

Distinct functional responses of producers and their consumers to climate shape trophic asymmetry in mutualistic networks

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8 **Abstract**

9 Functional traits are often used to infer the ecological processes that determine the
 10 composition of species assemblages. Whereas most trait-based approaches to infer
 11 community assembly processes focus on a single trophic level, traits also mediate
 12 interactions between trophic levels. Owing to the matching of traits facilitating in-
 13 teractions between producer and consumer assemblages, the functional trait diversity
 14 of different trophic levels is expected to covary in space. However, the differential
 15 response of consumers and producers to environmental gradients can cause a decou-
 16 pling of functional diversity between trophic levels, which we coin functional trophic
 17 asymmetry. Here, we develop a metric to quantify functional trophic asymmetry
 18 (FTA) and use it to infer the processes underpinning multitrophic community as-
 19 sembly and explore the role of these processes in shaping the topology of ecological
 20 networks.

21 We used digitally available data on the functional traits, pairwise mutualistic interac-
 22 tions, and geographic distributions of consumers (mammalian frugivores) and their
 23 producers (palms) to quantify FTA for species assemblages occurring in the Neotrop-
 24 ics. To cover major data gaps between species-level trait and interaction data at
 25 finer spatial grain, we trained machine learning models to downscale the continental
 26 meta-network to grid cell-level networks. For each grid-cell, we also estimated FTA
 27 for all combinations of interaction guilds. These guilds were defined as distinct sub-
 28 sets of producer and consumer assemblages playing similar roles within mutualistic
 29 networks and sharing partners in the other trophic level. We then used generalized
 30 additive models to relate geographic variation in FTA to variation in climatic vari-
 31 ables and assessed whether the strength of these relationship varied among pairwise
 32 interaction guilds. Finally, we then examined the relationship between FTA and
 33 network specialization across 1,072 grid cells in the Neotropics.

34 Our approach to model mutualistic network assembly identified 7 consumers x pro-
 35 ducer interaction guilds. Assemblage-wide FTA was negatively related to annual
 36 mean temperatures across the neotropics. When considering individual interaction
 37 guilds, precipitation seasonality was positively related to FTA. This relationship
 38 between FTA and precipitation seasonality was stronger for consumer and pro-
 39 ducer guild combinations with high predicted interaction strength. Finally, network
 40 specialization was positively related to FTA, regardless of the interaction guild com-
 41 bination.

42 Mutualistic networks in warm regions with seasonal rainfall, where the environment
 43 imposes a disproportionately strong selective pressure on palms relative to mammal
 44 frugivores, exhibit higher levels of functional trophic asymmetry. This relationship is
 45 particularly strong when considering guilds predicted to strongly interact in nature.
 46 Assemblages exhibiting high FTA also tend to have high levels of network special-
 47 ization, suggesting that differences in the strength of environmental selection among
 48 trophic levels favor the persistence of specialist species in these mutualistic interac-
 49 tion networks. We therefore conclude that future increases in temperature and the
 50 magnitude of precipitation seasonality caused by global climate change could lead to
 51 more specialized mutualistic networks which are more prone to collapse when facing
 52 further threats and local extinctions.

53 **0.1 Introduction**

54 Ecologists often examine patterns of functional trait diversity to investigate com-
 55 munity assembly processes (Ackerly, 2003; Kraft et al., 2015). To date, however,
 56 trait-based approaches in ecology often focus on a single trophic level, whereas ap-
 57 proaches that consider multiple trophic levels remain rare (Lavorel, 2013; Seibold
 58 et al., 2018). An approach that considers processes operating within and between
 59 trophic levels is necessary to better understand the assembly of multitrophic com-

60 munities (Allesina et al., 2008; Marjakangas et al., 2022; Saravia et al., 2022). More-
 61 over, considering trophic interactions while studying community assembly could shed
 62 new light on processes underpinning ecological networks (Allesina et al., 2008). Clas-
 63 sical approaches to study community assembly rely on the concept of environmental
 64 filtering, sorting or selection, where density independent conditions constrain the
 65 functional richness of species assemblages (HilleRisLambers et al., 2012; Kraft et al.,
 66 2015; Laliberté & Legendre, 2010; Villéger et al., 2008). Functional richness refers
 67 to the variability and relative frequency of different functional traits observed in a
 68 community. It is often used to estimate the strength of selection imposed by the
 69 environment (Kraft et al., 2008, 2015; Kraft & Ackerly, 2010). High functional richness
 70 can indicate weak environmental selection whereas low functional richness can
 71 indicate strong selection (Halpern & Floeter, 2008; Kraft et al., 2008; Paine et al.,
 72 2011). In a multitrophic context, the effects of environmental selection can cascade
 73 across trophic levels such that selection on consumer traits can shape the functional
 74 richness of their resources, modulated by their degree of reciprocal dependency or
 75 co-evolution (Lavorel, 2013). Moreover, the same environmental gradient could exert
 76 selective pressures of different strength on communities at distinct trophic levels
 77 (Marjakangas et al., 2022). Differences in the strength of selective pressure among
 78 trophic levels could then possibly constrain the structure or topologies of trophic
 79 networks (Blüthgen et al., 2007; Dehling et al., 2021; Schleuning et al., 2012)

80 Inferring the relative strength of environmental selection between trophic levels re-
 81 quires using high-dimensional approaches that can deal with sparse observations for
 82 many species (Rohr et al., 2010; Strydom et al., 2022). We introduce the concept of
 83 functional trophic asymmetry (FTA), which allows inferring the relative influence
 84 of environmental selection and trait matching on the composition of multitrophic
 85 assemblages (Figure 1). FTA is the difference in the richness of interaction-relevant
 86 traits between trophic levels in a multitrophic network. FTA can occur because
 87 traits mediating species interactions (i.e., interaction niches) across trophic levels
 88 can also mediate the responses of species to their abiotic environment (i.e., environ-
 89 mental niches) (Dehling et al., 2021; McCain & King, 2014; Moretti & Legg, 2009).
 90 As an example, plant seed size determines the outcome of animal-mediated seed dis-
 91 persal (Donoso et al., 2017, 2020) as well as physiological limits, such as tolerances
 92 of plant seedlings to desiccation (Hoekstra et al., 2001). High FTA could indicate
 93 differences in the strength of environmental selection over the interaction niches of
 94 distinct trophic levels within a multitrophic species assemblage. Alternatively, low
 95 FTA could indicate that the strength of the environment selection shaping inter-
 96 action niches is similar between trophic levels, e.g., equally weak or equally strong
 97 (Marjakangas et al., 2022). When interactions between producers and consumers are
 98 mutualistic, low FTA could also emerge under strong trait matching and therefore
 99 indicate the influence of trait co-evolution during multitrophic community assembly
 100 (Albrecht et al., 2018; Dehling et al., 2021). By studying spatial variation in FTA
 101 along environmental gradients, we could possibly identify the conditions promoting
 102 environmentally versus cross-trophic interaction- driven community assembly (Bello
 103 et al., 2023).

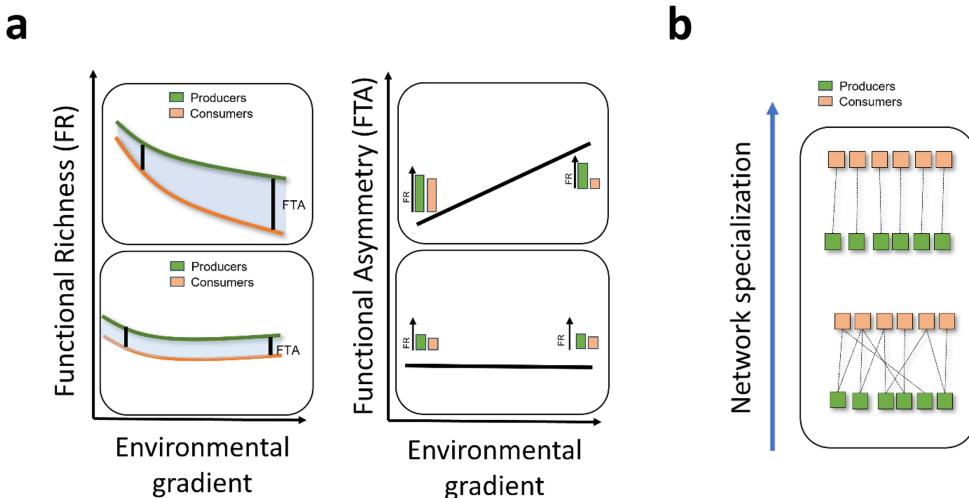


Figure 1: This conceptual model illustrates the dynamic relationship between functional diversity metrics—specifically Functional Richness (FR) and Functional Trait Asymmetry (FTA)—and environmental gradients within ecological networks. The left panel of Figure a) visualizes the variation in FR for producers (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 decline. 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 generalized interactions are between producers and consumers within ecological networks.

