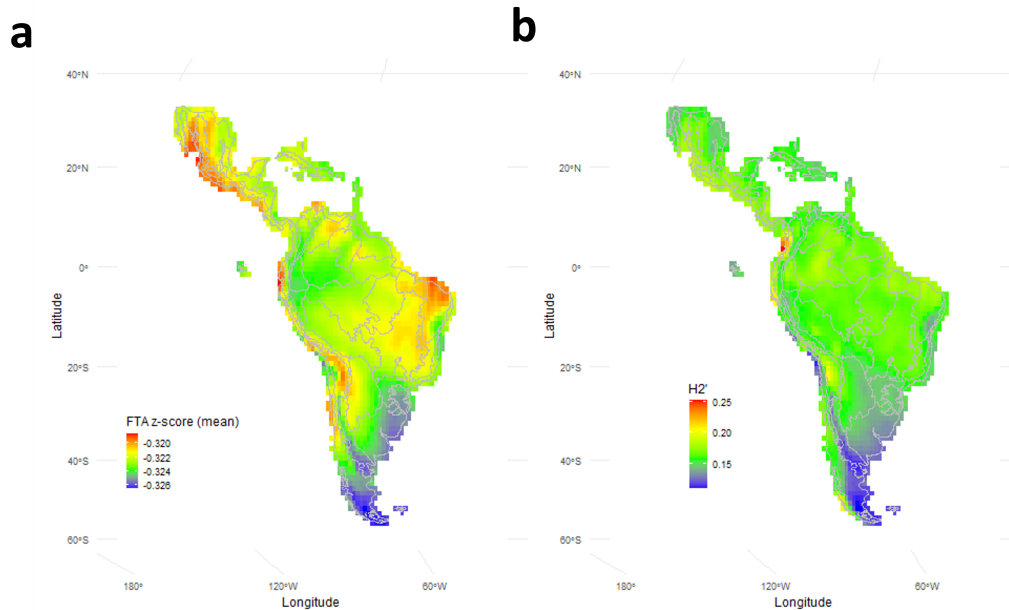


Figure 3: Spatial distribution of **(A)** FTA z-score (mean) and **(B)** H2' network specialization index across the Neotropics. Panel A depicts the geographic variation in the mean z-scores of the Functional Trophic Asymmetry (FTA). Areas with higher z-scores indicate greater asymmetry in the richness of interaction relevant traits between trophic levels, whereas lower scores suggest more balanced trait distributions. Panel B presents the spatial distribution the degree of species specialization of interactions within ecological networks. This panel reveals significant latitudinal gradients, particularly marked in the Andes and the Southern Cone.

- 535 Acevedo-Quintero, J. F., Zamora-Abrego, J. G., & García, D. (2020). From struc-
 536 ture to function in mutualistic interaction networks: Topologically important
 537 frugivores have greater potential as seed dispersers. *Journal of Animal Ecology*,
 538 89(9), 2181–2191.
- 539 Acevedo-Quintero, J. F., Saldaña-Vázquez, R. A., Mendoza, E., & Zamora-Abrego,
 540 J. G. (2020). Sampling bias affects the relationship between structural impor-
 541 tance and species body mass in frugivore-plant interaction networks. *Ecological*
 542 *Complexity*, 44, 100870.
- 543 Ackerly, D. D. (2003). Community assembly, niche conservatism, and adaptive evolu-
 544 tion in changing environments. *International Journal of Plant Sciences*, 164(S3),
 545 S165–S184.
- 546 Albrecht, J., Classen, A., Vollstädt, M. G., Mayr, A., Mollel, N. P., Schellenberger
 547 Costa, D., et al. (2018). Plant and animal functional diversity drive mutualistic
 548 network assembly across an elevational gradient. *Nature Communications*, 9(1),
 549 3177.
- 550 Allesina, S., Alonso, D., & Pascual, M. (2008). A general model for food web struc-
 551 ture. *Science*, 320(5876), 658–661.

- Antonelli, A., & Sanmartín, I. (2011). Why are there so many plant species in the neotropics? *Taxon*, 60(2), 403–414.
