Downscaling mutualistic networks from species to individuals reveals consistent interaction niches and roles within plant populations

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Author Contributions:

All authors conceptualized the study and provided data, E.Q., B.A.C., and J.I. curated data, E.Q. and F.R.S. developed software, E.Q. performed formal analyses and visualization, F.R.S. and P.J. supervised the study, P.J. provided funding acquisition and project management, E.Q. led writing, all authors contributed to writing, reviewing and editing.

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Abstract

Species-level networks emerge as the combination of interactions spanning multiple individuals, and their study has received considerable attention over the past 30 years. However, less is known about the structure of individual interaction configurations within species, being the fundamental scale at which ecological interactions occur in nature.

We compiled 46 empirical, individual-based, interaction networks on plant-animal seed dispersal mutualisms, comprising 1037 plant individuals across 29 species from various regions. We compare the structure of individual-based networks to that of species-based networks and, by extending the niche concept to interaction assemblages, we explore individual plant specialization. Using a Bayesian framework to account for uncertainty derived from sampling, we examine how plant individuals “explore” the interaction niche of their population.

Both individual-based and species-based networks exhibited high variability in network properties, lacking remarkable structural and topological differences between them. Within populations, frugivores' interaction allocation among plant individuals was highly heterogeneous, with one to three frugivore species dominating interactions. Regardless of species or bioregion, plant individuals displayed a variety of interaction profiles across populations, with a consistently small percentage of individuals playing a central role and exhibiting high diversity in their interaction assemblage. Plant populations showed varying mid to low levels of niche specialization; on average individuals' interaction niche ”breadth” accounted for 70% of the interaction diversity.

Our results emphasize the importance of downscaling from species to individual-based networks to understand the structuring of interactions within ecological communities and provide an empirical basis for the extension of niche theory to complex mutualistic networks.

Significance Statement

Ecological interactions in nature occur between individual partners rather than species, and their outcomes determine fitness variation. By examining among-individual variation in interaction niches, we can bridge evolutionary and ecological perspectives to understand interaction biodiversity. This study investigates individual plant variation in frugivore assemblages worldwide, exploring how plant individuals “build” their interaction profiles with animal frugivores. The structure of networks composed of individuals was surprisingly similar to networks composed of species. Within populations, only a few plants played a key role in attracting a high diversity of frugivores, making them central to the overall network structure. Individuals actually explored a substantial diversity of partners, with individual interaction “breadth” accounting for up to 70% of total interaction diversity on average.

Introduction

Species are a fundamental unit of study in most ecological research, resulting in numerous theoretical and methodological approaches to assess how their interactions support ecosystem functions. Food web theory and, recently, network ecology based on graph theory emerged as a useful framework to study these multi-species interactions simultaneously and assess the complexity of natural ecosystems (Solé & Valverde 2004, Fortuna & Bascompte 2008, Fontaine et al. 2011). Starting with food webs (Cohen 1978), network theory expanded its versatility to other ecological interaction modes such as mutualisms (Jordano 1987, Memmott 1999). Since then, abundant literature has revealed emergent and global properties of ecological networks, highlighting surprisingly similar architecture in the way they are assembled (McCann et al. 1998, Mora et al. 2018). Among ecological networks, mutualistic networks represent mutually beneficial interactions, and their structure and topology have been extensively explored (Bascompte & Jordano 2007). Plant-animal mutualistic networks are highly heterogeneous (i.e., most species have few interactions while a minority of species are much more connected) and nested (i.e., specialists interact with subsets of the species with which generalists interact), leading to asymmetric dependences among species (Jordano et al. 2003, Bascompte & Jordano 2007). Yet, it is not clear to what extent these properties percolate to networks at lower levels of organization, such as those composed of individual interactions.

Although interaction patterns are usually summarized at the species level, ecological interactions actually occur as encounters between individuals rather than species (Clark et al. 2011). For instance, while we may say that blackbirds (*Turdus merula*) consume and disperse raspberries (*Rubus idaeus*), it is actually certain individual raspberry plants that interact with individual blackbirds within a local population. By missing this individual-level resolution we miss two important opportunities: 1) the ability to effectively link individual trait variation with interaction outcomes (fitness effects) and thus connect ecological and

evolutionary perspectives; and 2) to bridge the gap between niche theory and complex interaction networks, i.e, to assess how individual-based interactions scale up into complex interaction networks.

Classical studies of frugivory interactions for animal-mediated seed dispersal have been plant-focused (e.g., Snow & Snow 1988), and provide a useful framework to zoom-in into the interactions established between a particular plant species and a set of animal frugivores. By considering individual-based networks, in which one set of nodes is composed of plant individuals, and the other set is composed of animal species (i.e., individual-species network), we can examine individual variation in “interactions build-up”, as well as its subsequent implications, in e.g., fitness (Rodríguez-Rodríguez et al. 2017). This is helpful not just for building a proper bridge between interaction ecology and demographic consequences (e.g., Quintero et al. 2023), but also for bridging network ecology with evolutionary consequences (Guimarães et al. 2011, Segar et al. 2020).

Network structure may not be consistent across hierarchical scales of organization (Tur et al. 2014, Wang et al. 2021). To begin with, the similarity in the set of partners available to individuals of the same species will be higher than that to different species. That is, the physical and phenological traits of conspecific individuals tend to be more similar than those among species (Siefert et al. 2015), discouraging major forbidden interactions (but see Albert et al. 2010, González-Varo & Traveset 2016) and likely increase overall network connectance. Thus, we might expect individual-based networks to exhibit architectural and structural properties different to those found in species-based networks; yet, this remains an underexplored question.

Downscaling the study of interactions to individuals allows us to observe how the variation among individuals in their partner use is distributed in the population (Fig. 1A-B). Since its origins, the niche concept has provided an ideal framework for studying individual variation in resource use (Grinnell 1917, Van Valen 1965, Bolnick et al. 2003). Even so, most previous

work has focused on antagonistic interactions such as predator-prey trophic niches (Bolnick et al. 2003, Araujo et al. 2011, Costa-Pereira et al. 2018, Costa-Pereira et al. 2019). It was only until very recently that niche theory was applied for understanding individual variation in mutualistic interactions (Tur et al. 2014, Albrecht et al. 2018, Phillips et al. 2020, Koffel et al. 2021, Arroyo-Correa et al. 2023, Gómez et al. 2023). However, the study on how a plant individual's interaction niche is distributed within a population remains largely unexplored, even less has been compared across different ecological systems. For this study, we rely on the concept of 'interaction niche' as the space defined by the set of species with which a population, or a plant individual, can interact (Fig. 1C) (Ponisio et al. 2019).

Interaction probabilities between plant individuals and animal species (i.e., probability of interspecific encounter, PIE; Chase & Knight 2013) are influenced by a myriad of factors such as population abundances, accessibility of resources, individual preferences or physiological needs (e.g., optimal foraging theory) as well as required matching in traits and phenology (Guimarães 2020). Intraspecific trait variability, neighborhood attributes and spatio-temporal context drive animal preferences for certain plant individuals, which will govern the establishment of interactions between plant individuals and their mutualistic partner species (Sallabanks 1993, Snell et al. 2019, Isla et al. 2023). In mutualistic systems such as pollination or seed dispersal, variation in the patterns of interaction or exploitation of niches (available partners) can play a determining role, as mutualists directly affect the reproductive outcome of individuals, influencing fitness variation and trait selection, which act as raw material for coevolution (Thompson 1999), as well as population dynamics and community assembly (Arroyo-Correa et al. 2023).

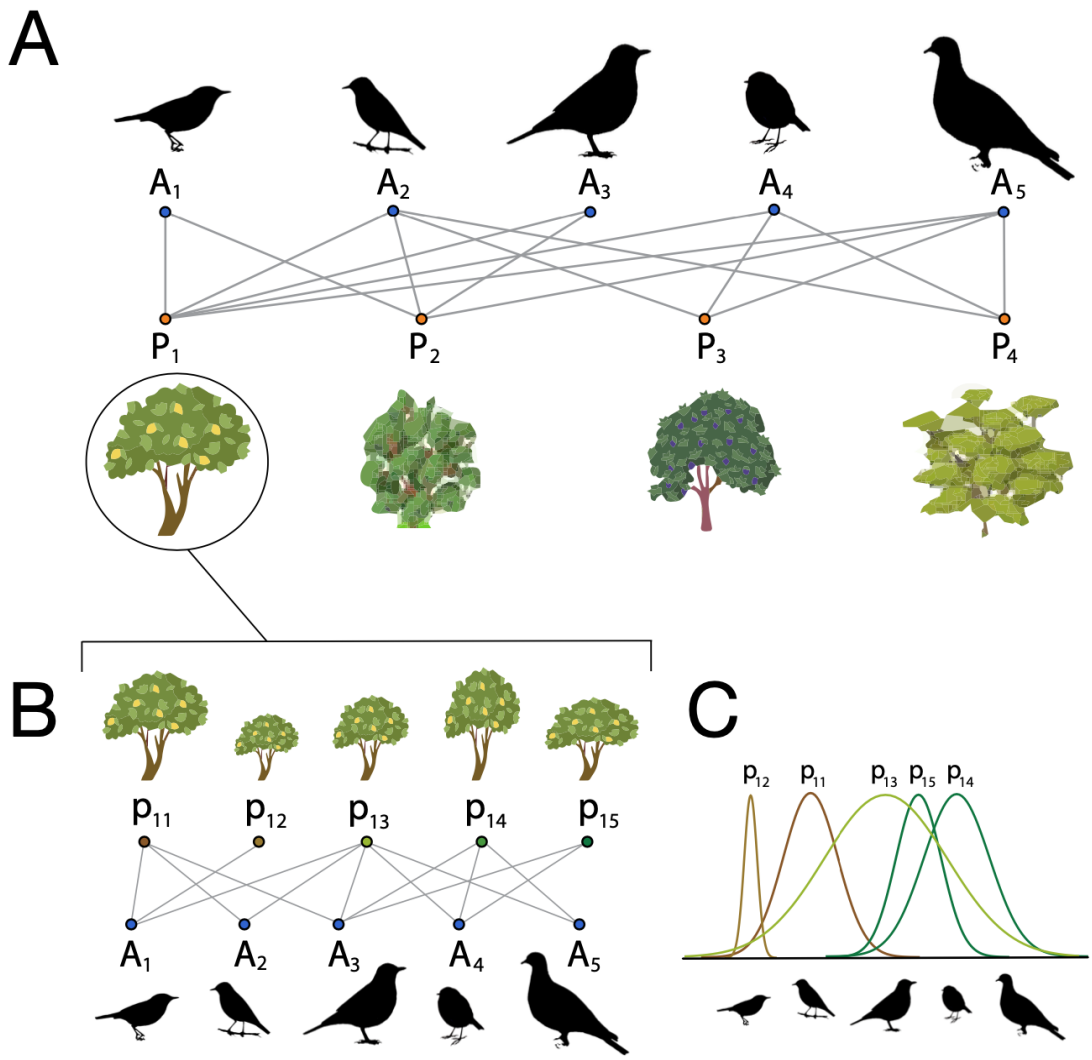

Figure 1. A) Schematic example of a species-based interaction network between four ornithochorous plant species (P_1 - P_4) and their frugivore assemblage with five animal species (A_1 - A_5) (top). B) A zoom in on the individual-based network of plant species P_1 depicting the interactions of its plant individuals (p_{11} - p_{15}) with five animal species, exemplifying the study focus of this paper. C) Different plant individuals (p_{11} - p_{14}) interact with frugivore assemblages of variable diversity, illustrating their individual interaction niches (exemplified by the five colored niche utilization curves within the inset which indicate the relative interaction frequency with each of the five animal species in the assemblage).

Quantifying variation in individual interaction niche-partitioning can shed light on the coexistence and stability of mutualistic communities. The patterns we observe when species interact arise from the way in which their individuals interact (Guimarães 2020). For instance, individuals in a population can behave as specialists or generalists when exploiting their interaction niche, and this may influence how these individuals are affected by interspecific competition and how partner diversity is promoted, determining, e.g., degree distributions in interaction networks (Bascompte & Jordano 2014). The extent to which individuals behave as specialists or generalists in a population can be elucidated by partitioning niche variation into its between- (BIC) and within-individual (WIC) components. This approach can prove useful to predict niche-shifts or niche expansion (Roughgarden, 1972, Bolnick et al. 2007). The levels of individual specialization in individual-based networks can be estimated as the proportion of the total niche width in the population (TNW; total partner diversity) due to within-individual variation (WIC; average partner diversity of individuals). Thus, the distribution of frugivore-partner species richness and interaction allocation among plant individuals can be highly variable in local populations (e.g., Jordano & Schupp 2000, Guerra et al. 2017, Miguel et al. 2018, Jácome-Flores et al. 2020, Quintero et al. 2023). By studying the levels of plant individual specialization and how frugivores allocate their interactions among plants, we aim to understand how variation in mutualistic interactions takes place within plant populations (Fig. 1). Understanding how the interaction niche is partitioned across individuals within populations on a global scale provides a unique ground to expand the concept of niche variation to mutualistic interactions and will open the door to the formulation of new hypotheses to be tested in the future.

A variety of node-level metrics for complex networks can provide insight into an individual's strategy within its population (Dormann 2011, Poisot 2012). Several studies have used node-level metrics to characterize individuals' positioning in the network, informing us

about their role and significance in their population (e.g., Gómez & Perfectti 2012, Rodríguez-Rodríguez et al. 2017, Crestani et al. 2019, Vissoto et al. 2022, Isla et al. 2023, Arroyo-Correa et al. 2023, Guerra et al. 2017). However, most of these studies have used a single or several metrics separately to understand the interaction profile of individuals and for single populations. By using a combination of node-level metrics, we aim to characterize interaction profiles of plant individuals with frugivore species and the distribution and frequencies of roles among and within populations in different geographic regions. Given contrasted differences in e.g., frugivore diversity and life histories across biogeographic realms, we could expect plant individuals from certain regions to exhibit similar interaction profiles, markedly different from those of individuals from other species and/or regions. Conversely, if life history or context-dependent effects were not determinant in structuring interactions between plant individuals and their frugivore partners, we could expect consistent individual interaction profiles across populations, irrespective of geographic location or biome type.

Obtaining an insightful picture of mutualistic network structure from field data is a challenging task. When sampling is limited, the inferred network structure can be noisy, even biased, and thus subject to sampling fluctuations. This issue becomes particularly relevant when comparing networks from different studies (Brimacombe et al. 2023). Here, we build upon Young et al. (2021) Bayesian framework for reconstructing mutualistic networks to infer each pairwise interaction in individual-based networks, accounting for sampling completeness and the inherent stochasticity of field observation data. We then propagate the uncertainty of all pairwise interactions down through niche specialization and network interaction profiles.