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 et al., 2021; Schleuning et al., 2012). 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 identity, number, and frequency of species interactions and therefore, network topology (Albrecht et al., 2018; Emer & Memmott, 2023; Marjakangas et al., 2022). As an example, constraints of varying intensities along climatic gradients, which limit the relative availability of interaction partners across trophic levels, could influence emergent patterns in network structure such as the specialization of multispecies interactions (Blüthgen et al., 2006, 2007; Marjakangas et al., 2022). 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 resources 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 et al., 2020; Dehling et al., 2022; Messeder et al., 2021). To effectively preserve these interactions, it is crucial to understand how co-occurring palm (producer) and mammalian frugivore (consumer) communities respond to environmental gradients. By examining co-variation in their functional richness across broad geographic scales and linking those patterns to spatial and/or temporal variation in climate, we can identify key abiotic factors that influence the assembly of their mutualistic relationships. Here, we ask (1) *which climatic variable(s) best explains geographic variation in the functional richness of palms and mammal frugivores*, (2) *whether differences in these relationships lead to functional trophic asymmetry (hereafter FTA)*, and (3) *which climatic variable best explains geographic variation in FTA across the Neotropics*. We also ask (4) *whether the strength of interactions between palm-frugivore interaction guilds relates to the strength of the relationship between FTA and climate*. Finally, we ask (5) *whether geographic variation in FTA relates to network specialization*.

0.2 Methods

0.2.1 Study system

We focused on multitrophic communities of Neotropical palms and their mutualistic, seed dispersing, mammalian frugivores (Figure S1). Palms (Plantae:Arecaceae) are a keystone plant family in tropical regions that provides fruit resources to a wide variety of vertebrate frugivores, including birds and mammals (Muñoz et al., 2019). 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 ectozoochorus dispersal (Messerder et al., 2021). Importantly, frugivory-related traits have notably underlain palm diversification and played a key role in the evolution of palm traits (Kissling et al., 2012; Onstein et al., 2014, 2017).

0.2.2 Data sources

0.2.2.1 Geographic distribution data

We obtained binary species distribution data (present/absent) on palms from the geographic range maps of (Bjørholm 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.

0.2.2.2 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., 2021). From this dataset, we selected only those species whose range in gridded multitrophic communities within a regular $1 \times 1^\circ$ latitude grid co-occur with at least 5 other palm and mammal frugivore species in the same grid. In total, we worked with a subset from this dataset of 494 palm species and 488 mammal frugivore species with linked trait and geographic data. Pairwise 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.

0.2.2.3 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 ($1 \times 1 \text{ km}^2$) to match the spatial resolution of our grid cell species-level data (Figure 2)

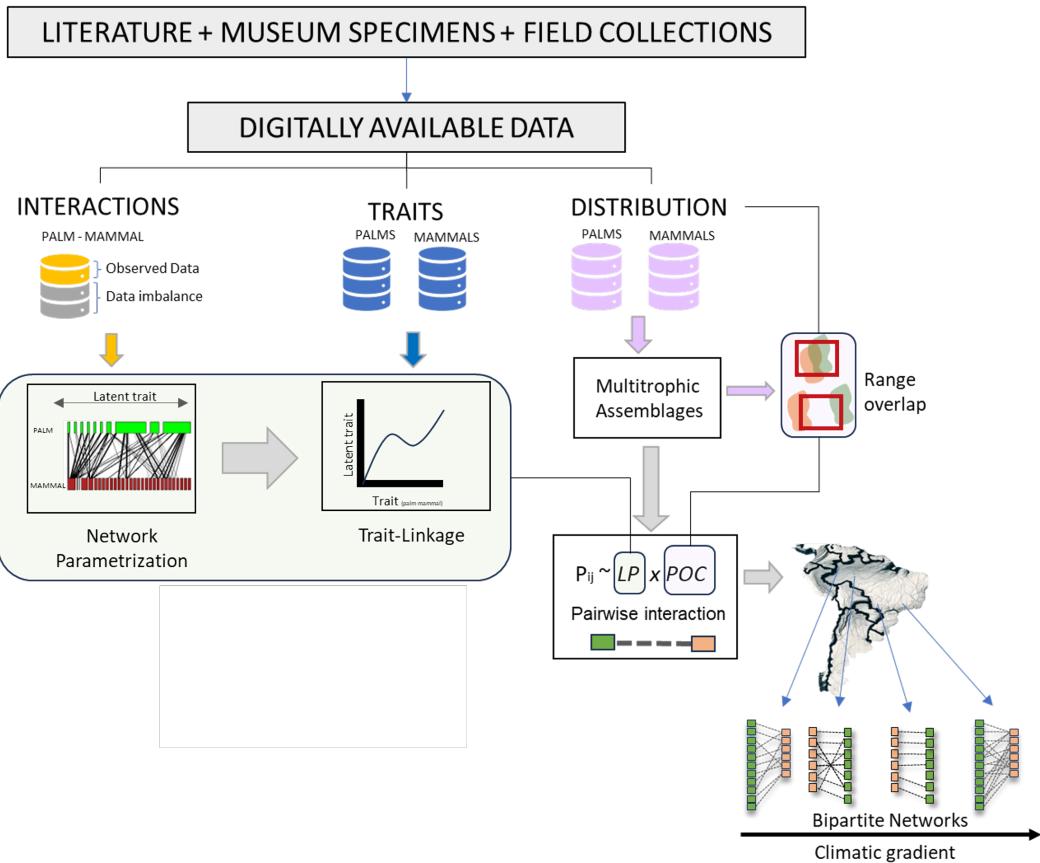


Figure 2: Workflow illustrating the integration of ecological and trait data from digital sources to model species interactions and predict ecological networks across geographic regions. The figure illustrates a workflow for integrating ecological interaction data derived from literature, museum specimens, and field collections into digitally available datasets. These datasets are used to build ecological network models and link species interactions to their biological traits. The approach involves parameterizing networks based on latent traits and identifying trait-linkages, which are subsequently utilized to predict ecological interactions and networks across different geographic locations (e.g. The Neotropics)

210 0.2.3 Statistical analysis

211 Building a probabilistic continental metaweb from aggregated binary interaction
 212 records Here, we fitted latent variable network structural models that vary in
 213 their assumptions to estimate interaction probabilities from observed binary data
 214 on species interactions. (Figure 3) Specifically, we tested: the stochastic block
 215 model (SBM), the connectance model, the trait-matching model, and the matching-
 216 centrality model (Terry & Lewis, 2020). The SBM assumes that ecological networks
 217 are modular, with species of consumers interacting more within their preferred
 218 groups of producers (i.e., interaction guilds). This model outputs three incidence
 219 matrices, reflecting predicted interactions: (i) one with guilds of palm species based
 220 on their modular interactions with mammals, (ii) a similar one for mammals, and
 221 (iii) one representing the interaction probabilities (Θ) among the guilds of each
 222 group (i.e., palm guilds-mammal-guild). The connectance model posits that inter-
 223 actions of specialist species are subsets of those of generalist species, optimiz-
 224 ing connectivity scores to recreate observed network patterns. The trait-matching model
 225 assumes non-random species interactions determined by trait differences, optimiz-

ing parameters along latent-trait axes. The matching-centrality model combines connectivity scores and latent-trait axes (Terry and 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 found that the SBM was the best supported model (Figure 3) and therefore focused on it in the rest of the manuscript. Additional details about the model assumptions are explained in Supplementary Text S1.