- Bello, C., Schleuning, M., & Graham, C. H. (2023). Analyzing trophic ecosystem functions with the interaction functional space. *Trends in Ecology & Evolution*.
- Bjorholm, S., Svenning, J.-C., Skov, F., & Balslev, H. (2005). Environmental and spatial controls of palm (arecaceae) species richness across the americas. *Global Ecology and Biogeography*, 14(5), 423–429.
- Blüthgen, N., & Klein, A.-M. (2011). Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology*, 12(4), 282–291.
- Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, 6(1), 1–12.
- Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B., & Blüthgen, N. (2007). Specialization, constraints, and conflicting interests in mutualistic networks. *Current Biology*, 17(4), 341–346.
- Bogoni, J. A., Peres, C. A., & Ferraz, K. M. (2020). Extent, intensity and drivers of mammal defaunation: A continental-scale analysis across the neotropics. *Scientific Reports*, 10(1), 14750.
- Carstensen, D. W., Lessard, J.-P., Holt, B. G., Krabbe Borregaard, M., & Rahbek, C. (2013). Introducing the biogeographic species pool. *Ecography*, 36(12), 1310–1318.
- Classen, A., Eardley, C. D., Hemp, A., Peters, M. K., Peters, R. S., Ssymank, A., & Steffan-Dewenter, I. (2020). Specialization of plant–pollinator interactions increases with temperature at mt. kilimanjaro. *Ecology and Evolution*, 10(4), 2182–2195.
- Cornell, H. V., & Harrison, S. P. (2014). What are species pools and when are they important? *Annual Review of Ecology, Evolution, and Systematics*, 45(1), 45–67.
- Dehling, D. M. (2018). The structure of ecological networks. *Ecological Networks in the Tropics: An Integrative Overview of Species Interactions From Some of the Most Species-Rich Habitats on Earth*, 29–42.
- Dehling, D. M., Töpfer, T., Schaefer, H. M., Jordano, P., Böhning-Gaese, K., & Schleuning, M. (2014). Functional relationships beyond species richness patterns: Trait matching in plant–bird mutualisms across scales. *Global Ecology and Biogeography*, 23(10), 1085–1093.
- Dehling, D. M., Peralta, G., Bender, I. M., Blendinger, P. G., Böhning-Gaese, K., Muñoz, M. C., et al. (2020). Similar composition of functional roles in andean seed-dispersal networks, despite high species and interaction turnover. *Ecology*, 101(7), e03028.
- Donoso, I., García, D., Martínez, D., Tylianakis, J. M., & Stouffer, D. B. (2017). Complementary effects of species abundances and ecological neighborhood on the occurrence of fruit-frugivore interactions. *Frontiers in Ecology and Evolution*, 133.
- Donoso, I., Sorensen, M. C., Blendinger, P. G., Kissling, W. D., Neuschulz, E. L., Mueller, T., & Schleuning, M. (2020). Downsizing of animal communities triggers stronger functional than structural decay in seed-dispersal networks. *Nature Communications*, 11(1), 1582.
- Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models: Analyzing bipartite ecological networks.
- Durand-Bessart, C., Cordeiro, N. J., Chapman, C. A., Abernethy, K., Forget, P.-M., Fontaine, C., & Bretagnolle, F. (2023). Trait matching and sampling effort shape the structure of the frugivory network in afrotropical forests. *New Phytologist*, 237(4), 1446–1462.
- Emer, C., Jordano, P., Pizo, M. A., Ribeiro, M. C., Silva, F. R. da, & Galetti, M. (2020). Seed dispersal networks in tropical forest fragments: Area effects, remnant species, and interaction diversity. *Biotropica*, 52(1), 81–89.

- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315.
- García, D., Donoso, I., & Rodríguez-Pérez, J. (2018). Frugivore biodiversity and complementarity in interaction networks enhance landscape-scale seed dispersal function. *Functional Ecology*, 32(12), 2742–2752.
- Gevrey, M., Dimopoulos, I., & Lek, S. (2003). Review and comparison of methods to study the contribution of variables in artificial neural network models. *Ecological Modelling*, 160(3), 249–264.
- Guzman, L. M., Germain, R. M., Forbes, C., Straus, S., O'Connor, M. I., Gravel, D., et al. (2019). Towards a multi-trophic extension of metacommunity ecology. *Ecology Letters*, 22(1), 19–33.