The overarching goal of this study is to investigate the role played by individuals in the assembly, structure and functioning of complex ecological interaction networks. To do so, we combine network and niche theory to characterize the interaction profile of plant

individuals in mutualistic seed dispersal systems across different bioregions aiming to illustrate the wide diversity of plant populations considered. We outline three main objectives: 1) examine whether networks composed of individuals exhibit different architectural and structural properties than those found in species-based networks, 2) understand how variation in frugivory interactions takes place at the plant population level by quantifying individual niche-partitioning and frugivore interaction allocation, and 3) characterize interaction profiles of plant individuals with frugivore species and assess the distribution and frequencies of roles among populations.

Results

Structure of individual versus species-based networks

We assembled a total of 46 individual-based plant-frugivore networks and compared them with 59 species-based networks using six network metrics (connectance, nestedness, modularity, assortativity, centralization and interaction evenness, see Methods). Networks showed a remarkable overlap in all metrics at both resolution scales (Fig. 2A). Species-based and individual-based networks presented wide variation in their structure and this variation was maintained when controlled by relative network size and interaction abundances (Table S3). Network metrics at both resolution scales deviated above and below null model expectations, suggesting that the underlying mechanisms driving the network structure are not well differentiated across scales. A few individual-based networks turned out to be more nested and less connected than expected by chance (Fig 2B).

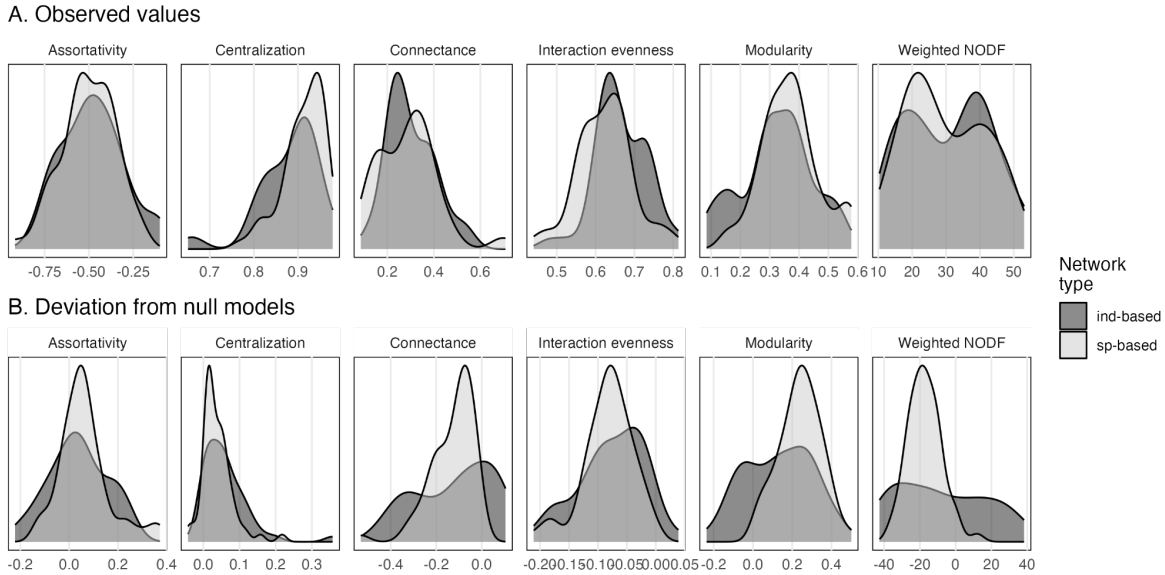

Figure 2. Distribution of (A) observed network-level metrics and (B) deviation of observed metric values from their corresponding null model of frugivory networks at different scales of resolution. Species-based networks are represented in light gray (n = 59) and individual-based networks in dark gray (n = 46). For each network metric, deviation from observed represents the difference between the observed value and the null expectation which represents a network of the same size and same relative abundances (i.e., Patefield's algorithm).

<u>Plant individuals' specialization in interaction niche</u>

The 46 populations included a total of 1037 plant individuals: 373 individuals (from 9 species) from the Mediterranean (Iberian Peninsula), 389 (17 species) from Tropical regions in Asia and America, and 275 (3 species) from Southern Temperate regions (Brazil and Argentina). Our aim in the compilation of individual-based networks was to showcase the diversity of environments and their associated variations; this analysis revealed major gaps in data coverage on the African continent and in the Australasian region (see Table S1). Most plant populations studied presented low to medium levels of individual specialization (mean WIC/TNW = 0.68; 90% CI = 0.32 - 0.95). Individual-based networks from the

Mediterranean region showed a higher proportion of generalized plant individuals (Fig. 3; mean WIC/TNW = 0.82), whereas southern temperate and tropical populations presented higher levels of individual specialization (mean WIC/TNW = 0.56 and 0.65 respectively, p-value < 0.01). Plant populations interacting with higher numbers of frugivore species had a wider interaction niche (TNW, i.e., Shannon diversity index, r = 0.53, p < 0.01), but not necessarily higher levels of individual specialization (WIC/TNW) (Fig. S3). The degree of individual specialization did not increase as TNW increased, because WIC increased in the same proportion as TNW (slope of log-log model = 1.000, SE = 0.005). That is, differences in the degree of individual specialization between bioregions were achieved via changes in both the BIC and the WIC components.

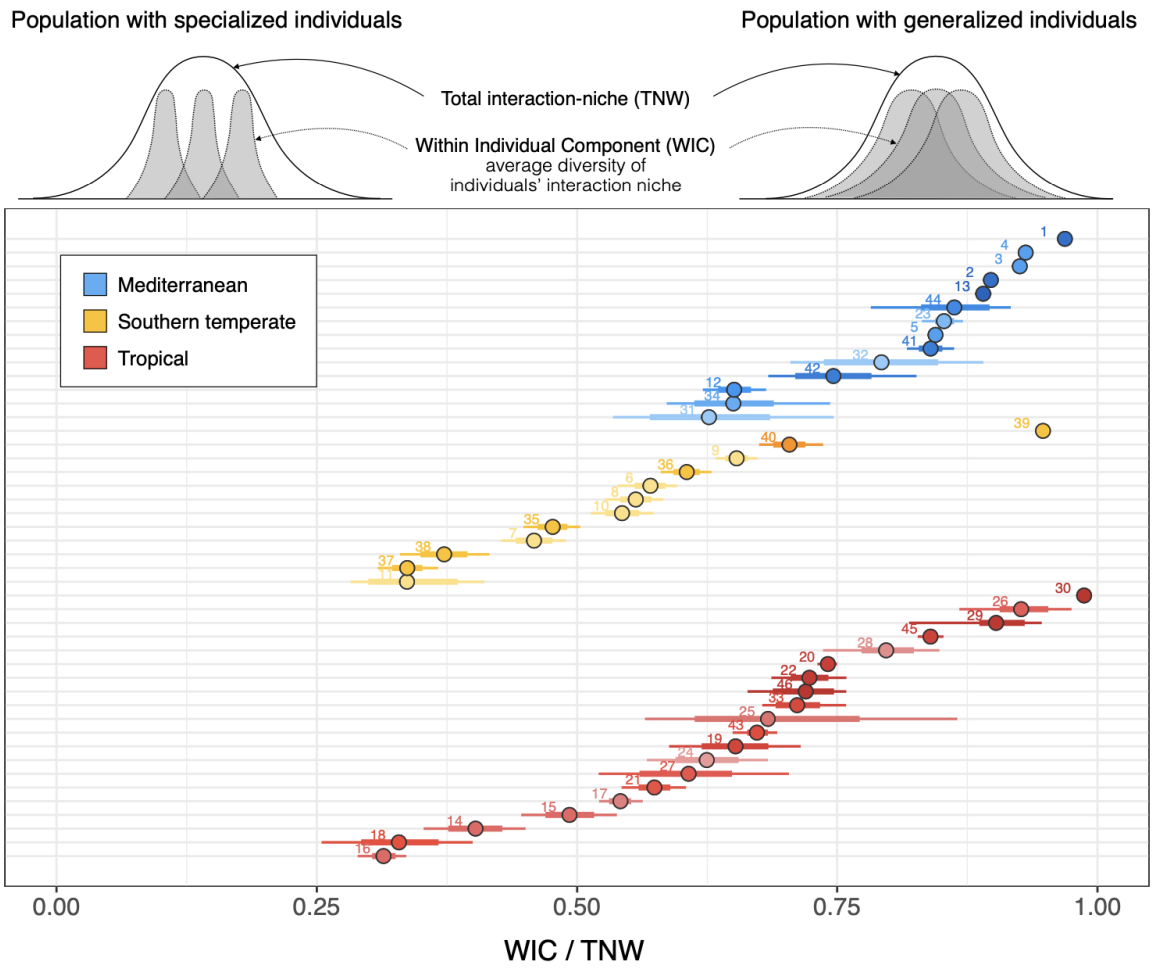

Figure 3. A schematic representation of two plant populations (top): the one on the left presents a population composed of highly specialized individuals (low WIC; low WIC/TNW) and the one on the right presents a population composed of highly generalized individuals (high WIC; high WIC/TNW). Values of WIC/TNW closer to 1 represent populations with generalized individuals where plants use most of the available interaction niche. On the other extreme, values closer to 0 indicate populations with specialized individuals that use a smaller subset of the available interaction niche (in this case plants do not tend to interact with the same frugivore species). Bottom panel: Values of individual specialization (WIC/TNW) for all plant populations studied (n = 46 networks). The total niche width (TNW) represents the interaction niche of the population, calculated as the Shannon diversity of interactions with frugivore species at the population level, i.e., aggregating across individuals. The within-individual component (WIC) is the average diversity of interactions with frugivores found within individual plants. Each point-interval in the graph represents an individual-based network (i.e., population), where the point indicates the mean WIC/TNW, and the thick and thin lines span the 60% and 90% credibility interval, respectively of each network posterior distribution. Colors represent the bioregions of the study site (see Table S1 for each network metadata).

Frugivore interactions within plant populations

Across all plant populations and regions, we found that just a reduced subset of frugivore species (generally between one and three) usually accumulated most of the interactions, while the rest of frugivore species contributed a minor proportion. On average, more than half of these interactions were contributed by less than 20% of frugivores (SD = 8.2%), regardless of the total number of frugivore species in the plant population (Fig. S4). The frugivores that contributed most interactions also tended to interact with a higher number of plant individuals (Spearman's rho = 0.81, Fig. 4). Remarkably, frugivore species with smaller

contributions interacted with a variable proportion of plant individuals, such proportion being higher in Mediterranean networks and lower in Southern Temperate networks (Fig. 4). Frugivores' body mass was not correlated with interaction contribution (rho = -0.08) nor with the proportion of plant individuals interacted (rho = -0.13).

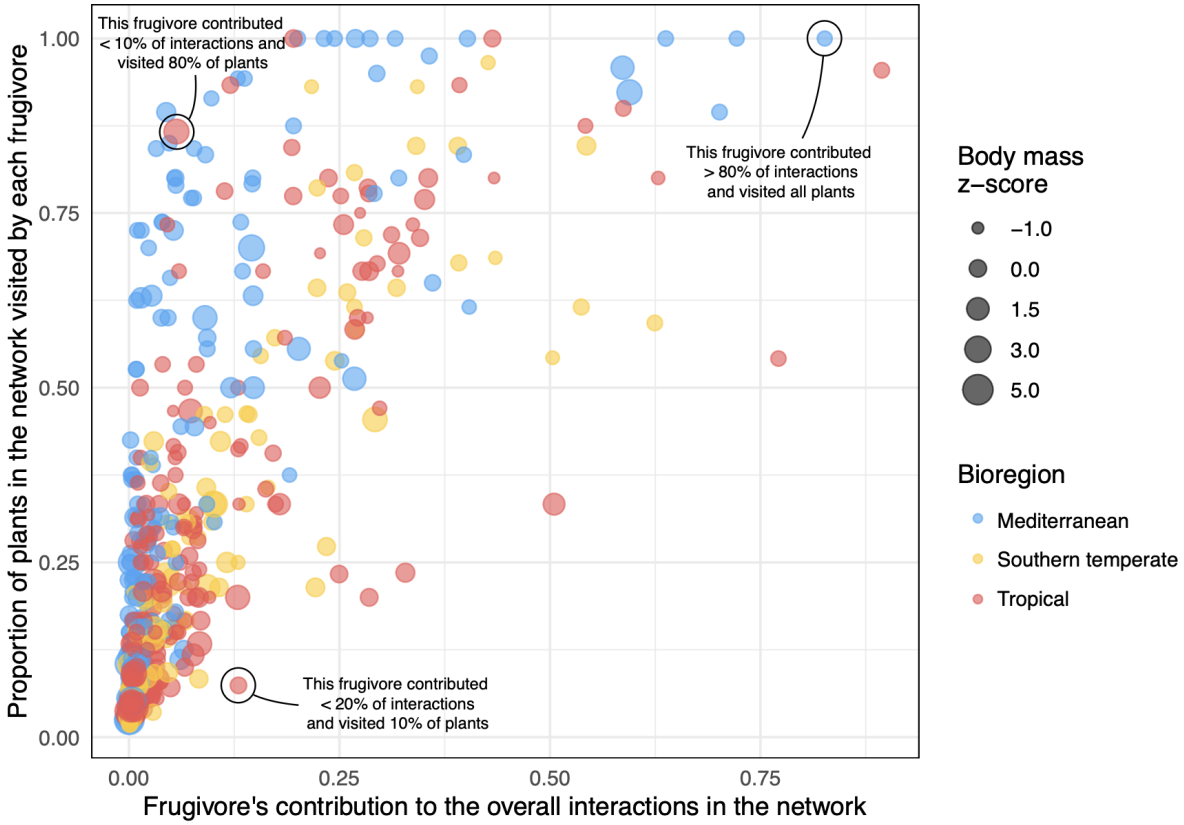

Figure 4. Relationship between the overall contribution to the total number of interactions by each frugivore species (i.e., link weights in the individual-based networks) and the proportion of plant individuals with which they interacted (i.e., animal degree). Each point represents a frugivore species in their respective plant population (individual-based network). Point color indicates the bioregion and point size represents the frugivore's body mass relative to its population (z-score).

Plant individuals' interaction profiles

A principal component analysis of all plant individuals on five node-level metrics (normalized degree, strength, specificity, overlap and weighted closeness; see Methods) did not produce distinct clusters by bioregion or population. Instead, individuals from different populations spread across the multidimensional space, suggesting ample within-population heterogeneity in plant individuals' interaction profiles (Fig. 5, Fig. S6). The first principal component (PC1), explaining more than half of the variation (51%), was mainly related to interaction degree and specificity index, thus capturing individual variation in frugivore richness and composition of the plant individual's assemblages. The second component (PC2) explained 24% of the variation and was correlated with niche overlap and interaction strength; these metrics are related to plant individuals' interaction patterns in relation to their conspecifics and affected by interaction frequency (link weight). Plant individuals with more unique frugivore assemblages were positioned in the upper area of the PCA, while many plants with highly-overlapping frugivore assemblages within their populations were positioned towards the bottom area. The third component (PC3; 10% variation explained; Table S4) was strongly related to weighted closeness, a measure of how strongly and well connected (i.e., central) individuals are within the network.