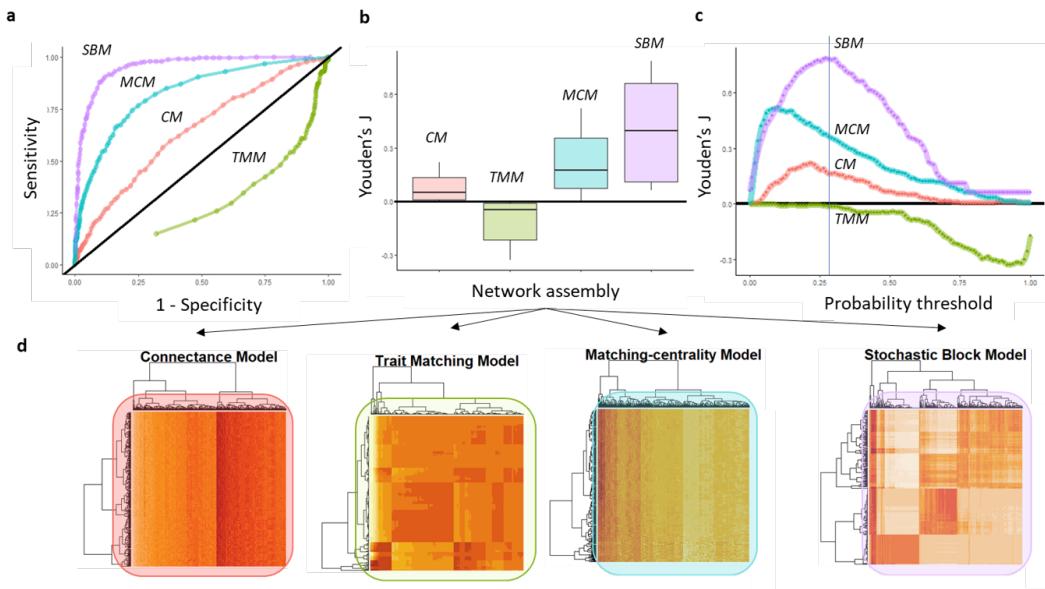


Figure 3: Model evaluation plots of distinct structural models fitted to predict the structure of the observed palm-mammal frugivore interactions in the Neotropics. In this figure we illustrate a comparison of ecological network assembly models using ROC curves (a), Youden's J index (b,c), and clustering heatmaps (d) to illustrate differences in predicting species interactions. Specifically, the figure compares four ecological network assembly models—Centrality Model (CM), Trait Matching Model (TMM), Matching Centrality Model (MCM), and Stochastic Block Model (SBM)—in their ability to accurately predict a observed binary pattern of species interactions. For our study, this observed pattern reflected the incidence of seed dispersal interactions between palms and their mammalian frugivores. The ROC curves (a) indicate model performance in terms of model sensitivity (i.e. true positive rate) versus model specificity (true negative rate). Curves further above the diagonal demonstrate stronger predictive ability, showing that the model performs significantly better than random guessing in identifying ecological interactions. If a ROC curve is close to or below this diagonal, the model's predictive performance is no better than random chance. The central boxplot summarizes the Youden's J index, where higher values reflect higher overall predictive accuracy. Panel (c) shows Youden's J index variation over different probability thresholds to materialize binary interactions. The heatmaps below visualize clustering patterns, highlighting structural differences in predicted interaction networks for each model.

0.2.3.1 Identifying interaction guilds

Since the hyperparameters of the Stochastic Block Model (SBM) provided the best fit for capturing the observed interactions, palm-frugivore interaction networks are

highly modular and certain groups of producers are more likely to interact with certain groups of consumers than others, and vice versa. In this context, we define an interaction guild as a distinct group of palm and mammal species within the continental metaweb that exhibits similar interaction patterns. Within each guild, both producer and resource species perform comparable functional roles in the network. Within and between each guild combination of consumers and producers, species pairs exhibit the same interaction strength, where interaction strength is defined as the magnitude or intensity of the effect that one species has on another within an ecological network. Here we estimate interaction strength as the probability that a species pair would interact in nature. The SBM estimates such interaction probabilities based on the frequency of interactions observed between species assigned to given guild of consumer or producer. The SBM model uses maximum likelihood to adjust the number of guilds and the distribution of interaction probabilities within and between guilds such that they best explain the observed pattern of interactions. Using SBMs largely reduces the complexity of dealing with interaction strengths by treating them as a guild-level phenomenon instead of a species-specific one.

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

The digital availability of primary biodiversity data on palms and their mammalian frugivores was imbalanced, with a high availability of distribution ranges and species traits, but a limited number of interaction records. Therefore, to downscale our initial metaweb to include interactions between every potentially co-occurring palm and mammal frugivore in every grid cell across the Neotropics, we used a twofold approach (Figure 2).

First, we employed multinomial logistic regression models to predict the species level SBM model results (i.e., interaction guild affiliation) from species-level trait data. We justify the choice of multinomial logistic regression models as these can handle the prediction of non-binary outcomes, such as the labeling of interaction guilds 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 use neural networks because they are useful when dealing with multicollinearity, as they can learn complex and non-linear relationships and interactions among multiple 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 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 grid cell. 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 their 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.

0.2.3.3 Estimating Functional Richness

We investigated the spatial variation in the relative distribution of species counts of producers and consumers across all guilds in a grid cell, as an interaction network-level indicator of the spatial distribution of producer and consumer species' functional richness. We estimated functional richness (FR) from the results of the SBM model fit, specifically, from the matrices representing the interaction guilds. Thus,

290 to measure functional richness for each trophic level, we calculated a grid-cell level
 291 vector representing the number of species across all interaction guilds ($n = 7$). To
 292 account for the differences in the total number of palm and mammal species across
 293 grid cells, we normalized this vector to the total sum of palm or mammal species
 294 counts within each grid cell.

295 0.2.3.4 Estimating Functional Trophic Asymmetry (FTA)

296 We quantified functional trophic asymmetry (FTA) as the absolute difference be-
 297 tween the functional richness vectors across trophic levels. Since each palm and
 298 mammal species in every grid cell had the potential to be affiliated with any of the
 299 seven interaction guilds and to interact with any species from the opposite trophic
 300 level both within and between guilds, we derived one FTA measures for each grid
 301 cell, and for each pairwise palm-mammal guild combination.

302 0.2.3.5 Estimating Network Specialization ($H2'$)

303 We estimated network specialization for each grid cell using the metric $H2'$. $H2'$ is a
 304 network-level index that varies between 0 and 1 (Blüthgen et al. 2007). High values
 305 indicate networks that are more specialized, meaning that species from one trophic
 306 level interact with only or few species in the opposite trophic level. Low $H2'$ values
 307 indicate that there is a low specificity of interactions in the network, meaning that
 308 species from one trophic level interact with multiple species at the other trophic
 309 level. Because inferred networks varied in their network size (i.e., number of unique
 310 interactions between palms and mammals), we rarefied the computation of $H2'$ to
 311 networks for each grid cell such that they would all have the same size (i.e., number
 312 of interactions). Specifically, we rarefied all networks to 100 pairwise interactions
 313 and repeated the procedure 999 times to get a distribution of rarefied $H2'$ values
 314 (Terry & Lewis, 2020). We then selected the median of this $H2'$ distribution as our
 315 grid cell-level measure of network specialization.

316 0.2.3.6 Assessing the influence of climate on FTA

317 To assess whether climate has an influence on FTA, we fitted a Generalized Addi-
 318 tive Model (GAM) to examine the relationships between FTA and four continuous
 319 bioclimatic predictors. The GAM approach allows for modelling flexible non-linear
 320 relationships between the predictors and the response variable using smoothed func-
 321 tions (Wood, 2017). The predictor variables included in our models were Mean
 322 annual temperature (Temp), Total annual precipitation (Prec), Temperature season-
 323 ality (TS), and Precipitation seasonality (PS). Collectively, are these climatic factors
 324 known contemporary factors influencing both the regional and global diversity of
 325 plants and mammals (Holt et al., 2018). We fitted separate splines for each of the
 326 climatic predictors.

327 Assessing how interaction strength mediates the influence of climate on FTA To
 328 assess whether the strength of interaction between producer and consumer guilds
 329 mediate the strength of the relationship between FTA and climate, we included in-
 330 teraction strength as an interaction term in the GAM, allowing splines between FTA
 331 and climate to vary non-linearly depending on interaction strength.

332 0.2.3.7 Assessing the relationship between FTA and $H2'$

333 We used Generalized Additive Model (GAM) to investigate the relationship be-
 334 tween rarefied grid cell network level specialization ($H2'$) as a response variable and
 335 FTA (z-scores) as the main predictor. We also added the effect of Mean annual
 336 temperature, Total annual precipitation, Precipitation seasonality, and Tempera-
 337 ture seasonality as covariate functions because these climate variables may influence
 338 $H2'$ independently of FTA, allowing us to isolate the specific impact of FTA on
 339 $H2'$ while controlling for the indirect effects of climate on FTA. Here, we estimated
 340 grid-cell level functional trophic asymmetry (FTA') by summing the FTA values
 341 across all interaction guilds, weighted by their respective interaction strengths. This

342 approach was selected as accounts for the uneven contributions of each guild to net-
 343 work structure, highlighting whether changes in network specialization are primarily
 344 driven by shifts in FTA within the more specialized interaction guilds.