- Halpern, B. S., & Floeter, S. R. (2008). Functional diversity responses to changing species richness in reef fish communities. *Marine Ecology Progress Series*, 364, 147–156.
- HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M., & Mayfield, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, 43, 227–248.
- Hoekstra, F. A., Golovina, E. A., & Buitink, J. (2001). Mechanisms of plant desiccation tolerance. *Trends in Plant Science*, 6(9), 431–438.
- Kissling, W. D., Dormann, C. F., Groeneveld, J., Hickler, T., Kühn, I., McInerney, G. J., et al. (2012). Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography*, 39(12), 2163–2178.
- Kissling, W. D., Balslev, H., Baker, W. J., Dransfield, J., Gödel, B., Lim, J. Y., et al. (2019). PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Scientific Data*, 6(1), 178.
- Kraft, N. J., & Ackerly, D. D. (2010). Functional trait and phylogenetic tests of community assembly across spatial scales in an amazonian forest. *Ecological Monographs*, 80(3), 401–422.
- Kraft, N. J., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree community assembly in an amazonian forest. *Science*, 322(5901), 580–582.
- Kraft, N. J., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29(5), 592–599.
- Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305.
- Lavorel, S., Storkey, J., Bardgett, R. D., De Bello, F., Berg, M. P., Le Roux, X., et al. (2013). A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science*, 24(5), 942–948.
- Lessard, J.-P., Belmaker, J., Myers, J. A., Chase, J. M., & Rahbek, C. (2012). Inferring local ecological processes amid species pool influences. *Trends in Ecology & Evolution*, 27(11), 600–607.
- Lim, J. Y., Svenning, J.-C., Gödel, B., Faurby, S., & Kissling, W. D. (2020). Frugivore-fruit size relationships between palms and mammals reveal past and future defaunation impacts. *Nature Communications*, 11(1), 4904.
- Marjakangas, E.-L., Muñoz, G., Turney, S., Albrecht, J., Neuschulz, E. L., Schleuning, M., & Lessard, J.-P. (2022). Trait-based inference of ecological network assembly: A conceptual framework and methodological toolbox. *Ecological Monographs*, 92(2), e1502.
- Marques Dracxler, C., & Kissling, W. D. (2022). The mutualism–antagonism continuum in neotropical palm–frugivore interactions: From interaction outcomes to ecosystem dynamics. *Biological Reviews*, 97(2), 527–553.

- McCain, C. M., & King, S. R. (2014). Body size and activity times mediate mammalian responses to climate change. *Global Change Biology*, 20(6), 1760–1769.
- McFadden, I. R., Fritz, S. A., Zimmermann, N. E., Pellissier, L., Kissling, W. D., Tobias, J. A., et al. (2022). Global plant-frugivore trait matching is shaped by climate and biogeographic history. *Ecology Letters*, 25(3), 686–696.
- Messeder, J. V. S., Guerra, T. J., Dáttilo, W., & Silveira, F. A. (2020). Searching for keystone plant resources in fruit-frugivore interaction networks across the neotropics. *Biotropica*, 52(5), 857–870.
- Moretti, M., & Legg, C. (2009). Combining plant and animal traits to assess community functional responses to disturbance. *Ecography*, 32(2), 299–309.
- Morrone, J. J. (2014). Biogeographical regionalisation of the neotropical region. *Zootaxa*, 3782(1), 1–110.
- Muñoz, G., Trøjelsgaard, K., & Kissling, W. D. (2019). A synthesis of animal-mediated seed dispersal of palms reveals distinct biogeographical differences in species interactions. *Journal of Biogeography*, 46(2), 466–484.
- Nagy, D. D., Magura, T., Horváth, R., Debnár, Z., & Tóthmérész, B. (2018). Arthropod assemblages and functional responses along an urbanization gradient: A trait-based multi-taxa approach. *Urban Forestry & Urban Greening*, 30, 157–168.
- Onstein, R. E., Carter, R. J., Xing, Y., & Linder, H. P. (2014). Diversification rate shifts in the cape floristic region: The right traits in the right place at the right time. *Perspectives in Plant Ecology, Evolution and Systematics*, 16(6), 331–340.