Few plants were highly central in the interaction network (high weighted closeness) and important for frugivore dependence (high species strength) (i.e., points in the upper-left area of the multivariate space). Most plant individuals showed uneven dependencies on frugivore species and/or medium-high frugivore overlap with other plants in the population. Yet plants with strong dependencies on one or few frugivore species tended to show lower overlap with other individuals in the frugivore assemblage, suggesting a trade-off between partner specialization and partner sharing (lower-right Fig. 5). Overall, plant individuals from the Mediterranean tended to have more similar frugivore assemblages (higher niche

overlap), while plant individuals from Southern Temperate regions presented less overlapping and more specialized frugivore assemblages (Fig. S7).

A cluster analysis further revealed consistent interaction profiles within plant populations, regardless of bioregion or species. All networks presented a variable but substantial proportion (mean = 44%; 90% CI = 17 - 77%) of plant individuals with “neutral” interaction profiles, which did not excel in any node-level metric (Fig. 5, Fig. S7). The clusters “specialized” (mean = 35%; 90% CI = 6 - 68%) and “overlapping” (mean = 39%; 90% CI = 3 - 93%) included a variable but substantial proportion of plants, most likely reflecting either distinct frugivore assemblages (e.g., the tropical biomes) or more overlapping in composition (mostly non-tropical), respectively. Notably, in most populations (36 out of 46), we detected a low proportion (mean = 12%, 90% CI = 3 - 27 %) of “keystone” individuals showing high strength and weighted closeness, accounting for a high proportion of interactions within their respective populations.

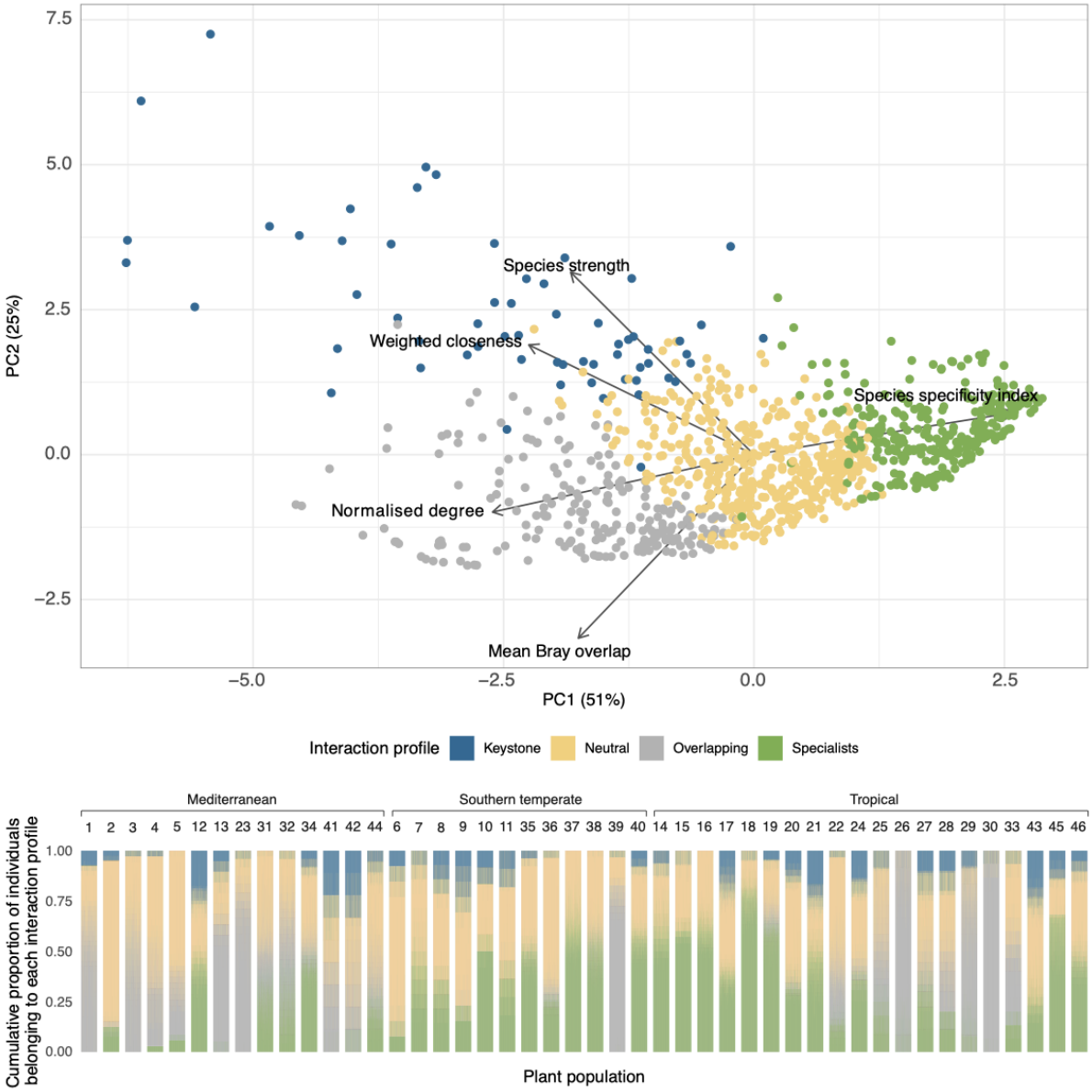

Figure 5. Principal Component Analysis for node-level metrics of individual plants in all plant populations with the most common cluster attribution for each individual depicted in color. Each plant individual is represented by the centroid of its 1000 node-metric values calculated with the full posterior distribution (Fig. S6). The panel below shows different plant populations as bars with a number code above (see Table S1) and the vertical lines composing the bars represent the cumulative percentage of individuals attributed to each cluster or interaction profile for each posterior sample (n = 1000).

Discussion

Our study provides new insights on how downscaling from species to individuals reveals new aspects of ecological interaction assembly, such as the consistency of structural properties of networks across biological organization scales, how mutualistic partner allocation takes place among plants in different populations around the world, as well as the similarity in the interaction profiles within populations regardless the species or ecological context.

Effects of downscaling resolution on network structure

The structure of plant-animal mutualistic networks revealed fundamental heterogeneity across networks and resolution scales. We did not find major deviations in the assembly patterns of interactions as we zoomed in from species to an individual-based scale. Previous research exploring the consequences of downscaling on network architecture found significant shifts in the structure of pollination networks (Tur el al. 2014, Wang et al. 2021): individual-based networks were less connected and individuals were more specialized than species. These studies, however, focused on a specific single community and used the same methodology for sampling both resolution scales. In contrast, our approach considers independent communities and populations from different regions of the world sampled with different methodologies, capturing much broader variation in interaction patterns. Compared to species-based networks, we found that individual-based networks were sometimes more nested than expected by chance. This result can be explained by the lack of major forbidden links in individual-based networks, as frugivores can potentially interact with most conspecific plant individuals, in contrast with species-based networks involving heterogeneous sets of plant species. We argue that the addition of new species or individuals with new traits to a network provides new link possibilities, yet in species-based networks, potential interactions must undergo stronger trait and

phenological matching filters than in individual-based networks (Sazatornil et al. 2016). Simply put, a given frugivore species may interact with a broader range of partners within a plant population than when interacting with the full range of available plant species in a plant community. The former set imposes less restricted limitations to interactions by including much more homogenous conspecific partners (despite intraspecific variation; see, González-Varo & Traveset 2016). In this way, downscaling from species to individuals fundamentally alters the probabilistic distribution of interactions among partners (Poisot et al. 2016).

Besides differences in the analytical approach, the structure of individual-based pollination and frugivory systems likely differs due to the nature of both ecological interactions (Wheelwright & Orians 1982, Jordano 1987). For instance, adjustment between the corolla and mouthparts in pollination systems usually requires stronger morphological coupling and is probably more favored (to avoid hybridization) than the adjustment between fruits and consumers' mouthparts in seed-dispersal systems (Wheelwright & Orians 1982, Jordano 1987), making pollination networks more specialized (see e.g., Mello et al. 2011).

Aside from minor differences in certain network metrics, the overall topology and structure of frugivory networks at different resolution scales were not sufficient to make clear distinctions. The convergence in network structure could indicate the lack of proper discriminatory tools or the existence of underlying forces that control ecological network configurations (e.g., the ultimate distribution of probabilities of interspecific encounters, PIEs). We argue that numerical effects are likely at the base of these emergent properties, governing interactions distribution across nodes and asymmetric interactions (Vázquez et al. 2007, Schleuning et al. 2011, Guimarães 2020). These numerical effects can be caused by varied organism abundances in the case of species, or traits and genotypes in the case of individuals that modulate the attractiveness of plants to frugivores, such as crop size, plant height, or phenology.

380 Individual specialization in the interaction niche

381 Individuals' interaction niches were narrower than that of their populations, supporting that
382 individual specialization in mutualisms is substantial and common in nature (Bolnick et al.
383 2003). Plant individuals' specialization levels were similar to specialization levels reported in
384 other animal taxa (Araujo et al. 2011). Interestingly, the degree of individual specialization
385 varied across biogeographic regions, yet most plant species showed WIC/TNW ratios >50
386 %, which indicates moderate generalization among plant individuals. Broader and more
387 overlapping frugivore assemblages in Mediterranean regions versus higher specialization
388 and variability in southern temperate and tropical networks (higher frequency of study cases
389 with WIC/TNW ratios <50 %) could not be attributed to differences in taxonomic diversity
390 as both regions presented similar total niche width (Fig. S3). Instead, plant individuals in
391 southern temperate regions presented smaller relative niches. Tropical populations
392 consisted of frugivore assemblages of variable diversity and displayed highly variable
393 individual specialization. The lack of differentiation in total niche breadth among bioregions
394 is consistent with findings for terrestrial food webs, where the latitude-niche breadth
395 hypothesis that predicts tropical populations to develop narrower niches was not confirmed
396 (Cirtwill et al. 2015). The large variation in individual specialization within bioregions may be
397 pointing to the role of fine-scale factors such as the local habitat, neighborhood effects, or
398 the influences of individual phenological variation. Further research is needed to evaluate
399 the ecological correlates of plant individuals' positions within these interaction networks
400 and their consequences.

401 Different levels of individual specialization can have implications for population stability and
402 niche expansion (Van Valen 1965). According to the niche variation hypothesis, populations
403 experiencing niche expansion achieve it through increasing their inter-individual variation
404 (Bolnick et al. 2007). Niche shifts and expansion have become exceptionally important for
405 adaptation to changing climate conditions (Hallfors et al 2023) as well as changes in

frugivore assemblages and fluctuating abundances (Campos-Celada et al. 2022). Therefore, the variation we found among populations in frugivore assemblage specialization will have a likely impact on the adaptation of plant–frugivore mutualistic interaction niche in current and future scenarios of global change.

In all plant populations just a few frugivore species, even within diversified assemblages, consistently perform most of the mutualistic interactions (Fig. S5; Rother et al. 2016, Guerra et al. 2017, Isla et al. 2023, Rehling et al. 2023, Thiel et al. 2023). Although frugivore body mass did not prove to be a good indicator of their contribution to interactions (although see Valenzuela-Ospina & Kattan 2021), it may play a role in seed dispersal effectiveness due to its positive correlation with the number of fruits consumed per visit or the frequency of long-distance seed dispersal events (Snow & Snow 1988, Jordano et al. 2007, Godínez-Álvarez et al. 2020). These highly uneven interaction patterns will result in asymmetric dependencies between plant individuals and frugivore species, where the main frugivore species show low specificity for specific plants, while most plant individuals rely mostly on the main frugivore's service (Quintero et al. 2023). Asymmetric dependency between partners also emerges at species–species interaction level (Vázquez & Aizen 2014, Bascompte et al. 2006); further downscaling into individual-individual interactions would help elucidate if asymmetry remains consistent across scales. Finally, our analysis reveals a consistent trend for frugivory and seed dispersal service in a given plant population (estimated from the proportion of plant individuals with which a frugivore species interacts) to increase with the overall contribution to the total number of interactions by each frugivore species (i.e., link weights in the individual-based networks). Thus, highly central frugivores in these within-population networks consistently span their interactions with a broad range of plant individuals, most likely an emergent result of the asymmetry discussed above.

430 Consistency of individual plants' interaction profiles across regions and populations

431 Plant individuals' interaction profiles were not explained by bioregion or species, pointing to
432 fundamental architectural patterns in the assemblage of mutualistic interactions that are not
433 strongly constrained by phylogeny or geographic location but rather by the interplay
434 between traits and numerical effects (Jordano 1987, Carnicer et al. 2009, Albrecht et al.
435 2018, Guimarães 2020). Remarkably, we found a consistent distribution of plant interaction
436 profiles within populations, in which a substantial fraction of individuals act in an average
437 manner, a variable fraction of individuals stand out for their specialization or redundancy
438 and only very few individuals stand out for their central role, high diversity of interactions,
439 and strong frugivores' dependence on them ("keystone" individuals). Similar results have
440 been found in food webs, revealing the presence of a core group of species fulfilling similar
441 ecological roles alongside peripheral species exhibiting idiosyncratic profiles (Mora et al.
442 2018). It is likely that within frugivory networks these key individuals present unique
443 phenotypic traits, such as abundant fruit crops or advantageous locations that make them
444 reliable to many frugivores (Snell et al. 2019, Isla et al. 2023).

445 Although some of the plant species considered in this study were generalists within their
446 community, individuals in their population also showed narrower and specialized interaction
447 niche breadths (Guerra et al. 2017), illustrating how ecological generalists are in fact
448 heterogeneous collections of relative generalist and specialist individuals (Arroyo-Correa et
449 al. 2023, Bolnick et al. 2007). This admixing illustrates how plant species interacting with a
450 wide range of partners actually emerge as a combination of plant individuals with broad
451 interaction generalization and other individuals with higher interaction specificity.

452 Concluding remarks

453 We found consistent patterns of interaction assembly across biological scales using a set of
454 biologically informative network metrics. On top of the absence of a clear hierarchy

differentiation in network structure between individuals and species, we found that almost every network included a similar representation of individual interaction profiles, evidencing a common backbone in the way interactions are organized (Mora et al. 2018). Conducting future analyses on interaction modes or motifs of individual-based networks may provide us with new insights, as these approaches have proven effective in distinguishing networks between and within ecological systems (Mora et al. 2018, Michalska-Smith et al. 2022, Pichon et al. 2023).