345 0.3 Results

346 0.3.1 Interaction guild delineation

347 The Theta matrix derived from the SBM (Stochastic Block Model) analysis (Figure
 348 4) reflects the modular pattern assumed by this model, here identified as the best
 349 for frugivore-mammal interactions. Therefore, these interactions are stronger within
 350 rather than between guild pairs. Given the associations found with the theta matrix,
 351 we can derive that the following high-level trait-trait associations: a) Tall palms with
 352 medium-sized fruits can associate strongly with small to medium sized mammals
 353 that consume moderate to high amounts of fruit. b) Acaulescent or small-stemmed
 354 palms with small to large fruits correlate strongly with either small, moderately
 355 frugivorous mammals or small mammals with relatively low frugivory. Finally, c)
 356 medium-sized to large sized mammals with moderate to low frugivory levels interact
 357 with species with intermediate palm traits (e.g., moderately tall erect palms with
 358 medium-sized fruits) (Figure S1).

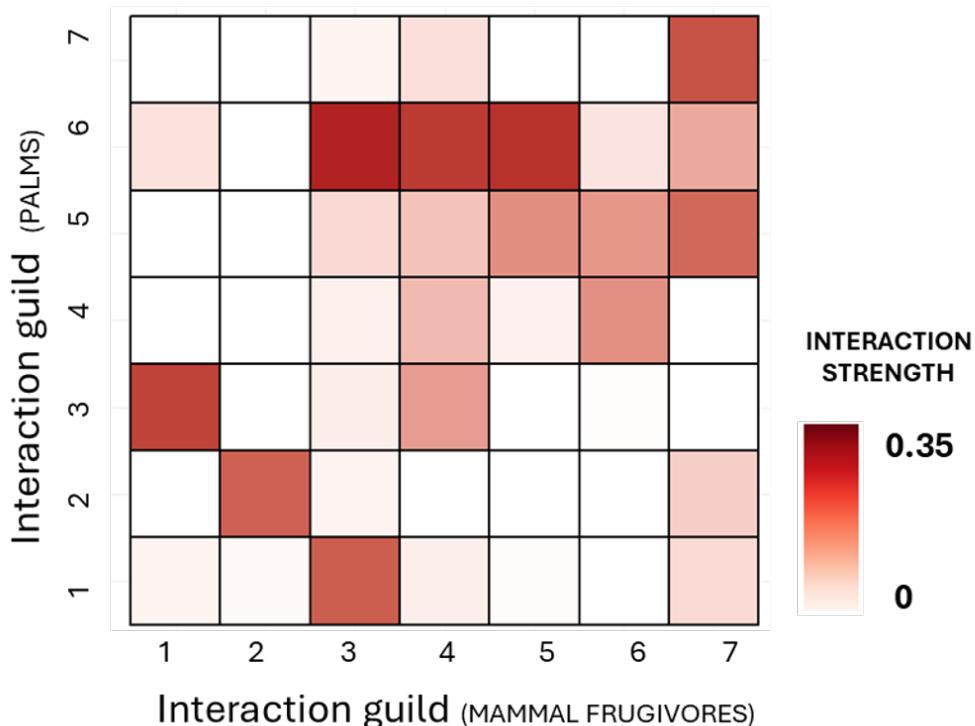


Figure 4: Heatmap depicting the probability of interaction between palm and mammal interaction guilds defined as blocks by the Stochastic Block Model (SBM). The intensity of red shading correlates with the strength of these interactions, where darker shades signify higher probabilities of interaction between species within or between interaction guilds (SBM blocks), where the probability was inferred using the Stochastic Block Model's estimated interaction parameters (theta Matrix) derived from fitting the model to observed binary (presence = 1, absence = 0) interaction data compiled from scientific literature.

359 **0.3.2 The influence of climate on functional richness**

360 At the grid-cell level, when ignoring interaction guild affiliations, neither the func-
 361 tional richness of palms or mammals relates to geographic variation in climate (Ta-
 362 ble S1a,b). The functional richness of palms does not relate to temperature ($F =$
 363 3.00, $P < 0.05$), precipitation ($F = 1.19$, $P = 0.23$), temperature seasonality ($F =$
 364 -0.27, $P = 0.79$) or precipitation seasonality ($F = 0.68$, $P = 0.50$). The functional
 365 richness of mammals positively relates to mean annual temperature ($F = 10.60$, P
 366 < 0.05) but not to precipitation ($F = 0.001$, $P = 1.00$), temperature seasonality (F
 367 = 0.52, $P = 0.60$) or precipitation seasonality ($F = 1.67$, $P = 0.10$). When consider-
 368 ing guild affiliation in our analyses, there are marked differences in the relationship
 369 between functional richness and climate among trophic levels (Figure 4a,b). The
 370 functional richness of palm positively relates to precipitation seasonality for guilds
 371 5 ($F = 5.62$, $P < 0.01$) and negatively relates to precipitation seasonality for guild 6
 372 ($F = 8.37$, $P = 0.01$). In contrast, the relationship between the functional richness
 373 of mammals and precipitation seasonality does not vary among guilds. However, the
 374 relationship with temperature does vary among guilds. Specifically, the functional
 375 richness of guild 3 positively relates to temperature ($F = 11.21$, $P < 0.01$) whereas
 376 that of other guilds does not relate to temperature.

Table 1

Source: Article Notebook

Parametric coefficients

	Estimate	Std. Error	t value	p-value
Intercept	0.21	0	271.5	>0.001 ***

Source: Article Notebook

Smooth Terms

	edf	Ref.df	F	p-value
Mean Annual Temperature	1.00	1	5.97	0.01 *
Mean Annual Temperature x interaction strength	0.00	27	0.00	0.57
Precipitation seasonality	1.00	1	0.30	0.59
Precipitation seasonality x interaction strength	1.67	27	0.14	0.05.
Temperature seasonality	1.00	1	0.19	0.67
Temperature seasonality x interaction strength	0.00	27	0.00	0.54
Total Annual Precipitation	1.00	1	0.28	0.60
Total Annual Precipitation x interaction strength	0.00	27	0.00	0.47
Interaction strength	5.00	5	746.20	>0.001 ***

Source: Article Notebook

378 **0.3.3 The influence of climate on FTA**

379 The distribution of functional trophic asymmetry (FTA) exhibited a bi-modal pat-
 380 tern, with a primary cluster centered around local maxima of FTA = 0.09 and a
 381 secondary cluster near a second local maxima of FTA = 0.49. A similar cluster-
 382 ing pattern after standardizing FTA by the strength of interaction guilds, however,
 383 the cluster of low FTA values due to low or minimal interaction strength is more
 384 apparent (Figure 4c, 4d). The maximum FTA record across all guilds was 0.93.
 385 Within individual guilds, the highest FTA values were associated with interactions

386 between tall, erect palms bearing medium to large fruits (guild 3) and highly fru-
387 givorous mammals (guild 1) (Figure S5). Similarly, medium-sized palms with small
388 to medium fruits (guild 5) interact with large mammals exhibiting low levels of fru-
389 givory (guild 6) also contributed significantly to high FTA standardized values In
390 contrast, interactions involving acaulescent or short-stemmed palms with medium-
391 sized fruits (guild 6) and small mammals with limited frugivory intake (guild 3)
392 consistently yielded the lowest FTA standardized values (Figure S5) When ignoring
393 interaction guilds, functional trophic asymmetry (FTA) is positively related to mean
394 annual temperature ($F = 5.97, P = 0.01$). FTA is not related to precipitation (F
395 = 0.28, $P = 0.13$), precipitation seasonality ($F = 0.30, P = 0.59$) or temperature
396 seasonality ($F = 0.19, P = 0.67$) (Table 1). When considering interaction guild affil-
397 iation in our analyses, there are marked differences in how temperature (Temp) and
398 Precipitation seasonality (PS) interact among distinct interaction guild combinations
399 (Figure 5). Specifically, an increase in the relative richness of frugivores with low lev-
400 els of fruit in their diet (i.e. mammal interaction guilds 3, 6 and 7) with increasing
401 Temperature drove changes in FTA along the temperature gradient (Figure 5a, 5c),
402 while along increasing precipitation seasonality, FTA was driven by the reduction
403 in the richness of short palms with low to medium fruit sizes (guild 5) and of tall
404 palms with low fruit sizes (guild 2), coupled with an increase in the relative richness
405 of short stemmed and acaulescent palms with medium to large fruits (guild 6) across
406 the climatic gradient (Figure 5b,5d).