- Onstein, R. E., Baker, W. J., Couvreur, T. L., Faurby, S., Svenning, J.-C., & Kissling, W. D. (2017). Frugivory-related traits promote speciation of tropical palms. *Nature Ecology & Evolution*, 1(12), 1903–1911.
- Paine, C. T., Baraloto, C., Chave, J., & Hérault, B. (2011). Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos*, 120(5), 720–727.
- Peña, R., Schleuning, M., Dalerum, F., Donoso, I., Rodríguez-Pérez, J., & García, D. (2023). Abundance and trait-matching both shape interaction frequencies between plants and birds in seed-dispersal networks. *Basic and Applied Ecology*, 66, 11–21.
- Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods in Ecology and Evolution*, 14(5), 1333–1345.
- Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict. *Functional Ecology*, 30(12), 1878–1882.
- Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., et al. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*, 48(7), 1552–1563.
- Préau, C., Dubos, N., Lenormand, M., Denelle, P., Le Louarn, M., Alleaume, S., & Luque, S. (2022). Dispersal-based species pools as sources of connectivity area mismatches. *Landscape Ecology*, 1–15.
- Pyron, R. A., Costa, G. C., Patten, M. A., & Burbrink, F. T. (2015). Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. *Biological Reviews*, 90(4), 1248–1262.
- Rohr, R. P., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling food webs: Exploring unexplained structure using latent traits. *The American Naturalist*, 176(2), 170–177.
- Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3), 630–642.
- Schlägel, U. E., Grimm, V., Blaum, N., Colanelli, P., Dammhahn, M., Eccard, J. A., et al. (2020). Movement-mediated community assembly and coexistence. *Biological Reviews*, 95(4), 1073–1096.

- Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M., et al. (2012). Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology*, 22(20), 1925–1931.
- Schleuning, M., Ingmann, L., Strauss, R., Fritz, S. A., Dalsgaard, B., Matthias Dehling, D., et al. (2014). Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecology Letters*, 17(4), 454–463.
- Schleuning, M., Fründ, J., Schweiger, O., Welk, E., Albrecht, J., Albrecht, M., et al. (2016). Ecological networks are more sensitive to plant than to animal extinction under climate change. *Nature Communications*, 7(1), 13965.
- Schleuning, M., Neuschulz, E. L., Albrecht, J., Bender, I. M., Bowler, D. E., Dehling, D. M., et al. (2020). Trait-based assessments of climate-change impacts on interacting species. *Trends in Ecology & Evolution*, 35(4), 319–328.
- Schleuning, M., García, D., & Tobias, J. A. (2023). Animal functional traits: Towards a trait-based ecology for whole ecosystems. *Functional Ecology*. Wiley Online Library.
- Seibold, S., Cadotte, M. W., MacIvor, J. S., Thorn, S., & Müller, J. (2018). The necessity of multitrophic approaches in community ecology. *Trends in Ecology & Evolution*, 33(10), 754–764.
- Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., et al. (2022). Food web reconstruction through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*, 13(12), 2838–2849.
- Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047.
- Thuiller, W., Calderón-Sanou, I., Chalmandrier, L., Gaüzère, P., O'Connor, L. M., Ohlmann, M., et al. (2024). Navigating the integration of biotic interactions in biogeography. *Journal of Biogeography*, 51(4), 550–559.
- Villéger, S., Mason, N. W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290–2301.
- Webb, S. D. (2006). The great american biotic interchange: Patterns and processes1. *Annals of the Missouri Botanical Garden*, 93(2), 245–257.
- Whiteman-Jennings, W. (2015). INTO THE TROPICS: A QUANTITATIVE STUDY OF MAMMALS IN THE GREAT AMERICAN BIOTIC INTERCHANGE.
- Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.*, 36, 519–539.
- Wilman, H., Belmaker, J., Simpson, J., Rosa, C. de la, Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: Ecological archives E095-178. *Ecology*, 95(7), 2027–2027.
- Zona, S., & Henderson, A. (1989). A review of animal-mediated seed dispersal of palms. *Selbyana*, 6–21.