Intraspecific variation was at the core mutualistic interactions configuration, driven by the widespread interaction profiles of frugivore species with individual plants. High levels of intraspecific variation have been shown to confer greater stability to mutualistic systems (Arroyo-Correa et al. 2023). By zooming in on ecological interactions this study provides valuable insights into how mutualistic interactions are structured at the individual level and reveal underlying patterns of role assignment within populations and across bioregions.

Methods

Dataset acquisition

We compiled studies on frugivory ecological networks with publicly-available data, both at the species and the plant individual level. Species-based networks were gathered from 40 published studies at the community scale (see Table S1). For individual-based networks, which are scarcer, we compiled phyto-centric studies (plant-based), with quantitative information on frugivore visitation on plant individuals within populations. We combined published studies with unpublished datasets, gathering data for 21 different study systems, including datasets from our own field studies with different Mediterranean species (n = 9). Some of the studies selected presented more than one network from different communities (in species-based studies) or populations (in individual-based studies) (Table S1). These

480 datasets document interactions between plant species and animal frugivore species (in
481 species-based studies) or interactions between plant individuals of a single species and
482 animal frugivore species (in individual-based studies). None of the datasets collected are
483 nested, that is, individual-based networks are not sampled within the same study as a
484 species-based network, which prevents a direct structure dependence between the two
485 scales of the datasets. Data was entered as adjacency matrices, where rows represent
486 plant species (or individuals) and columns represent animal species, with matrix elements a_{ij}
487 indicating interaction frequency (visitation frequency to plants). In order to ensure networks
488 were sufficiently sampled to robustly characterize their structure and interaction profiles, we
489 only kept those that were reasonably complete. We checked for sampling coverage of
490 individual-based networks using iNext R package (Hsieh et al. 2016) (Table S2). To do so,
491 we converted the adjacency matrix data to an incidence frequency-data and considered
492 plant individuals as sampling units and the number of frugivore species detected at each
493 plant (species richness). We discarded networks in which the number of interacting nodes
494 (plants and frugivore species) was less than 15 or plants were less than six (n = 13
495 networks). Our final dataset consisted of 105 networks with an average size of 384 potential
496 links or cells (range = 65 - 2904) and 90 unique interactions (range = 22 - 419). Forty-six
497 were individual-based networks and 59 were species-based networks (Table S1). When
498 possible we referred the interaction value to the coarsest level, that is, frugivore visitation
499 events, otherwise number of fruits consumed.

500

501 Network-level metrics

502 For both the individual and species-based networks, we calculated several network-level
503 metrics, using R packages bipartite (Dormann et al. 2008) and igraph (Csárdi & Nepusz
504 2006). We selected a representative set of metrics that had suitable biological interpretation

and were not highly correlated (Variance Inflation Factor < 3) and/or not strongly affected by the number of species/individuals sampled or overall network size (Fig. S1, S2).

Selected network-level metrics were:

1. Connectance *(topology).* This metric gives the proportion of realized over potential links in the network. Calculated as the sum of realized links (unweighted) divided by the number of cells in the matrix. Values range from 0 (no links) to 1 (fully connected networks where all nodes interact among them) (Dunne et al. 2002).

2. Weighted nestedness wNODF *(structure)*. It informs on the way interactions are organized. A highly nested structure is one in which nodes with fewer connections tend to interact with a subset of highly connected nodes that in turn interact with the highly connected ones (Bascompte et al. 2003). Values of 0 indicate non-nestedness, those of 100 perfect nesting (Almeida-Neto & Ulrich 2011).

3. Assortativity *(topology)*. This metric indicates the level of homophily among nodes in the graph. It ranges from -1 to 1, when high it means that nodes tend to connect with nodes of similar degree; when low, nodes of low-degree connect with nodes of high-degree (disassortative) (Newman 2002, Barabasi 2016).

4. Modularity *(structure - clustering)*. It reflects the tendency of a network to be organized in distinct clusters or modules (Bascompte & Jordano 2014). This metric ranges from 0 (no clusters) to 1, where nodes within a module interact more among them than with nodes from other modules (highly compartmentalized network; Newman 2006).

5. Eigenvector centralization *(centrality)*. This metric quantifies how centralized or decentralized the distribution of eigenvector centrality scores is across all nodes in a network (Freeman et al. 1979). The eigenvector centrality of a given node in a network is a measure of the influence of that node, taking into account both the node's direct connections and the connections of its neighbors. Nodes with high eigenvector

centrality are connected to other nodes that are also central, giving them a higher score (de Oliveira Lima et al. 2020). Therefore, the network-level eigenvector centralization provides a measure of the extent to which a few nodes dominate the network in terms of influence. In a network with low centralization, the centrality scores are relatively evenly distributed among the nodes, suggesting a more decentralized structure where many nodes contribute to the overall connectivity of the network, and therefore to the interaction services. On the other hand, a network with high centralization indicates that only a small number of nodes have a higher centrality, suggesting a more centralized structure where a few nodes play a crucial role in the network's overall connectivity. We normalized this measure to ensure that the centralization value is relative to the maximum centralization for a network of a given size.

6. Interaction evenness (*interaction diversity*). Also known as Pielou's evenness, quantifies how balanced the distribution of interactions is across nodes (Blüthgen et al. 2008). This metric considers all links as species, and their weight as a measure of their abundance. It quantifies link diversity using Shannon index and divides it by the theoretical maximum richness of all possible links (i.e., logarithm of Shannon). It ranges from 0 to 1, where low values indicate high unevenness and high values approach perfect evenness in interaction distribution.

<u>Bayesian modeling of individual-based network structure</u>

Reconstructing mutualistic network structure from field data is a challenging task. Interaction data are hard to collect and require typically large sampling efforts, particularly to characterize infrequent interactions. Inferred network structure is highly sensitive to sampling design, effort, and completeness. Comparing networks from different studies without accounting for these sampling effects may lead to mistaken inferences (Brimacombe et al. 2023). Here, we build upon Young et al. (2021) Bayesian framework for

reconstructing mutualistic networks to infer the posterior probability of each pairwise interaction in individual-based networks, accounting for sampling completeness and the inherent stochasticity of field observation data.

Following Young et al. (2021), pairwise interaction counts can be modeled as determined by the sampling effort spent on each plant, the relative interaction abundance of each plant and animal in the population, the (inferred) existence of an interaction link among both partners, and the "preference" parameter, which relates how many visits or interactions occur for interacting partners compared to the number of visits or interactions for non-mutualists (no link inferred). Here we adapted Young et al. (2021) model to allow for varying preferences (i.e., interaction counts) among different frugivore species. Following Young et al. (2021) we used exponential priors with rate parameters beta = 0.01 for those preference parameters. We fitted a Bayesian model to each individual-based network using the newly developed 'BayesianNetworks' R Package (Rodríguez-Sánchez & Young 2024). 'BayesianNetworks' relies on Stan (Stan Development Team 2024) and cmdstanr (Gabry et al. 2024) for parameter estimation, and includes functions to facilitate modeling of bipartite mutualistic networks, including data preparation, model fitting, checking and visualization. As model output, we obtained 1000 samples of the posterior count expected for each pairwise interaction. Posterior predictive checks showed the expected increase of uncertainty in poorly sampled networks, and overall confirmed the good match between the observed data and predicted counts. Posterior distributions of pairwise interaction counts were then propagated all the way down to individual node metrics and analysis of niche specialization.

<u>Network standardization</u>

All posterior interaction counts were rounded to integer numbers. When sampling effort among plant individuals was heterogeneous within the population (21 out of 46 nets), we divided the posterior interaction counts (e.g., number of visits) by the amount of time

observed and/or the area sampled in each plant, so that interaction counts were comparable.

Once all individual-based networks were controlled by sampling effort and rounded, we scaled both individual-based and species-based networks by dividing the weight of each pairwise interaction by the total number of interactions in the matrix (grand total standardization; Quintero et al. 2022). Therefore, the interaction values (matrix cells) represent the relative frequency of a plant individual (in individual-based networks) or a plant species (in species-based networks) interacting with a given frugivore species, and the sum of all relative frequencies equals one.

Niche specialization

We estimated populations' niche specialization using the Shannon approximation of the WIC/TNW index for discrete data (Roughgarden 1979, Bolnick et al. 2002). In this case, we define as a niche-resource the available coterie of visiting frugivore species in a given population. This index computes the relative degree of individual specialization as the proportion of total niche width (TNW) explained by within-individual variation (WIC). Total niche width (TNW) is calculated as the total diversity of frugivore species visiting the plant population, using Shannon index. The within-individual variation (WIC) is calculated as the average Shannon diversity of frugivores for each plant individual, weighted by the relative proportion of all frugivore interactions in the population that are used by each individual. Finally, WIC is divided by TNW. Values closer to 1 indicate a population composed of generalist individuals that are using most of the population niche. On the contrary, values closer to 0 indicate a population of specialist individuals using small subsets of the population niche, with large differences in resource-use among them. WIC and TNW estimates were calculated for the Bayesian output of each network, rendering a credibility interval for each population. To test differences in individual specialization (i.e., WIC/TNW)

between different bioregions (n = 3) we fitted a mixed-effects linear model with a normal distribution where the network and study were present as random factors (Bates et al. 2015).

Node-level metrics

To characterize plant individuals' interaction profiles in their populations, we computed a set of node-level indices for each plant individual using R package bipartite (Dormann et al. 2008). Additionally, we calculated average niche overlap using Bray-Curtis dissimilarity index (vegan R package; Oksanen et al. 2022). We computed these metrics for the full posterior distribution of each individual, obtaining 1000 values for each individual and index. We selected a representative set of metrics that had a suitable biological interpretation for assessing the individuals' interaction profiles and were not highly correlated nor affected by the number of individuals sampled (Fig. S5).

Selected node-level metrics were:

7. Normalized degree *(interaction diversity).* It represents the richness of partners for a given node and is scaled relative to the rest of nodes in the network. This metric ranges from 0 to 1, where a plant individual would score 1 if it interacts with all the frugivore species available (Dormann 2011).

8. Species specificity index *(interaction diversity)*. This metric informs about the variation in the distribution of interactions with frugivore species partners. It is estimated as a coefficient of variation of interactions for each plant individual, normalized to range between 0 and 1 (Julliard et al. 2006, Poisot et al. 2012). High values indicate higher variation in dependence on frugivore species. Plants with high dependence on few or a single frugivore species yield values close to 1, and plants that distribute their interactions equally with many frugivore species show low values.

9. Species strength *(interaction intensity).* It quantifies the dependence of the community on a given node (Dormann 2011), in this case, the frugivores represent the community and the plant individuals the nodes. It is calculated as the sum of the dependencies of each frugivore species (i.e., the fraction of all visits to a given plant individual coming from a particular frugivore species) (Bascompte et al. 2006).

10. Weighted closeness *(node position).* This metric provides an index of the magnitude to which a given node has short connection paths to all other nodes in the network (Opsahl et al. 2010). It is influenced by the intensity and number of links and indicates to what extent a node is in the "center" of the connections of the graph. This metric is calculated on the unipartite projection of the individual-based network for the plant individuals, in which links between plant individuals represent the number of frugivore interactions shared. In this context, the weighted closeness of a plant individual is estimated as the inverse of the sum of all path lengths (link weights) between this plant individual and all other plant individuals in the unipartite network. Therefore, plant individuals with higher values of weighted closeness are strongly connected with more plant individuals in the population through shared frugivore species.

11. Mean interaction overlap using Bray-Curtis index *(node similarity).* This measure of interaction overlap informs on the average similarity in frugivore use between pairs of plant individuals. This metric indicates how different the frugivore assemblage of a given plant individual is compared to the rest of the population (e.g., Gómez et al. 2010). Higher values (i.e., higher overlap) indicate a higher similarity in interaction assemblage for a given plant individual with respect to other individuals in the population.

654 Data analysis for network metrics

655 In order to determine variation distribution in interaction structuring and node topology we
656 performed a principal component analysis (PCA). Previous studies have used PCA for
657 comparing network metrics (e.g., Sazima et al. 2010, Mora et al. 2018, Medeiros et al. 2018,
658 Burin et al. 2021, Acevedo-Quintero et al 2023). In order to compare plant individuals'
659 interaction profiles, we performed a PCA using the full set of node-level metric distributions
660 estimated for plant individuals within their population (i.e., individual node metrics derived
661 from the full Bayesian posterior of each individual). This resulted in an ordination of
662 elements (1000 points per each plant individual, single values sampled from the full
663 posterior distributions of each individual-based network) in relation to the multivariate space
664 defined by node-level metrics. Thus, such PCA provides an exploratory analysis of how
665 plant individuals span the multivariate space of network metrics, where the location of each
666 individual characterizes its interaction profile.

667 With the aim of identifying distinct plant individual profiles we performed a discriminant
668 analysis of principal components (DAPC) using the adegenet R package (Jombart et al.
669 2023). We performed 1000 DAPCs using node-level metrics derived from the samples of
670 the full posterior distributions of the individual-based networks. A predetermined number of
671 groups equal to 4 was used to run the analysis and plant individuals were assigned to the
672 group with the highest probability as calculated with the DAPC. This analysis was based on
673 the variation captured by the first 3 PCs which together explained 86% of the variance, with
674 eigenvalues >0.7. Cluster groups were then named according to plants' relative position in
675 the PCA and we quantified the percentage of individuals assigned to these four groups for
676 each plant population in each of the 1000 repetitions.