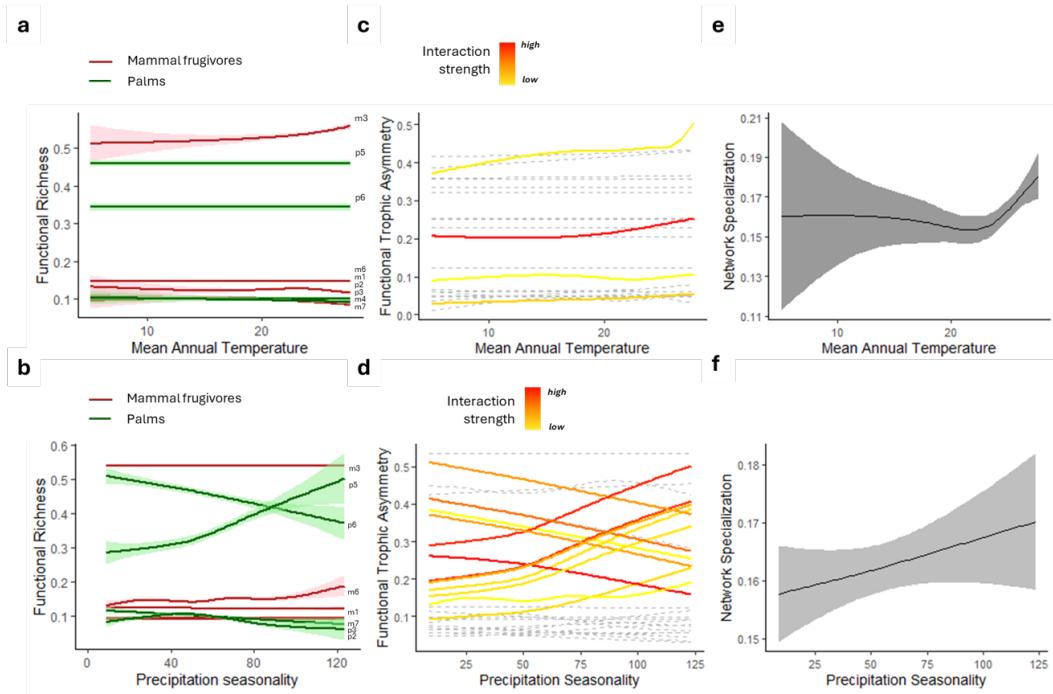


Figure 5: Relationships between environmental gradients, functional diversity, and network properties in the multitrophic system of mutualistic palm-mammal frugivore networks in Neotropics. (a, b) Trends in the functional richness of palms (green) and mammals (red) as a function of mean annual temperature (a) and precipitation seasonality (b), with shaded areas representing confidence intervals. Each trendline estimates the change in Functional Richness of an interaction guild. Each interaction guild corresponds to the species groupings found with the Stochastic Block Model and it is identified with labels at the higher end of the climatic gradient. (c, d) Functional trophic asymmetry (FTA) across temperature (c) and precipitation seasonality (d) for all combinations of potential interactions among and within guilds. Interaction strength indicated by a color gradient from yellow (low) to red (high). Trendlines for interaction guild combinations which are significantly affected with the changes in the climatic gradient are colored and shown in continuous lines. Trendlines for interaction guild combinations which are not responsive to climate are shown in gray and stippled lines. (e, f) Network specialization (z-score) along gradients of mean annual temperature (e) and precipitation seasonality (f), with shaded areas denoting confidence intervals. Network specialization is measured with the specialization index (H'), rarefied to be measured in networks of the same number of interactions, and z-score standardized for networks across sites by using a null model that simulates stochastic multispecies assembly.

407 0.3.4 Does interaction strength mediates the influence of climate on 408 FTA?

409 The strength of interaction between guilds of consumers and producers had an over-
410 all positive effect on FTA (Figure S6). FTA values showed a bi-modal distribution
411 with peaks at high and low ends of the interaction strength spectrum (Figure S6).
412 However, we did not find strong evidence supporting that the relationship between
413 FTA and climate depends on the strength of interaction between interaction guilds
414 ($F = 746$, $P > 0.05$). The interaction term between guild interaction strength and
415 precipitation seasonality had a marginally significant, and positive, effect on FTA.
416 ($F = 0.14$, $P = 0.051$) (Table 1). Assessing the relationship between FTA' and H_2'
417 We found that palm-mammalian frugivore networks have moderate levels of trophic

specialization (H_2') ranging from 0.12 to 0.25, where 0 means species have no preference or specialization in their interaction partners and 1 represents networks where each species interacts only with a specific subset of interaction partners (Figure S7).

Geographic variation in H_2' positively relates to variation in FTA' ($F = 24.36$; $P < 0.001$) (Figure 6c, 6d). H_2' also positively relates to the mean annual temperature of the atmosphere ($F = 2.12$, $P = 0.03$), however, effect uncertainty is stronger in cold regions than in warm regions (Figure 5e). Similarly, H_2' is positively related to precipitation seasonality PS ($F = 2.29$, $P = 0.02$). (Figure 5f) Finally, variation in H_2' does not relate to variation in temperature seasonality or total annual precipitation (both $P > 0.05$). The deviance explained by this model was 17.6%. (Table 2)

Table 2

Source: Article Notebook

Parametric coefficients

	Estimate	Std. Error	t value	p-value
Intercept	0.16	0	86.33	<2e-16

Smooth Terms

	edf	Ref.df	F	p-value
FTA = s(sum_fta)	5.97	7.18	24.37	<2e-16
Mean Annual Temperature = s(Temp)	5.86	7.04	2.13	0.04
Precipitation seasonality = s(PS)	5.42	6.56	2.29	0.03
Temperature seasonality = s(TS)	1.00	1.00	0.74	0.39
Total Annual Precipitation = s(Prec)	5.29	6.39	0.93	0.48

Source: Article Notebook

428

0.4 Discussion

Our study reveals that producers and consumers differ in their functional responses to climatic gradient thereby giving rise to trophic asymmetry (FTA). The degree of FTA in palm-mammal frugivore assemblages varies across the Neotropics, with the highest value recorded in regions with a warm climate and a seasonal precipitation regime. Furthermore, species assemblages with high FTA also exhibited a high level of specialization in their trophic interaction networks. Taken together, our results suggest that distinct community assembly processes operate simultaneously across trophic levels, reinforcing the idea that network assembly emerges from a dynamic interplay of bottom-up and top-down processes (Marjakangas et al., 2022; Moretti & Legg, 2009; Schleuning et al., 2023) which are context dependent.

Palms and mammal frugivore assemblages differ in their response to climatic gradients across the Neotropics. There is a positive relationship between the functional richness of mammal assemblages and temperature, mainly driven by an increase in the richness of small-bodied, opportunistic mammal frugivores with broad diets (Figure 5a, Figure S1). Warm regions have high primary productivity, which translates into an abundance of fruits and other resources that support a great diversity of mammal species and interaction traits (Gorczyński et al., 2021; Losada et al., 2024). Among those, small tropical frugivores tend to have narrower climatic niches as they tend to be restricted to the warmest regions. As opposed to larger bodied mammals,

449 they are less suited to cold climatic conditions because they more easily lose heat
 450 (Shipley & McGuire, 2024). In addition, in warm regions, small frugivorous mammals
 451 invest less energy in thermoregulation and can allocate more energy to feeding
 452 and breeding (Arends & McNab, 2001; Merritt, 2010). Higher reproductive rates
 453 and shorter generation times over evolutionary time can create opportunities for
 454 adaptation or speciation (Allen et al., 2006). Finally, warm, and stable climates over
 455 evolutionary time could have lowered extinction rates, allowing these climatically
 456 sensitive small frugivore lineages to persist through time (Sandel et al., 2011).