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References

1. Acevedo-Quintero, J. F., Zamora-Abrego, J. G., & Mancera-Rodríguez, N. J. (2023). Structural but not functional resistance of frugivore-plant interaction networks to the defaunation process. *Food Webs*, e00322. https://doi.org/10.1016/j.fooweb.2023.e00322

2. Alatalo, R. V. (1981). Problems in the measurement of evenness in ecology. *Oikos*, *37*(2), 199. https://doi.org/10.2307/3544465

3. Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P., & Lavorel, S. (2010). Intraspecific functional variability: Extent, structure and sources of variation. *Journal of Ecology*, *98*(3), 604–613. https://doi.org/10.1111/j.1365-2745.2010.01651.x

4. Albrecht, J., Classen, A., Vollstädt, M. G. R., Mayr, A., Mollel, N. P., Schellenberger Costa, D., Dulle, H. I., Fischer, M., Hemp, A., Howell, K. M., Kleyer, M., Nauss, T., Peters, M. K., Tschapka, M., Steffan-Dewenter, I., Böhning-Gaese, K., & Schleuning, M. (2018). Plant and animal functional diversity drive mutualistic network assembly across an elevational gradient. *Nature Communications*, *9*(1), 3177. https://doi.org/10.1038/s41467-018-05610-w

5. Almeida-Neto, M., & Ulrich, W. (2011). A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling & Software*, *26*(2), 173–178. https://doi.org/10.1016/j.envsoft.2010.08.003

6. Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, *14*(9), 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

7. Arroyo-Correa, B., Jordano, P., & Bartomeus, I. (2023). Intraspecific variation in species interactions promotes the feasibility of mutualistic assemblages. *Ecology Letters*, *24*, 448–459. https://doi.org/10.1111/ele.14163

8. Barabási, A. L. (2016). *Network science*. Cambridge University Press.

9. Bascompte, J., & Jordano, P. (2007). Plant-animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

10. Bascompte, J., & Jordano, P. (2014). *Mutualistic networks*. Princeton University Press. https://doi.org/10.1515/9781400848720

11. Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences*, *100*(16), 9383–9387. https://doi.org/10.1073/pnas.1633576100

12. Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, *312*, 431–433. https://doi.org/10.1126/science.1123412

13. Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

14. Blüthgen, N., Frund, J., Vázquez, D. P., & Menzel, F. (2008). What do interaction network metrics tell us about specialization and biological traits? *Ecology*, 89(12), 3387–3399. https://doi.org/10.1890/07-2121.1

15. Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C., & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, *26*(4), 183–192. https://doi.org/10.1016/j.tree.2011.01.009

16. Bolnick, D. I., Svanbäck, R., Araújo, M. S., & Persson, L. (2007). Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences*, *104*(24), 10075–10079. https://doi.org/10.1073/pnas.0703743104

17. Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, *106*(1), 1–28.

18. Bolnick, D. I., Yang, L. H., Fordyce, J. A., Davis, J. M., & Svanbäck, R. (2002). Measuring individual-level resource specialization. *Ecology*, *83*(10), 2936–2941. https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2

19. Burin, G., Guimarães Jr, P. R., & Quental, T. B. (2021). Macroevolutionary stability predicts interaction patterns of species in seed dispersal networks. *Science*, *372*, 733–737. https://doi.org/10.1126/science.abf0556

20. Campo-Celada, M., Jordano, P., Benítez-López, A., Gutiérrez-Expósito, C., Rabadán-González, J., & Mendoza, I. (2022). Assessing short and long-term variations in diversity, timing and body condition of frugivorous birds. *Oikos*, *2022*, e08387. https://doi.org/10.1111/oik.08387

21. Carnicer, J., Jordano, P., & Melián, C. J. (2009). The temporal dynamics of resource use by frugivorous birds: A network approach. *Ecology*, *90*(7), 1958–1970. https://doi.org/10.1890/07-1939.1

22. Chase, J. M., & Knight, T. M. (2013). Scale-dependent effect sizes of ecological drivers on biodiversity: Why standardised sampling is not enough. *Ecology Letters*, *16*(s1), 17–26. https://doi.org/10.1111/ele.12112

23. Cirtwill, A. R., Stouffer, D. B., & Romanuk, T. N. (2015). Latitudinal gradients in biotic niche breadth vary across ecosystem types. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1819), 20151589. https://doi.org/10.1098/rspb.2015.1589

24. Clark, J. S., Bell, D. M., Hersh, M. H., Kwit, M. C., Moran, E., Salk, C., Stine, A., Valle, D., & Zhu, K. (2011). Individual-scale variation, species-scale differences: Inference needed to understand diversity: Individual-scale variation, species-scale differences. Ecology Letters, 14(12), 1273–1287. https://doi.org/10.1111/j.1461-0248.2011.01685.x

25. Cohen, J. E. (1978). *Food webs and niche space*. Princeton University Press.

26. Costa-Pereira, R., Araújo, M. S., Souza, F. L., & Ingram, T. (2019). Competition and resource breadth shape niche variation and overlap in multiple trophic dimensions. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1902), 20190369. https://doi.org/10.1098/rspb.2019.0369

27. Costa-Pereira, R., Rudolf, V. H. W., Souza, F. L., & Araújo, M. S. (2018). Drivers of individual niche variation in coexisting species. *Journal of Animal Ecology*, *87*(5), 1452–1464. https://doi.org/10.1111/1365-2656.12879

28. Crestani, A. C., Mello, M. A. R., & Cazetta, E. (2019). Interindividual variations in plant and fruit traits affect the structure of a plant-frugivore network. *Acta Oecologica*, *95*, 120–127. https://doi.org/10.1016/j.actao.2018.11.003

29. Csárdi, G., & Nepusz, T. (2006). The igraph software package for complex network research <http://igraph.org>. *InterJournal Complex Systems*, *1695*, 1–9.

30. de Oliveira Lima, G., Leite, A. V., Souza, C. S., Castro, C. C., & de Santana Bezerra, E. L. (2020). A multilayer network in an herbaceous tropical community reveals multiple roles of floral visitors. *Oikos*, *129*(8), 1141–1151. https://doi.org/10.1111/oik.06565

31. Dormann, C. F. (2011). How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology*, *1*(1), 1–20.

32. Dormann, C. F., Gruber, B., & Fruend, J. (2008). Introducing the bipartite package: Analysing ecological networks. *R News*, *8*(2), 8–11.

33. Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences*, *99*(20), 12917–12922. https://doi.org/10.1073/pnas.192407699

34. Fontaine, C., Guimarães Jr, P. R., Kéfi, S., Loeuille, N., Memmott, J., van der Putten, W. H., van Veen, F. J. F., & Thébault, E. (2011). The ecological and evolutionary implications of merging different types of networks. *Ecology Letters*, *14*(11), 1170–1181. https://doi.org/10.1111/j.1461-0248.2011.01688.x

35. Fortuna, M. A., & Bascompte, J. (2008). The network approach in ecology. In *Unity in diversity: Reflections on ecology after the legacy of Ramon Margalef*. Fundación BBVA.

36. Freeman, L. C., Roeder, D., & Mulholland, R. R. (1979). Centrality in social networks: II. Experimental results. *Social Networks*, *2*(2), 119–141. https://doi.org/10.1016/0378-8733(79)90002-9

37. Gabry J, Češnovar R, Johnson A, Bronder S (2024). cmdstanr: R Interface to 'CmdStan'. R package version 0.8.1, https://discourse.mc-stan.org, https://mc-stan.org/cmdstanr/

38. Godínez-Alvarez, H., Ríos-Casanova, L., & Peco, B. (2020). Are large frugivorous birds better seed dispersers than medium- and small-sized ones? Effect of body mass on seed dispersal effectiveness. *Ecology and Evolution*, *10*(12), 6136–6143. https://doi.org/10.1002/ece3.6285

39. Gómez, J. M., Abdelaziz, M., Lorite, J., Jesús Muñoz-Pajares, A., & Perfectti, F. (2010). Changes in pollinator fauna cause spatial variation in pollen limitation. *Journal of Ecology*, *98*(5), 1243–1252. https://doi.org/10.1111/j.1365-2745.2010.01691.x

40. Gómez, J. M., González-Megías, A., Armas, C., Narbona, E., Navarro, L., & Perfectti, F. (2023). The role of phenotypic plasticity in shaping ecological networks. *Ecology Letters*, *26*(S1), S47–S61. https://doi.org/10.1111/ele.14192

41. Gómez, J. M., & Perfectti, F. (2012). Fitness consequences of centrality in mutualistic individual-based networks. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1734), 1754–1760. https://doi.org/10.1098/rspb.2011.2244

42. González-Varo, J. P., & Traveset, A. (2016). The labile limits of forbidden interactions. *Trends in Ecology & Evolution*, *31*(9), 700–710. https://doi.org/10.1016/j.tree.2016.06.009

43. Grinnell, J. (1917). The niche-relationships of the California thrasher. *The Auk*, *34*(4), 427–433. https://doi.org/10.2307/4072271

44. Guerra, T. J., Dayrell, R. L. C., Arruda, A. J., Dáttilo, W., Teixido, A. L., Messeder, J. V. S., & Silveira, F. A. O. (2017). Intraspecific variation in fruit–frugivore interactions: Effects of fruiting neighborhood and consequences for seed dispersal. *Oecologia*, *185*(2), 233–243. https://doi.org/10.1007/s00442-017-3943-z

45. Guimarães, P. R. (2020). The structure of ecological networks across levels of organization. *Annual Review of Ecology, Evolution, and Systematics*, *51*(1), 433–460. https://doi.org/10.1146/annurev-ecolsys-012220-120819

46. Guimarães, P. R., Jordano, P., & Thompson, J. N. (2011). Evolution and coevolution in mutualistic networks. *Ecology Letters*, *14*(9), 877–885. https://doi.org/10.1111/j.1461-0248.2011.01649.x

47. Hällfors, M. H., Heikkinen, R. K., Kuussaari, M., Lehikoinen, A., Luoto, M., Pöyry, J., Virkkala, R., Saastamoinen, M., & Kujala, H. (2023). Recent range shifts of moths,

butterflies, and birds are driven by the breadth of their climatic niche. *Evolution Letters*, qrad004. https://doi.org/10.1093/evlett/qrad004

48. Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, *54*(2), 427–432. https://doi.org/10.2307/1934352

49. Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

50. Isla, J., Jácome-Flores, M., Arroyo, J. M., & Jordano, P. (2023). The turnover of plant–frugivore interactions along plant range expansion: Consequences for natural colonization processes. *Proceedings of the Royal Society B: Biological Sciences*, *290*(1999), 20222547. https://doi.org/10.1098/rspb.2022.2547

51. Jácome-Flores, M. E., Jordano, P., Delibes, M., & Fedriani, J. M. (2020). Interaction motifs variability in a Mediterranean palm under environmental disturbances: The mutualism–antagonism continuum. *Oikos*, *129*(3), 367–379. https://doi.org/10.1111/oik.06688

52. Jombart, T., Kamvar, Z. N., Collins, C., Lustrik, R., Beugin, M.-P., Knaus, B. J., Solymos, P., Mikryukov, V., Schliep, K., Maié, T., Morkovsky, L., Ahmed, I., Cori, A., Calboli, F., Ewing, R. J., Michaud, F., DeCamp, R., Courtiol, A., Clark, L. V., & Dimens, P. (2023). *adegenet: Exploratory Analysis of Genetic and Genomic Data* (2.1.10) [Computer software]. https://cran.r-project.org/web/packages/adegenet/index.html

53. Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. *The American Naturalist*, *129*(5), 657–677. https://doi.org/10.1086/284665

54. Jordano, P., Bascompte, J., & Olesen, J. M. (2003). Invariant properties in coevolutionary networks of plant-animal interactions: Invariant properties in coevolutionary networks. *Ecology Letters*, *6*(1), 69–81. https://doi.org/10.1046/j.1461-0248.2003.00403.x

55. Jordano, P., García, C., Godoy, J. A., & García-Castaño, J. L. (2007). Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences*, *104*(9), 3278–3282. https://doi.org/10.1073/pnas.0606793104

56. Jordano, P., & Schupp, E. W. (2000). Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, *70*(4), 591–615. https://doi.org/10.2307/2657187

57. Julliard, R., Clavel, J., Devictor, V., Jiguet, F., & Couvet, D. (2006). Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, *9*(11), 1237–1244. https://doi.org/10.1111/j.1461-0248.2006.00977.x

58. Koffel, T., Daufresne, T., & Klausmeier, C. A. (2021). From competition to facilitation and mutualism: A general theory of the niche. *Ecological Monographs*, *91*(3), e01458. https://doi.org/10.1002/ecm.1458

59. McCann, K., Hastings, A., & Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature*, *395*(6704), Article 6704. https://doi.org/10.1038/27427

60. Medeiros, L. P., Garcia, G., Thompson, J. N., & Guimarães, P. R. (2018). The geographic mosaic of coevolution in mutualistic networks. *Proceedings of the National Academy of Sciences*, *115*(47), 12017–12022. https://doi.org/10.1073/pnas.1809088115

61. Mello, M. A. R., Marquitti, F. M. D., Guimarães, P. R., Kalko, E. K. V., Jordano, P., & De Aguiar, M. A. M. (2011). The missing part of seed dispersal networks: Structure and robustness of bat-fruit interactions. *PLoS ONE*, *6*(2), e17395. https://doi.org/10.1371/journal.pone.0017395

62. Memmott, J. (1999). The structure of a plant-pollinator food web. *Ecology Letters*, *2*(5), 276–280. https://doi.org/10.1046/j.1461-0248.1999.00087.x

63. Michalska-Smith, M., Song, Z., Spawn-Lee, S. A., Hansen, Z. A., Johnson, M., May, G., Borer, E. T., Seabloom, E. W., & Kinkel, L. L. (2022). Network structure of resource use and niche overlap within the endophytic microbiome. *The ISME Journal*, *16*(2), 435–446. https://doi.org/10.1038/s41396-021-01080-z

64. Miguel, M. F., Jordano, P., Tabeni, S., & Campos, C. M. (2018). Context-dependency and anthropogenic effects on individual plant-frugivore networks. *Oikos*, *127*(7), 1045–1059. https://doi.org/10.1111/oik.04978

65. Mora, B. B., Gravel, D., Gilarranz, L. J., Poisot, T., & Stouffer, D. B. (2018). Identifying a common backbone of interactions underlying food webs from different ecosystems. *Nature Communications*, *9*(1), 2603. https://doi.org/10.1038/s41467-018-05056-0

66. Müller, C. B., Adriaanse, I. C. T., Belshaw, R., & Godfray, H. C. J. (1999). The structure of an aphid–parasitoid community. *Journal of Animal Ecology*, *68*(2), 346–370. https://doi.org/10.1046/j.1365-2656.1999.00288.x

67. Newman, M. E. J. (2002). Assortative mixing in networks. *Physical Review Letters*, *89*(20), 208701. https://doi.org/10.1103/PhysRevLett.89.208701

68. Newman, M. E. J. (2006). Modularity and community structure in networks. *Proceedings of the National Academy of Sciences*, *103*(23), 8577–8582. https://doi.org/10.1073/pnas.0601602103

69. Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M. D.,

Durand, S., … Weedon, J. (2022). *vegan: Community Ecology Package* (2.6-4) [Computer software]. https://cran.r-project.org/web/packages/vegan/index.html

70. Opsahl, T., Agneessens, F., & Skvoretz, J. (2010). Node centrality in weighted networks: Generalizing degree and shortest paths. *Social Networks*, *32*(3), 245–251. https://doi.org/10.1016/j.socnet.2010.03.006

71. Phillips, R. D., Peakall, R., Van Der Niet, T., & Johnson, S. D. (2020). Niche perspectives on plant–pollinator interactions. *Trends in Plant Science*, *25*(8), 779–793. https://doi.org/10.1016/j.tplants.2020.03.009

72. Pichon, B., Goff, R. L., Morlon, H., & Perez-Lamarque, B. (2023). Telling mutualistic and antagonistic ecological networks apart by learning their multiscale structure. *bioRxiv*. https://doi.org/10.1101/2023.04.04.535603

73. Poisot, T., Canard, E., Mouquet, N., & Hochberg, M. E. (2012). A comparative study of ecological specialization estimators. *Methods in Ecology and Evolution*, *3*(3), 537–544. https://doi.org/10.1111/j.2041-210X.2011.00174.x

74. Poisot, T., Cirtwill, A. R., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. B. (2016). The structure of probabilistic networks. *Methods in Ecology and Evolution*, *7*(3), 303–312. https://doi.org/10.1111/2041-210X.12468

75. Ponisio, L. C., Valdovinos, F. S., Allhoff, K. T., Gaiarsa, M. P., Barner, A., Guimarães, P. R., Hembry, D. H., Morrison, B., & Gillespie, R. (2019). A network perspective for community assembly. *Frontiers in Ecology and Evolution*, *7*, 103. https://doi.org/10.3389/fevo.2019.00103

76. Quintero, E., Isla, J., & Jordano, P. (2022). Methodological overview and data-merging approaches in the study of plant–frugivore interactions. *Oikos*, *e08379*, 1–18. https://doi.org/10.1111/oik.08379

77. Quintero, E., Rodríguez-Sánchez, F., & Jordano, P. (2023). Reciprocity and interaction effectiveness in generalised mutualisms among free-living species. *Ecology Letters*, *26*(1), 132–146. https://doi.org/10.1111/ele.14141

78. Rehling, F., Jongejans, E., Schlautmann, J., Albrecht, J., Fassbender, H., Jaroszewicz, B., Matthies, D., Waldschmidt, L., Farwig, N., & Schabo, D. G. (2023). Common seed dispersers contribute most to the persistence of a fleshy-fruited tree. *Communications Biology*, *6*(1), 330. https://doi.org/10.1038/s42003-023-04647-y

79. Rodríguez-Rodríguez, M. C., Jordano, P., & Valido, A. (2017). Functional consequences of plant-animal interactions along the mutualism-antagonism gradient. *Ecology*, *98*(5), 1266–1276. https://doi.org/10.1002/ecy.1756

80. Rodríguez-Sánchez, Francisco, and Jean-Gabriel Young. 2024. *BayesianNetworks: Bayesian Modelling of Bipartite Networks.* https://github.com/Pakillo/BayesianNetworks

81. Rother, D. C., Pizo, M. A., & Jordano, P. (2016). Variation in seed dispersal effectiveness: The redundancy of consequences in diversified tropical frugivore assemblages. *Oikos*, *125*(3), 336–342. https://doi.org/10.1111/oik.02629

82. Roughgarden, J. (1972). Evolution of niche width. *The American Naturalist*, *106*(952), 683–718.

83. Roughgarden, J. (1979). *Theory of population genetics and evolutionary ecology: An introduction*. MacMillan.

84. Sallabanks, R. (1993). Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology*, *74*(5), 1326–1336. https://doi.org/10.2307/1940063

85. Sazatornil, F. D., Moré, M., Benitez-Vieyra, S., Cocucci, A. A., Kitching, I. J., Schlumpberger, B. O., Oliveira, P. E., Sazima, M., & Amorim, F. W. (2016). Beyond neutral and forbidden links: Morphological matches and the assembly of mutualistic hawkmoth–plant networks. *Journal of Animal Ecology*, *85*(6), 1586–1594. https://doi.org/10.1111/1365-2656.12509

86. Sazima, C., Guimarães, P. R., Dos Reis, S. F., & Sazima, I. (2010). What makes a species central in a cleaning mutualism network? *Oikos*, *119*(8), 1319–1325. https://doi.org/10.1111/j.1600-0706.2009.18222.x

87. Schleuning, M., Blüthgen, N., Flörchinger, M., Braun, J., Schaefer, H. M., & Böhning-Gaese, K. (2011). Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. *Ecology*, *92*(1), 26–36. https://doi.org/10.1890/09-1842.1

88. Segar, S. T., Fayle, T. M., Srivastava, D. S., Lewinsohn, T. M., Lewis, O. T., Novotny, V., Kitching, R. L., & Maunsell, S. C. (2020). The role of evolution in shaping ecological networks. *Trends in Ecology & Evolution*, *35*(5), 454–466. https://doi.org/10.1016/j.tree.2020.01.004

89. Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., de L. Dantas, V., de Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*(12), 1406–1419. https://doi.org/10.1111/ele.12508

90. Snell, R. S., Beckman, N. G., Fricke, E., Loiselle, B. A., Carvalho, C. S., Jones, L. R., Lichti, N. I., Lustenhouwer, N., Schreiber, S. J., Strickland, C., Sullivan, L. L., Cavazos, B. R., Giladi, I., Hastings, A., Holbrook, K. M., Jongejans, E., Kogan, O., Montaño-Centellas, F., Rudolph, J., … Schupp, E. W. (2019). Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. *AoB PLANTS*, *11*(4), plz016. https://doi.org/10.1093/aobpla/plz016

91. Snow, B. K., & Snow, D. (1988). *Birds and Berries*. T & AD Poyser.

92. Solé, R. V., & Valverde, S. (2004). Information theory of complex networks: On evolution and architectural constraints. In E. Ben-Naim, H. Frauenfelder, & Z. Toroczkai (Eds.), *Complex Networks* (Vol. 650, pp. 189–207). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-44485-5_9

93. Stan Development Team. (2024). Stan Modeling Language Users Guide and Reference Manual, 2.32.2. https://mc-stan.org

94. Thiel, S., Willems, F., Farwig, N., Rehling, F., Schabo, D. G., Schleuning, M., Shahuano Tello, N., Töpfer, T., Tschapka, M., Heymann, E. W., & Heer, K. (2023). Vertically stratified frugivore community composition and interaction frequency in a liana fruiting across forest strata. *Biotropica*, *55*, 650–664. https://doi.org/10.1111/btp.13216

95. Thompson, J. N. (1999). The raw material for coevolution. *Oikos*, *84*(1), 5. https://doi.org/10.2307/3546861

96. Tur, C., Vigalondo, B., Trøjelsgaard, K., Olesen, J. M., & Traveset, A. (2014). Downscaling pollen-transport networks to the level of individuals. *Journal of Animal Ecology*, *83*(1), 306–317. https://doi.org/10.1111/1365-2656.12130

97. Valenzuela-Ospina, L., & Kattan, G. H. (2022). Downscaling plant-frugivore interaction networks in an assemblage of fig consumers. *Biota Colombiana*, *23*(1), e1011. https://doi.org/10.21068/2539200X.1011

98. Van Valen, L. (1965). Morphological variation and width of ecological niche. *The American Naturalist*, *99*(908), 377–390.

99. Vázquez, D. P., & Aizen, M. A. (2004). Asymmetric specialization: A pervasive feature of plant–pollinator interactions. *Ecology*, *85*(5), 1251–1257. https://doi.org/10.1890/03-3112

100. Vázquez, D. P., Melián, C. J., Williams, N. M., Blüthgen, N., Krasnov, B. R., & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, *116*(7), 1120–1127. https://doi.org/10.1111/j.0030-1299.2007.15828.x

101. Vissoto, M., Vizentin-Bugoni, J., Sendoya, S. F., Gomes, G. C., & Dias, R. A. (2022). Plant height and spatial context influence individual connectivity and specialization on seed dispersers in a tree population. *Oecologia*, *198*(3), 721–731. https://doi.org/10.1007/s00442-022-05142-7

102. Wang, L.-L., Yang, Y.-P., & Duan, Y.-W. (2021). Pollinator individual-based networks reveal the specialized plant–pollinator mutualism in two biodiverse communities. *Ecology and Evolution*, *11*(23), 17509–17518. https://doi.org/10.1002/ece3.8384

103. Wheelwright, N. T., & Orians, G. H. (1982). Seed dispersal by animals: Contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *The American Naturalist*, *119*(3), 402–413.

Individual-based networks references:

1. Crestani, A. C., Mello, M. A. R., & Cazetta, E. (2019). Interindividual variations in plant and fruit traits affect the structure of a plant-frugivore network. *Acta Oecologica*, *95*, 120–127. https://doi.org/10.1016/j.actao.2018.11.003

2. Friedemann, P., Côrtes, M. C., de Castro, E. R., Galetti, M., Jordano, P., & Guimarães Jr, P. R. (2022). The individual-based network structure of palm-seed dispersers is explained by a rainforest gradient. *Oikos*, *2022*, e08384. https://doi.org/10.1111/oik.08384

3. Gopal, A., Mudappa, D., Raman, T. R. S., & Naniwadekar, R. (2020). Forest cover and fruit crop size differentially influence frugivory of select rainforest tree species in Western Ghats, India. *Biotropica*, *52*(5), 871–883. https://doi.org/10.1111/btp.12810

4. Guerra, T. J., Dayrell, R. L. C., Arruda, A. J., Dáttilo, W., Teixido, A. L., Messeder, J. V. S., & Silveira, F. A. O. (2017). Intraspecific variation in fruit–frugivore interactions: Effects of fruiting neighborhood and consequences for seed dispersal. *Oecologia*, *185*(2), 233–243. https://doi.org/10.1007/s00442-017-3943-z

5. Isla, J., Jácome-Flores, M., Arroyo, J. M., & Jordano, P. (2023). The turnover of plant–frugivore interactions along plant range expansion: Consequences for natural colonization processes. *Proceedings of the Royal Society B: Biological Sciences*, *290*(1999), 20222547. https://doi.org/10.1098/rspb.2022.2547

6. Jácome-Flores, M. E., Jordano, P., Delibes, M., & Fedriani, J. M. (2020). Interaction motifs variability in a Mediterranean palm under environmental disturbances: The mutualism–antagonism continuum. *Oikos*, *129*(3), 367–379. https://doi.org/10.1111/oik.06688

7. Jayanth, A., Isvaran, K., & Naniwadekar, R. (2024). Drivers of intraspecific variation in seed dispersal can differ across two species of fleshy-fruited savanna plants. *Biotropica*, 56, e13322. https://doi.org/10.1111/btp.13322.

8. Jordano, P. (1995). Frugivore-mediated selection on fruit and seed size: Birds and St. Lucie's cherry, *Prunus mahaleb*. *Ecology*, *76*(8), 2627–2639. https://doi.org/10.2307/2265833

9. Jordano, P. (2024). *Material for the course: Curso Posgraduação Frugivoria 2016, UNESP Rio Claro, Brazil*(course_materials) [dataset]. Zenodo. https://doi.org/10.5281/zenodo.10478535

10. Jordano, P., & Schupp, E. W. (2000). Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, *70*(4), 591–615. https://doi.org/10.2307/2657187

11. Lamperty, T., Karubian, J., & Dunham, A. E. (2021). Ecological drivers of intraspecific variation in seed dispersal services of a common neotropical palm. *Biotropica*, *53*(4), 1226–1237. https://doi.org/10.1111/btp.12966

12. Miguel, M. F., Jordano, P., Tabeni, S., & Campos, C. M. (2018). Context-dependency and anthropogenic effects on individual plant-frugivore networks. *Oikos*, *127*(7), 1045–1059. https://doi.org/10.1111/oik.04978

13. Quintero, E., Rodríguez-Sánchez, F., & Jordano, P. (2023). Reciprocity and interaction effectiveness in generalised mutualisms among free-living species. *Ecology Letters*, *26*(1), 132–146. https://doi.org/10.1111/ele.14141

14. Ramaswami, G., Somnath, P., & Quader, S. (2017). Plant-disperser mutualisms in a semi-arid habitat invaded by Lantana camara L. *Plant Ecology*, *218*(8), 935–946. https://doi.org/10.1007/s11258-017-0741-y

15. Rodriguez-Sanchez, F. (2010). *An integrative framework to investigate species responses to climate change: Biogeography and ecology of relict trees in the mediterranean*. Universidad de Sevilla.

16. Thiel, S., Willems, F., Farwig, N., Rehling, F., Schabo, D. G., Schleuning, M., Shahuano Tello, N., Töpfer, T., Tschapka, M., Heymann, E. W., & Heer, K. (2023). Vertically stratified frugivore community composition and interaction frequency in a liana fruiting across forest strata. *Biotropica*, *55*, 650–664. https://doi.org/10.1111/btp.13216

17. Vergara-Tabares, D. L., Blendinger, P. G., Tello, A., Peluc, S. I., & Tecco, P. A. (2022). Fleshy-fruited invasive shrubs indirectly increase native tree seed dispersal. *Oikos*, *2022*(2). https://doi.org/10.1111/oik.08311

18. Villalva, P., Arroyo-Correa, B., Calvo, G., Homet, P., Isla, J., Mendoza, I., Moracho, E., Quintero, E., Rodríguez-Sánchez, F., & Jordano, P. (2023). *FRUGIVORY CAMTRAP: A dataset of plant-animal interactions recorded with camera traps* [Text/csv]. DIGITAL.CSIC. https://doi.org/10.20350/DIGITALCSIC/15623

19. Vissoto, M., Vizentin-Bugoni, J., Sendoya, S. F., Gomes, G. C., & Dias, R. A. (2022). Plant height and spatial context influence individual connectivity and specialization on seed dispersers in a tree population. *Oecologia*, *198*(3), 721–731. https://doi.org/10.1007/s00442-022-05142-7

Species-based network references:

1. Albrecht, J., Bohle, V., Berens, D. G., Jaroszewicz, B., Selva, N., & Farwig, N. (2015). Variation in neighbourhood context shapes frugivore-mediated facilitation and competition among co-dispersed plant species. *Journal of Ecology*, *103*(2), 526–536. https://doi.org/10.1111/1365-2745.12375
2. Alves, K. J. F. (2008). *Composição da avifauna e frugivoria por aves em um mosaico sucessional na mata Atlântica*. Universidade Estadual Paulista.
3. Andrade, P. C., Mota, J. V. L., & de Carvalho, A. A. F. (2011). Interações mutualísticas entre aves frugívoras e plantas em um fragmento urbano de Mata Atlântica, Salvador, BA. *Revista Brasileira de Ornitologia*, *19*(1), 63–73.
4. Athiê, S. (2009). *Composição da avifauna e frugivoria por aves em um mosaico de vegetação secundária em Rio Claro, região centro-leste do estado de São Paulo*. Universidade Federal de São Carlos.
5. Baird, J. W. (1980). The selection and use of fruit by birds in an eastern forest. *Wilson Bulletin*, *92*(1), 63–73.
6. Beehler, B. (1983). Frugivory and polygamy in birds of paradise. *The Auk*, *100*(1), 1–12. https://www.jstor.org/stable/4086272
7. Burns, K. C. (2013). What causes size coupling in fruit–frugivore interaction webs? *Ecology*, *94*(2), 295–300. https://doi.org/10.1890/12-1161.1
8. Castro, E. R. de. (2007). *Fenologia reprodutiva do palmito* Euterpe edulis *(Arecaceae) e sua influência na abundância de aves frugívoras na floresta atlântica*. Universidade Estadual Paulista.
9. Correia, J. M. de S. (1997). *Utilização de espécies frutíferas de mata Atlântica na alimentação da avifauna da reserva biológica de Poço das Antas, RJ*. Universidade de Brasília.
10. Crome, F. (1975). The ecology of fruit pigeons in tropical Northern Queensland. *Wildlife Research*, *2*(2), 155–185. https://doi.org/10.1071/WR9750155
11. Fadini, R. F., & de Marco Jr, P. (2004). Interações entre aves frugívoras e plantas em um fragmento de mata atlântica de Minas Gerais. *Ararajuba*, *12*(2), 97–103.
12. Frost, P. G. H. (1980). Fruit-frugivore interactions in a South African coastal dune forest. In R. Nöhring (Ed.), *Acta XVII Congressus Internationalis Ornithologici* (Vol. 2, pp. 1179–1184). Verlag der Deutschen Ornithologen-Gesellschaft.
13. Galetti, M., & Pizo, M. A. (1996). Fruit eating by birds in a forest fragment in southeastern Brasil. *Ararajuba*, *4*(2), 71–79.
14. Garcia, Q. S., Rezende, J. L. P., & Aguiar, L. M. S. (2000). Seed dispersal by bats in a disturbed area of Southeastern Brazil. *Revista de Biología Tropical*, *48*(1), 125–128.
15. García-Castaño, J. L. (2001). *Consecuencias demográficas de la dispersión de semillas por aves y mamíferos frugívoros en la vegetación Mediterránea de montaña*. Universidad de Sevilla.
16. Gorchov, D. L., Cornejo, F., Ascorra, C. F., & Jaramillo, M. (1995). Dietary overlap between frugivorous birds and bats in the Peruvian Amazon. *Oikos*, *74*(2), 235. https://doi.org/10.2307/3545653
17. Guitián, J. (1984). Ecología de una comunidad de passeriformes en un bosque montano de la Cordillera Cantábrica Occidental [Http://purl.org/dc/dcmitype/Text, Universidade de Santiago de Compostela]. In *Ecología de una comunidad de*

passeriformes en un bosque montano de la Cordillera Cantábrica Occidental. https://investigacion.usc.es/documentos/5d1df66029995204f766a2ba?lang=es

18. Hasui, E. (1994). *O papel das aves frugívoras na dispersão de sementes em um fragmento de floresta estacional semidecídua secundária, em São Paulo, SP* [Universidade de São Paulo]. https://repositorio.usp.br/item/000742034
19. Heleno, R. H., Olesen, J. M., Nogales, M., Vargas, P., & Traveset, A. (2013). Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1750), 20122112. https://doi.org/10.1098/rspb.2012.2112
20. Hernández-Montero, J. R., Saldaña-Vázquez, R. A., Galindo-González, J., & Sosa, V. J. (2015). Bat-fruit interactions are more specialized in shaded-coffee plantations than in tropical mountain cloud forest fragments. *PLOS ONE*, *10*(5), e0126084. https://doi.org/10.1371/journal.pone.0126084
21. Lopez, J. E., & Vaughan, C. (2004). Observations on the role of frugivorous bats as seed dispersers in Costa Rican secondary humid forests. *Acta Chiropterologica*, *6*(1), 111–119. https://doi.org/10.3161/001.006.0109
22. Menke, S., Böhning-Gaese, K., & Schleuning, M. (2012). Plant-frugivore networks are less specialized and more robust at forest-farmland edges than in the interior of a tropical forest. *Oikos*, *121*(10), 1553–1566. https://doi.org/10.1111/j.1600-0706.2011.20210.x
23. Noma, N., & Yumoto, T. (1997). Fruiting phenology of animal-dispersed plants in response to winter migration of frugivores in a warm temperate forest on Yakushima Island, Japan. *Ecological Research*, *12*(2), 119–129. https://doi.org/10.1007/BF02523777
24. Olesen, J. M., Bascompte, J., Dupont, Y. L., Elberling, H., Rasmussen, C., & Jordano, P. (2011). Missing and forbidden links in mutualistic networks. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1706), 725–732. https://doi.org/10.1098/rspb.2010.1371
25. Palmeirim, J. M., Gorchov, D. L., & Stoleson, S. (1989). Trophic structure of a neotropical frugivore community: Is there competition between birds and bats? *Oecologia*, *79*(3), 403–411. https://doi.org/10.1007/BF00384321
26. Passos, F. C., Silva, W. R., Pedro, W. A., & Bonin, M. R. (2003). Frugivoria em morcegos (Mammalia, Chiroptera) no Parque Estadual Intervales, sudeste do Brasil. *Revista Brasileira de Zoologia*, *20*(3), 511–517. https://doi.org/10.1590/S0101-81752003000300024
27. Pedro, W. A. (1992). *Estrutura de uma taxocenose de morcegos da reserva do Panga (Uberlandia, MG), com ênfase nas relações tróficas em Phyllostomidae (Mammalia: Chiroptera)*. Universidade Estadual de Campinas.
28. Pizo, M. A. (2004). Frugivory and habitat use by fruit-eating birds in a fragmented landscape of southeast brazil. *Ornitologia Neotropical*, *15*(Suppl.), 117–126.
29. Poulin, B., Wright, S. J., Lefebvre, G., & Calderón, O. (1999). Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. *Journal of Tropical Ecology*, *15*(2), 213–227. https://doi.org/10.1017/S0266467499000760

30. Ribeiro Da Silva, F., Montoya, D., Furtado, R., Memmott, J., Pizo, M. A., & Rodrigues, R. R. (2015). The restoration of tropical seed dispersal networks: Restoration of tropical seed dispersal networks. *Restoration Ecology*, *23*(6), 852–860. https://doi.org/10.1111/rec.12244
31. Robinson, V. (2015). *Índice de importância de diferentes espécies de plantas na atração de aves para uma área reflorestada em Piracicaba*. Universidade Estadual Paulista.
32. Rodrigues, S. B. M. (2015). *Rede de interações entre aves frugívoras e plantas em uma área de mata Atlântica no sudeste do Brasil*. Universidade Federal de São Carlos.
33. Saavedra, F., Hensen, I., Beck, S. G., Böhning-Gaese, K., Lippok, D., Töpfer, T., & Schleuning, M. (2014). Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. *Oecologia*, *176*(3), 837–848. https://doi.org/10.1007/s00442-014-3056-x
34. Sarmento, R., Alves-Costa, C. P., Ayub, A., & Mello, M. A. R. (2014). Partitioning of seed dispersal services between birds and bats in a fragment of the Brazilian Atlantic Forest. *Zoologia (Curitiba)*, *31*(3), 245–255. https://doi.org/10.1590/S1984-46702014000300006
35. Schleuning, M., Blüthgen, N., Flörchinger, M., Braun, J., Schaefer, H. M., & Böhning-Gaese, K. (2011). Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. *Ecology*, *92*(1), 26–36. https://doi.org/10.1890/09-1842.1
36. Silva, R. F. de M. (2011). *Interações entre plantas e aves frugívoras no campus da Universidade Federal Rural do Rio de Janeiro*. Universidade Federal Rural do Rio de Janeiro.
37. Snow, B. K., & Snow, D. (1988). *Birds and Berries*. T & AD Poyser.
38. Snow, B. K., & Snow, D. W. (1971). The feeding ecology of tanagers and honeycreepers in trinidad. *The Auk*, *88*(2), 291–322. https://doi.org/10.2307/4083882
39. Stiebel, H., & Bairlein, F. (2008). Frugivorie mitteleuropäischer Vögel I: Nahrung und Nahrungserwerb. *Vogelwarte*, *46*, 1–23.
40. Yang, S., Albert, R., & Carlo, T. A. (2013). Transience and constancy of interactions in a plant-frugivore network. *Ecosphere*, *4*(12), art147. https://doi.org/10.1890/ES13-00222.1

Supporting information for

Downscaling mutualistic networks from species to individuals reveals consistent interaction niches and roles within plant populations

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Network characteristics and sampling effort

Table S1. List of networks providing the identification code used in figures, the type (ind: individual-based, sp: species-based), the focal plant species in the case of individual-based networks, the country where network was sampled, number of plants and frugivore species present in the network, network size (potential interactions), number of unique interactions (realized interactions), the name of the population where sampling took place in case of several populations for the same study, and the reference of the study from which the network was extracted.

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
1	ind	*Pistacia lentiscus* (Anacardiaceae)	Spain	40	27	1080	392	El Puntal	Camera traps and DNA-barcoding	Quintero, E., Rodríguez-Sánchez, F., & Jordano, P. (2023). Reciprocity and interaction effectiveness in generalised mutualisms among free-living species. Ecology Letters, 26(1), 132–146.
2	ind	*Pistacia lentiscus* (Anacardiaceae)	Spain	40	16	640	134	Laguna de las Madroñas	DNA-barcoding	
3	ind	*Juniperus phoenicea* (Cupressaceae)	Spain	35	10	350	137	Colonizacion	Camera traps and DNA-barcoding	Isla, J., Jácome-Flores, M., Arroyo, J. M., & Jordano, P. (2023). The turnover of plant–frugivore interactions along plant range expansion: Consequences for natural colonization processes. Proceedings of the Royal Society B: Biological Sciences, 290(1999), 20222547.
4	ind	*Juniperus phoenicea* (Cupressaceae)	Spain	35	10	350	154	Ojillo	Camera traps and DNA-barcoding	
5	ind	*Juniperus phoenicea* (Cupressaceae)	Spain	35	11	385	148	El Marqués	Camera traps and DNA-barcoding	
6	ind	*Lithraea molleoides* (Anacardiaceae)	Argentina	13	10	130	37	Los Hornillos	Focal observations	Vergara-Tabares, D. L., Blendinger, P. G., Tello, A., Peluc, S. I., & Tecco, P. A. (2022). Fleshy-fruited invasive shrubs indirectly increase native tree seed dispersal. Oikos, 2022(2).
7	ind	*Lithraea molleoides* (Anacardiaceae)	Argentina	14	10	140	33	Las Calles	Focal observations	
8	ind	*Lithraea molleoides* (Anacardiaceae)	Argentina	14	13	182	46	La Poblacion	Focal observations	
9	ind	*Lithraea molleoides* (Anacardiaceae)	Argentina	13	12	156	41	San Javier	Focal observations	

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
10	ind	*Lithraea molleoides* (Anacardiaceae)	Argentina	12	11	132	29	Las Rabonas	Focal observations	
11	ind	*Lithraea molleoides* (Anacardiaceae)	Argentina	11	7	77	25	Los Molles	Focal observations	
12	ind	*Laurus nobilis* (Lauraceae)	Spain	18	17	306	87		Focal observations	Rodríguez-Sánchez, F. (2010). An integrative framework to investigate species responses to climate change: Biogeography and ecology of relict trees in the Mediterranean. PhD Thesis. Universidad de Sevilla, Spain.
13	ind	*Prunus mahaleb* (Rosaceae)	Spain	19	20	380	211		Focal observations	Jordano, P. (1995). Frugivore-mediated selection on fruit and seed size: birds and St. Lucie's cherry, *Prunus mahaleb*. Ecology, 76(8), 2627–2639. Jordano, P., & Schupp, E. W. (2000). Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. Ecological Monographs, 70(4), 591-615.
14	ind	*Euterpe edulis* (Arecaceae)	Brazil	17	9	153	31	Restinga	Focal observations	Friedemann, P., Côrtes, M. C., de Castro, E. R., Galetti, M., Jordano, P., & Guimarães Jr, P. R. (2022). The individual-based network structure of palm-seed dispersers is explained by a rainforest gradient. Oikos, 2022, e08384.
15	ind	*Euterpe edulis* (Arecaceae)	Brazil	15	7	105	25	Lowland	Focal observations	
16	ind	*Euterpe edulis* (Arecaceae)	Brazil	30	8	240	50	Premontane	Focal observations	
17	ind	*Cecropia glaziovii* (Urticaceae)	Brazil	27	37	999	124		Focal observations	Jordano, P. 2024. Material for the course: Curso Posgraduação Frugivoria 2016, UNESP Rio Claro, Brazil. doi: 10.5281/zenodo.10478535.
18	ind	*Heynea trijuga* (Meliaceae)	India	24	11	264	48		Focal observations	Gopal, A., Mudappa, D., Raman, T. S., & Naniwadekar, R. (2020). Forest cover and fruit crop

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
19	ind	*Myristica dactyloides* (Myristicaceae)	India	25	7	175	45		Focal observations	size differentially influence frugivory of select rainforest tree species in Western Ghats, India. Biotropica, 52(5), 871-883.
20	ind	*Persea macrantha* (Lauraceae)	India	32	21	672	186		Focal observations	
21	ind	*Henriettea succosa* (Melastomataceae)	Brazil	18	22	396	77		Focal observations	Crestani, A. C., Mello, M. A. R., & Cazetta, E. (2019). Interindividual variations in plant and fruit traits affect the structure of a plant-frugivore network. Acta Oecologica, 95, 120-127.
22	ind	*Prestoea decurrens* (Arecaceae)	Ecuador	31	9	279	100		Camera traps	Lamperty, T., Karubian, J., & Dunham, A. E. (2021). Ecological drivers of intraspecific variation in seed dispersal services of a common neotropical palm. Biotropica, 53(4), 1226–1237.
23	ind	*Corema album* (Ericaceae)	Spain	24	15	360	129		Camera traps	Villalva, P., Arroyo-Correa, B., Calvo, G., Homet, P., Isla, J., Mendoza, I., Moracho, E., Quintero, E., Rodríguez-Sánchez, F., & Jordano, P. (2023). FRUGIVORY CAMTRAP: A dataset of plant-animal interactions recorded with camera traps. https://doi.org/10.20350/DIGITALCSIC/15623
24	ind	*Bursera penicillata* (Burseraceae)	India	15	11	165	43		Focal observations	Ramaswami, G., Somnath, P., & Quader, S. (2017). Plant-disperser mutualisms in a semi-arid habitat invaded by Lantana camara L. Plant Ecology, 218, 935-946.
25	ind	*Erythroxylum monogynum* (Erythroxylaceae)	India	12	6	72	29		Focal observations	
26	ind	*Flacourtia indica* (Salicaceae)	India	13	5	65	33		Focal observations	
27	ind	*Flueggea leucopyrus* (Phyllanthaceae)	India	10	8	80	22		Focal observations	