457 The functional richness of palms does not relate to variation in temperature, but it
 458 is negatively related negatively related to precipitation seasonality. Palms, being
 459 megathermal plants, evolved in and require warm conditions year-round (Eiserhardt
 460 et al., 2011; Reichgelt et al., 2018). However, given the overall warm conditions of
 461 Neotropics, geographic variation in mean annual temperature exerts little constraints
 462 on palm functional richness. Studies show that variations in mean temperature
 463 within the tropical-subtropical range affect palm growth rates rather than commu-
 464 nity composition (Eiserhardt et al., 2011). Unlike temperature, annual precipitation
 465 seasonality strongly relates to palm functional richness. When precipitation becomes
 466 seasonal, the overall number of palms species tends to decline, and drought-tolerant
 467 palm types are more represented in palm assemblages (Eiserhardt et al., 2011; Sousa
 468 et al., 2020) (Figure 5b). As such these habitats favor species with water-saving
 469 strategies (e.g. large-nuts) over water-spending ones (e.g. fast growth and large
 470 leaves) (Eiserhardt et al., 2011; Emilio et al., 2019). In warm and wet habitats, both
 471 strategies coexist since water is abundant (Eiserhardt et al., 2011).

472 Functional Trophic Asymmetry (FTA) varied geographically, peaking in warm re-
 473 gions with highly seasonal precipitation (Figure 6). Overall, average annual temper-
 474 ature has a small but positive effect on FTA. This is mainly due to a proportionally
 475 greater representation of guilds with small generalist mammals frugivores in as-
 476 semblages of warm regions relative to the functional richness of interacting palm
 477 assemblages. As such, variation in mean annual temperature and its effects on FTA
 478 were associated with shifts in the functional richness of mammals rather than shifts
 479 in the functional diversity of palms. These results support the view that the mode of
 480 assembly in palm-frugivore networks inhabiting the warmest regions of the neotrop-
 481 ics is top-down (i.e. consumer-driven) (Albrecht et al., 2018; Dehling et al., 2016,
 482 2022; Marjakangas et al., 2022; Sonne et al., 2016). In contrast, the significant in-
 483 fluence of precipitation seasonality on the functional richness of palm assemblages
 484 supports the view that the mode of assembly in palm-frugivore networks inhabiting
 485 areas with highly seasonal precipitations is bottom-up (producer-driven).

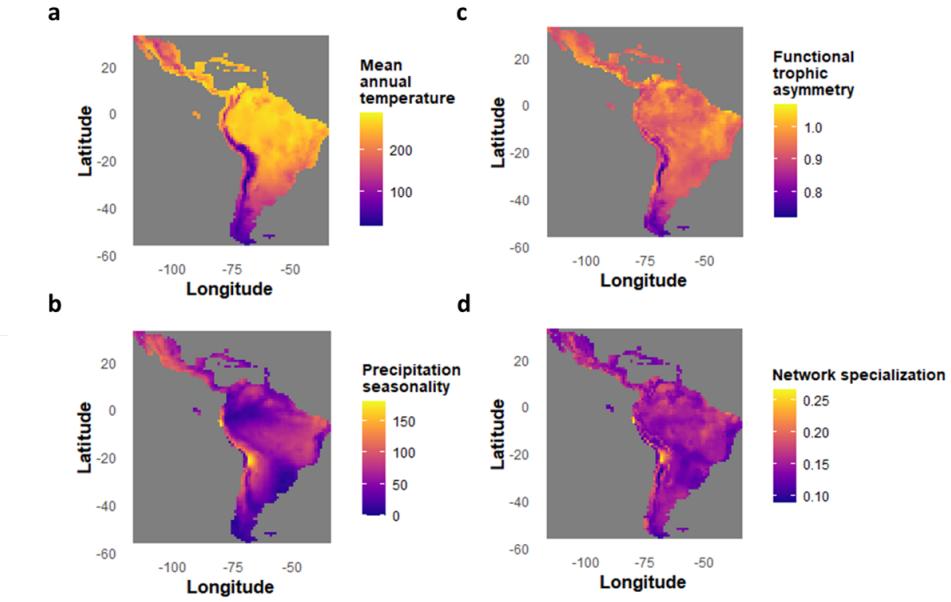


Figure 6: Spatial distribution of climate, functional trophic asymmetry, and network specialization for palm-mammal frugivore seed dispersal networks across the Neotropics. Panels (a) and (b) show the geographical variation in mean annual temperature and precipitation seasonality, respectively, with warmer colors indicating higher values. Panels (c) and (d) depict the spatial patterns of functional trophic asymmetry (FTA) and network specialization (H^2'), where higher values are also represented by warmer colors. FTA (Panel c) reflects variation in functional trophic asymmetry across regions, with higher values concentrated in areas of higher temperature and seasonality. Network specialization (Panel d) indicates the degree of exclusive interactions within ecological networks. Color scales for each map are shown in adjacent legends.

Interaction strength, representing the intensity of the effect that one species has on another within an ecological network, varies significantly across palms and mammal frugivore guilds. Moreover, variation in the strength of interaction between palm-frugivore guilds mediates the response of FTA to precipitation seasonality. Specifically, strongly interacting guilds show a more significant and positive relationship between FTA and precipitation seasonality. In other words, palm species among guilds with more specialized seed dispersal are more common while palm species among guilds with a generalist seed dispersal strategy become rarer towards regions where rainfall is seasonal (Figure 5b, 5d). As precipitation becomes more seasonal, palm functional richness shifts towards large-fruited species and mammal frugivore generalists become scarcer. Our results align with findings such as from bat-plant mutualistic pollination networks, where interacting species exhibit lower niche overlap in highly seasonal environments, and for avian-frugivory networks where weaker trait matching is found towards the tropics (Huang et al., 2025; Schleuning et al., 2012), but also contrast with others that report stronger trait-matching and interaction strength towards the tropics in plant-hummingbird pollination networks (Sonne et al., 2020) and avian-palm frugivory (McFadden et al., 2022).

The concept of functional trophic asymmetry (FTA) offers a valuable framework to examine how multitrophic ecological communities respond to shifting environmental conditions. Our results suggest that as global climate change accelerates, rising tem-

peratures and altered precipitation regimes are likely to increase FTA multitrophic palm-frugivore communities and increase specialization in palm seed dispersal networks. A likely consequence is also the loss of ecosystem function, namely plant functional connectivity —the dispersal of plant propagules between habitat patches—, which has been shown to decrease with increased specialization and reduced plant functional diversity (Landim et al., 2025). The same could be true of other ecosystem functions in other types of mutualistic networks, but it remains to be explored (Acosta-Rojas et al., 2023; Landim et al., 2025; Nowak et al., 2025; Rabeau et al., 2025). In addition to climate change, habitat fragmentation and human-induced landscape modifications can independently alter resource and consumer functional diversity, thereby affecting FTA (Béllo Carvalho et al., 2023; Guevara et al., n.d.). Although differences in the extent of landscape fragmentation were not directly investigated in this study, previous research shows that deforestation has a greater impact on the diversity and redundancy of functional roles in plants than in their hummingbird pollinators, suggesting a decline in plant functional roles as forests are lost. Such results reinforce the role of FTA as a key indicator in predicting shifts in ecosystem function (Bello et al., 2023; Brodie et al., 2021; Montoya & Raffaelli, 2010) as species distributions shift in response to climate change (Aizen et al., 2012; Bartley et al., 2019; Hurtado et al., 2024; Valiente-Banuet et al., 2015). Adding additional information such as geographical variation in population density, land-use change, or spatial movement data (e.g., GPS tracking of frugivores) would improve realism and generalization of our models (Beumer et al., 2025; Borah et al., 2022; Cousens et al., 2010). Future work can integrate these elements into our data pipelines once the relevant data becomes available.

530 0.5 Supplementary material:

531 0.5.1 Supplementary figures

532 0.5.2 Figure S1

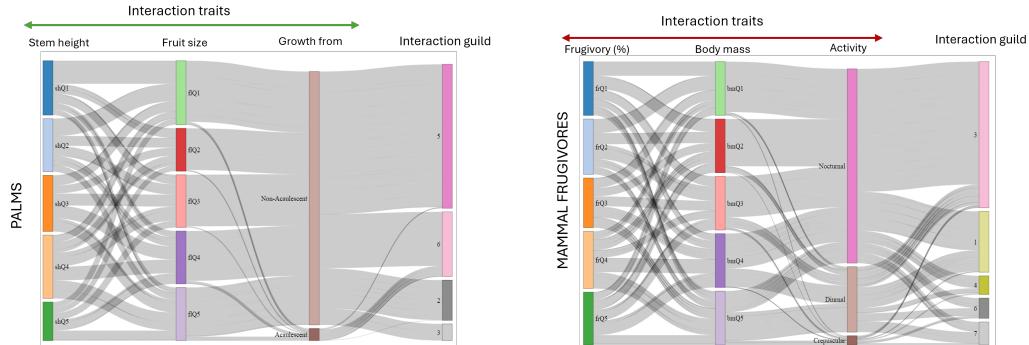
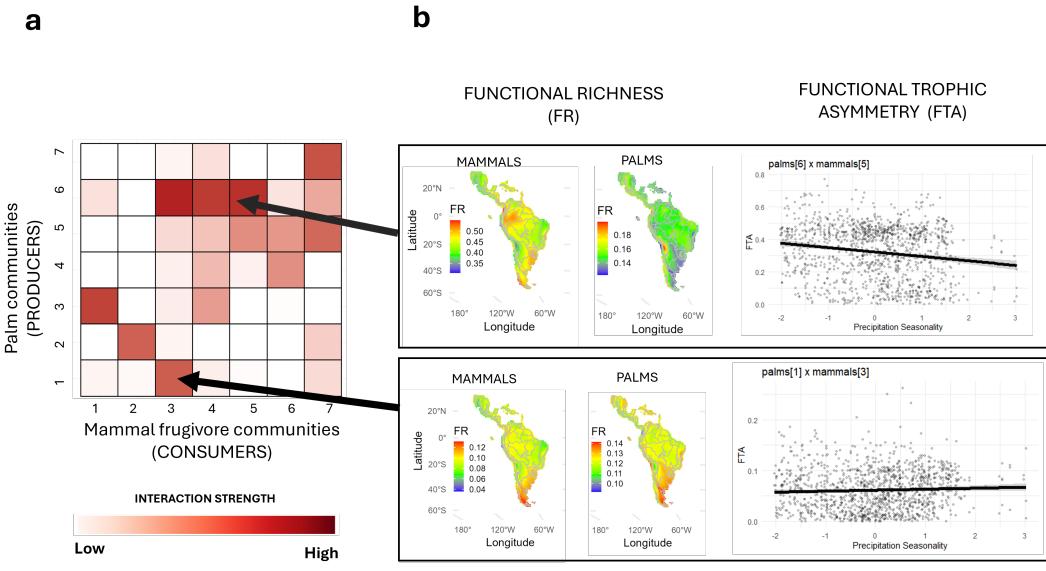


Figure 7: Sankey diagrams illustrating the differences in trait associations to an interaction guild across trophic levels. Top panel - palms: Relationships between stem height and fruit size, followed by a growth form classification (Aculescent vs. Non-Aculescent). Bottom panel-mammal frugivores: Relationships between percentage frugivory in diet and body size categorized into different activity periods (Nocturnal, Diurnal, and Crepuscular). Stem height, Fruit size, Frugivory (%) and Body mass are continuous traits that are grouped into quintiles for visualization purposes. Interaction guilds are defined for both groups with Stochastic Block Modelling of the palm-mammal frugivore interaction aggregated metaweb for the Neotropics. Trait associations to interaction guilds were discovered through multinomial classification modelling using a neural network backend.

533 **0.5.3 Figure S2**

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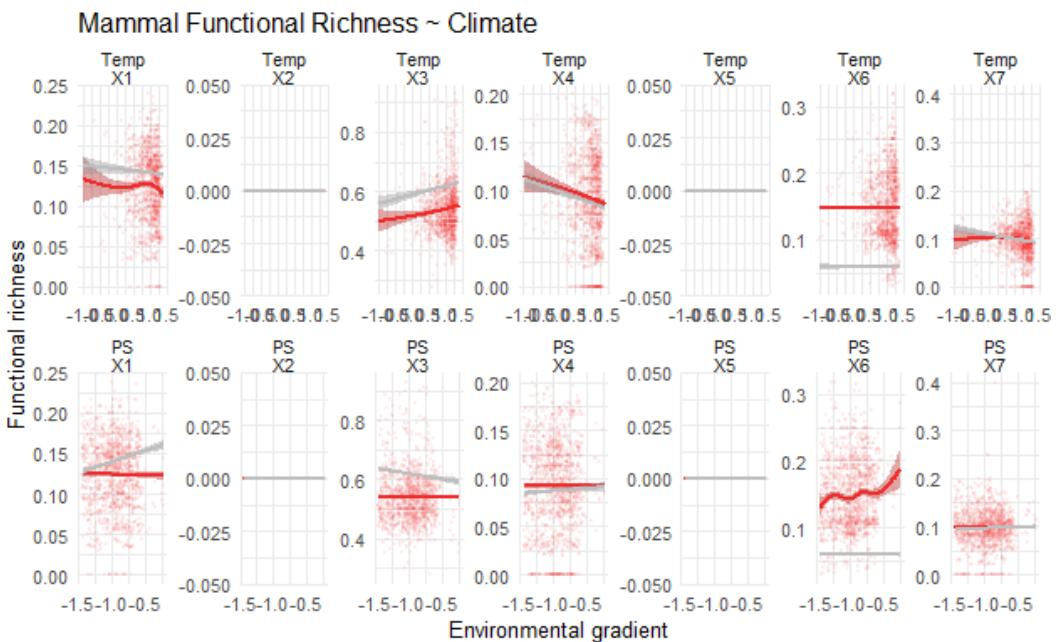
535 **0.5.4 Figure S3**

Figure 8: Changes in the functional richness of mammals along gradients of temperature and precipitation seasonality. Each pane represents the trend of the communities of mammals in a single interaction guild. Red lines represent observed trends, gray lines represent expected trends from a null model

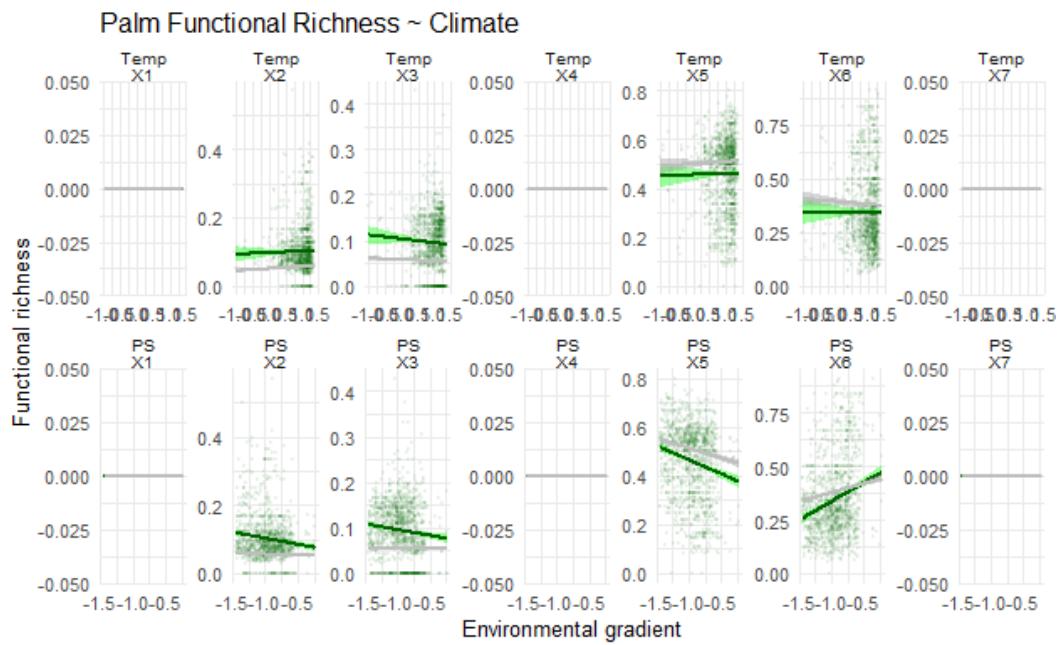
536 **0.5.5 Figure S4**

Figure 9: Changes in the functional richness of palms along gradients of temperature and precipitation seasonality. Each pane represents the trend of the communities of mammals in a single interaction guild. Green lines represent observed trends, gray lines represent expected trends from a null model.

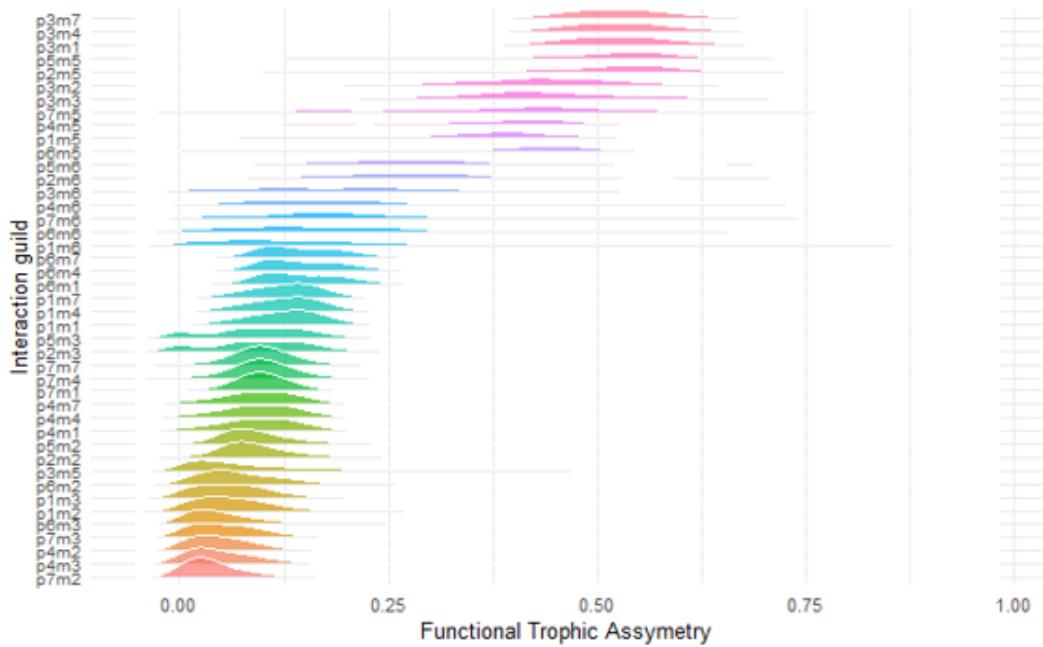
537 **0.5.6 Figure S5**

Figure 10: Functional trophic asymmetry across interaction guilds. Histograms show the distribution of FTA across each combination of palm (p) and mammal (m) guilds across the Neotropics.

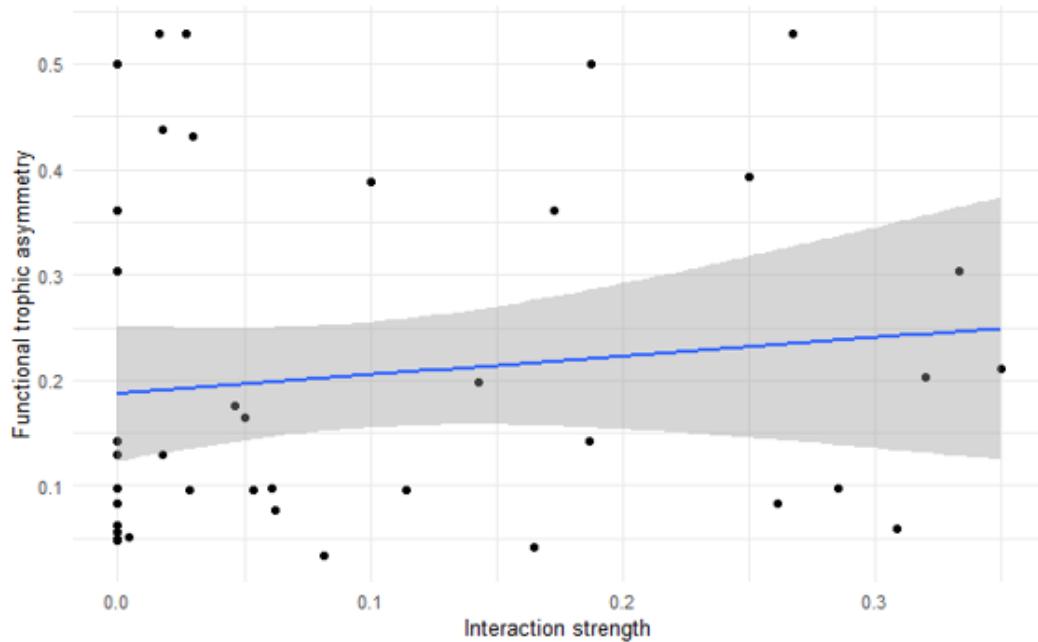
538 **0.5.7 Figure S6**

Figure 11: The relationship between Functional Trophic Asymmetry and Interaction Strength. The y-axis represents the median FTA of an interaction guild. The x-axis represents the interaction strength, measured by their interaction probability between guilds modelled by a stochastic block model (SBM)

539 **0.5.8 Figure S7**

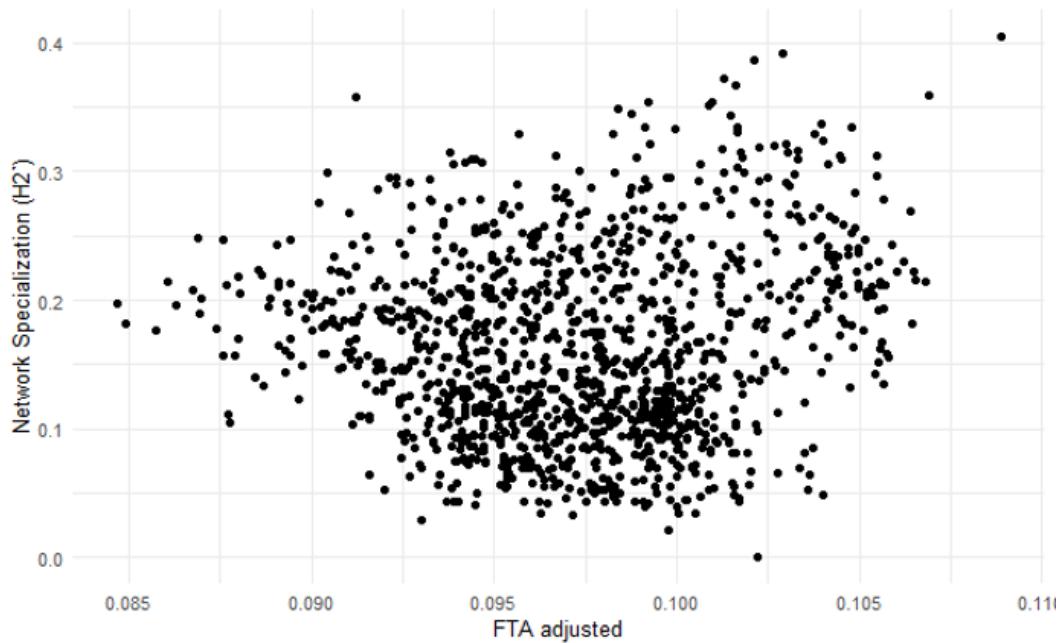
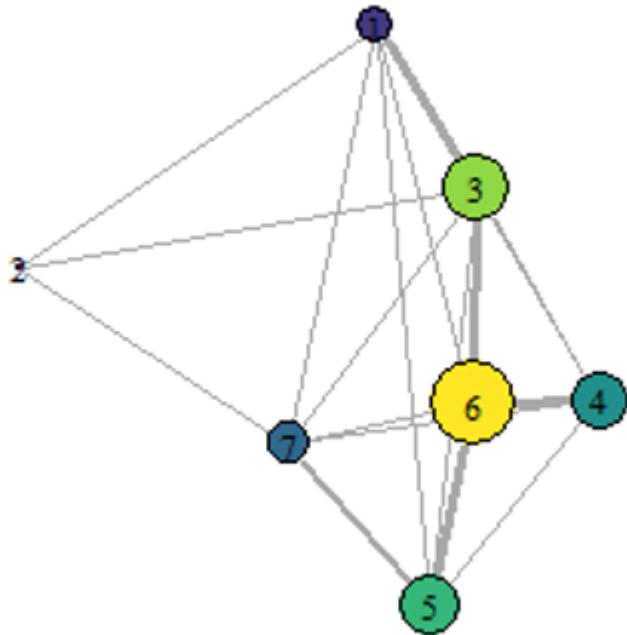


Figure 12: The relationship between Network specialization and FTA (adjusted for interaction strength)

540 **0.5.9 Figure S8**

541
542 Figure 13: The relative influence of distinct interaction guilds on maintaining the
543 Neotropical seed dispersal networks. Nodes represent a con-
544 sumer/producer guild and links represents interactions among them. The size of nodes
545 highlights the node-centrality, a measure of connectivity and influence over other nodes in
546 the network.
547

548 **0.6 Supplementary tables**
549 **Supplementary text**

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