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
28	ind	*Canthium coromandelicum* (Rubiaceae)	India	10	8	80	30		Focal observations	
29	ind	*Santalum album* (Santalaceae)	India	14	10	140	38		Focal observations	
30	ind	*Ziziphus oenopolia* (Rhamnaceae)	India	15	13	195	102		Focal observations	
31	ind	*Chamaerops humilis* (Arecaceae)	Spain	39	6	234	76	Matasgordas	Footprint traps	Jácome-Flores, M. E. et al. 2020. Interaction motifs variability in a Mediterranean palm under environmental disturbances: the mutualism–antagonism continuum. Oikos 129: 367–379.
32	ind	*Chamaerops humilis* (Arecaceae)	Spain	24	6	144	57	Martinazo	Footprint traps	
33	ind	*Miconia irwinii* (Melastomataceae)	Brazil	15	9	135	59		Focal observations	Guerra, T. J. et al. 2017. Intraspecific variation in fruit–frugivore interactions: effects of fruiting neighborhood and consequences for seed dispersal. Oecologia 185: 233–243.
34	ind	*Juniperus macrocarpa* (Cupressaceae)	Spain	26	11	286	72		Camera traps	Villalva, P., Arroyo-Correa, B., Calvo, G., Homet, P., Isla, J., Mendoza, I., Moracho, E., Quintero, E., Rodríguez-Sánchez, F., & Jordano, P. (2023). FRUGIVORY CAMTRAP: A dataset of plant-animal interactions recorded with camera traps. https://doi.org/10.20350/DIGITALCSIC/15623
35	ind	*Prosopis flexuosa* (Fabaceae)	Argentina	26	9	234	72	Araya-San Ignacio	Camera traps	Miguel, M.F., Jordano, P., Tabeni, S. and Campos, C.M. (2018), Context-dependency and anthropogenic effects on individual plant–frugivore networks. Oikos, 127: 1045-1059.
36	ind	*Prosopis flexuosa* (Fabaceae)	Argentina	28	10	280	84	El Bonito	Camera traps	

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
37	ind	*Prosopis flexuosa* (Fabaceae)	Argentina	54	10	540	112	El Doménico	Camera traps	
38	ind	*Prosopis flexuosa* (Fabaceae)	Argentina	35	8	280	61	MaB Ñacuñán Reserve Protected 1	Camera traps	
39	ind	*Prosopis flexuosa* (Fabaceae)	Argentina	29	9	261	99	MaB Ñacuñán Reserve Protected 2	Camera traps	
40	ind	*Schinus terebinthifolia* (Anacardiaceae)	Brazil	26	16	416	93		Focal observations	Vissoto, M., Vizentin-Bugoni, J., Sendoya, S. F., Gomes, G. C., & Dias, R. A. (2022). Plant height and spatial context influence individual connectivity and specialization on seed dispersers in a tree population. Oecologia, 198(3): 721-731.
41	ind	*Phillyrea angustifolia* (Oleaceae)	Spain	10	16	160	72	El Puntal	DNA-barcoding	Unpublished data. SUMHAL project. IP: Pedro Jordano - 2021-2022.
42	ind	*Phillyrea angustifolia* (Oleaceae)	Spain	9	12	108	41	Laguna de las Madroñas	DNA-barcoding	
43	ind	*Marcgravia longifolia* (Marcgraviaceae)	Peru	24	43	1032	127		Focal observations	Thiel, S., Willems, F., Farwig, N., Rehling, F., Schabo, D. G., Schleuning, M., Shahuano Tello, N., Töpfer, T., Tschapka, M., Heymann, E. W., & Heer, K. (2023). Vertically stratified frugivore community composition and interaction frequency in a liana fruiting across forest strata. Biotropica, 55, 650–664
44	ind	*Osyris lanceolata* (Santalaceae)	Spain	19	14	266	62		DNA-barcoding	Unpublished data. SUMHAL project. IP: Pedro Jordano - 2021-2022

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
45	ind	*Naringi crenulata* (Rutaceae)	India	22	12	264	62		Focal observations	Jayanth, A., Isvaran, K., & Naniwadekar, R. (2024). Drivers of intraspecific variation in seed dispersal can differ across two species of fleshy-fruited savanna plants. Biotropica, 56(3), e13322. https://doi.org/10.1111/btp.13322
46	ind	*Ziziphus oenopolia* (Rhamnaceae)	India	20	13	260	57		Focal observations and mist-netting	
47	sp		Spain	25	36	900	228	Cazorla	Focal observations	Olesen JM, Bascompte J, Dupont YL, Elberling H, Rasmussen C, Jordano P. (2011). Missing and forbidden links in mutualistic networks. Proceedings of the Royal Society B-Biological Sciences 278: 725-732.
48	sp		Spain	16	17	272	120	Hato Ratón	Mist-netting	
49	sp		Spain	17	28	476	130	Spain	Focal observations	García-Castaño, J.L. (2001). Consecuencias demográficas de la dispersión de semillas por aves y mamíferos frugívoros en la vegetación mediterránea de montaña. PhD Thesis. Universidad de Sevilla, Spain.
50	sp		Papua New Guinea	31	9	279	119		Focal observations	Beehler B. (1983) Frugivory and polygamy in birds of paradise. Auk, 100, 1-11.
51	sp		South Africa	16	10	160	110		Focal observations	Frost P.G.H. (1980) Fruit-frugivore interactions in a South African coastal dune forest. In: Acta XVII Congressus Internationalis Ornithologici (ed. Noring R), pp. 1179-1184. Deutsche Ornithologische Ges., Berlin, Germany.
52	sp		Spain	12	7	84	40		Mist-netting	Guitián J. (1983) Relaciones entre los frutos y los passeriformes en un bosque montano de la cordillera Cantabrica occidental. PhD Thesis. Universidad de Santiago, Spain.
53	sp		Brazil	35	29	1015	146		Focal observations	Galetti M. & Pizo M.A. (1996) Fruit eating birds in a forest fragment in southeastern Brazil. Ararajuba, Rev. Brasil. Ornitol., 4, 71-79.

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
54	sp		England	11	14	154	47		Focal observations	Snow, B.K. & Snow, D.W. (1988). Birds and berries. T. and A.D. Poyser, Calton, England.
55	sp		Japan	15	8	120	38		Focal observations	Noma, N. & Yumoto, T. (1997). Fruiting phenology of animal-dispersed plants in response to winter migration of frugivores in a warm temperate forest on Yakushima Island, Japan. Ecological Research, 12, 119-129.
56	sp		Australia	71	7	497	142		Focal observations	Crome, F. H.J. (1975). The ecology of fruit pigeons in tropical Northern Queensland. Aust Wildl Res, 2, 155-185.
57	sp		Trinidad and Tobago	50	14	700	234		Focal observations	Snow B.K. & Snow D.W. (1971) The feeding ecology of tanagers and honeycreepers in Trinidad. Auk, 88, 291-322.
58	sp		United States	7	21	147	50		Focal observations	Baird, J.W. (1980). The selection and use of fruit by birds in an Eastern forest. Wilson Bulletin, 92, 63-73.
59	sp		Kenya	8	30	240	69	Interior little disturbed	Focal observations	Menke, S., Böhning-Gaese, K. & Schleuning, M. (2012). Plant-frugivore networks are less specialized and more robust at forest-farmland edges than in the interior of a tropical forest. Oikos, 121, 1553-1566.
60	sp		Kenya	7	38	266	104	Edge little disturbed	Focal observations	
61	sp		Kenya	8	34	272	88	Interior highly disturbed	Focal observations	
62	sp		Kenya	8	39	312	115	Edge highly disturbed	Focal observations	
63	sp		Brazil	15	49	735	143		Focal observations	Pizo, M.A. (2004). Frugivory and habitat use by fruit-eating birds in a fragmented landscape of southeast Brazil. Ornitologia Neotropical, 15, 117-126.

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
64	sp		Kenya	33	88	2904	419		Focal observations	Schleuning M, Bluthgen N, Florchinger M, Braun J, Schaefer HM, Bohning-Gaese K. 2011. Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. Ecology 92: 26-36.
65	sp		Brazil	49	16	784	131		Focal observations	Castro, E.R.D. (2007). Fenologia reprodutiva do palmito Euterpe edulis (Erecaceae) e sua influência na abundância de aves frugívoras na floresta atlântica. PhD Thesis. Instituto de Biociencias. Universidade Estadual Paulista "Juio de Mesquita Filho" Rio Claro, SP, Brazil.
66	sp		Brazil	13	45	585	183		Focal observations	Correia, J.M.S. (1997). Utilização de espécies frutíferas de mata Atlântica na alimentação da avifauna da reserva biológica de Poço das Antas, RJ. MSc Thesis. Instituto de Biologia. UNB, Brazil.
67	sp		Brazil	13	30	390	145		Focal observations	Alves, K.J.F. (2008). Composição da avifauna e frugivoria por aves em um mosaico sucessional na mata Atlântica. MSc Thesis. Instituto de Biociencias. Universidade Estadual Paulista, Julio de Mesquita Filho, Rio Claro, SP, Brazil.
68	sp		Brazil	9	30	270	92		Focal observations	Athie, S. (2009). Composição da avifauna e frugivoria por aves em um mosaico de vegetação secundária em Rio Claro, região centro-leste do estado de São Paulo. MSc Thesis. Universidade Federal de São Carlos, Brazil.
69	sp		Brazil	25	28	700	90		Focal observations	Ferreira Fadini, R. & De Marco Jr., P. (2004). Interações entre aves frugívoras e plantas em um fragmento de mata atlântica de Minas Gerais. Ararajuba, 12, 97-103.

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
70	sp		Brazil	26	22	572	79		Focal observations and mist-netting	Hasui, Erica. (1994). O papel das aves frugivoras na dispersao de sementes em um fragmento de floresta semidecidua secundaria em Sao Paulo, SP. MSc thesis. USP Sao Paulo, Brazil.
71	sp		Brazil	22	20	440	67		Focal observations	Silva, R. F. d. M. (2011). Interações entre plantas e aves frugívoras no campus da Universidade Federal Rural do Rio de Janeiro. In: Instituto de Florestas. Universidade Federal do Rio de Janeiro Rio de Janeiro, Brazil.
72	sp		Brazil	12	15	180	32	15-year-old restored plot	Focal observations	Ribeiro da Silva, F., Montoya, D., Furtado, R., Memmott, J., Pizo, M.A. and Rodrigues, R.R. (2015), The restoration of tropical seed dispersal networks. Restor Ecol, 23: 852-860.
73	sp		Brazil	23	29	667	129	25-year-old restored plot	Focal observations	
74	sp		Brazil	14	14	196	35	57-year-old restored plot	Focal observations	
75	sp		Brazil	6	28	168	50		Focal observations	Robinson, V. (2015). Interações entre aves frugívoras e plantas em um fragmento de mata atlântica de Minas Gerais. In: Instituto de Biociencias. Universidade Estadual Paulista "Julio de Mesquita Filho" Rio Claro, SP, Brazil.
76	sp		Brazil	30	58	1740	240		Focal observations	Rodrigues, S. B. M. (2015). Rede de interações entre aves frugivoras e plantas em una área de mata Atlântica no sudeste do Brasil. Universidade Federal de Sao Carlos, Campus Sorocaba Sorocaba, SP, Brazil.
77	sp		New Zealand	18	8	144	102		Focal observations	Burns, K.C. (2013). What causes size coupling in fruit-frugivore interaction webs? Ecology, 94, 295-300.
78	sp		Poland	8	12	96	38	site_11	Focal observations	

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
79	sp		Poland	7	11	77	32	site_13	Focal observations	Albrecht, J., Bohle, V., Berens, D. G., Jaroszewicz, B., Selva, N., & Farwig, N. (2015). Variation in neighbourhood context shapes frugivore-mediated facilitation and competition among co-dispersed plant species. Journal of Ecology, 103(2), 526–536.
80	sp		Poland	9	13	117	42	site_15	Focal observations	
81	sp		Poland	8	13	104	36	site_30	Focal observations	
82	sp		Poland	8	10	80	29	site_35	Focal observations	
83	sp		Poland	8	10	80	30	site_36	Focal observations	
84	sp		Poland	8	11	88	33	site_102	Focal observations	
85	sp		Poland	10	13	130	42	site_111	Focal observations	
86	sp		Poland	8	15	120	57	site_112	Focal observations	
87	sp		Poland	9	16	144	41	site_203	Focal observations	
88	sp		Poland	6	20	120	43	site_301	Focal observations	
89	sp		Poland	8	19	152	56	site_315	Focal observations	
90	sp		Brazil	22	17	374	78		Focal observations	Andrade, P., Mota, J. & Carvalho, A. (2011). Mutual interactions between frugivorous birds and plants in an urban fragment of Atlantic Forest, Salvador, BA. Revista Brasileira de Ornitologia, 19, 63-73.
91	sp		Puerto Rico	34	20	680	95		Focal observations	Yang, S., Albert, R. & Carlo, T.A. (2013). Transience and constancy of interactions in a plant-frugivore network. Ecosphere, 4(12): 147.
92	sp		Brazil	14	6	84	22		Mist-netting	Garcia, Q.S., Rezende, J.L.P. & Aguiar, L.M.S. (2000). Seed dispersal by bats in a disturbed area of Southeastern Brazil. Revista de Biología Tropical, 48, 125-128.

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
93	sp		Peru	77	18	1386	196		Mist-netting	Gorchov, D.L., Cornejo, F., Ascorra, C.F. & Jaramillo, M. (1995). Dietary overlap between frugivorous birds and bats in the peruvian amazon. Oikos, 74, 235-250.
94	sp		Costa Rica	35	14	490	95		Mist-netting	Palmeirim, J.M., Gorchov, D.L. & Stoleson, S. (1989). Trophic structure of a neotropical frugivore community: is there competition between birds and bats? Oecologia (Berl.), 79, 403-411.
95	sp		Costa Rica	35	14	490	119		Mist-netting	Lopez, J.E. & Vaughan, C. (2004). Observations on the Role of Frugivorous Bats as Seed Dispersers in Costa Rican Secondary Humid Forests. Acta Chiropterologica, 6, 111-119.
96	sp		Ecuador	43	15	645	97		Animal feces (mist-netting and transects)	Heleno, R.H., Olesen, J.M., Nogales, M., Vargas, P. & Traveset, A. (2013). Seed dispersal networks in the Galapagos and the consequences of alien plant invasions. Proc Biol Sci, 280, 20122112.
97	sp		Mexico	22	7	154	47	Tropical montane cloud forest fragment	Mist-netting	Hernandez-Montero, J.R., Saldana-Vazquez, R.A., Galindo-Gonzalez, J. & Sosa, V.J. (2015). Bat-fruit interactions are more specialized in shaded-coffee plantations than in tropical mountain cloud forest fragments. PLoS ONE, 10, e0126084.
98	sp		Mexico	19	6	114	34	Shaded-coffee plantation	Mist-netting	
99	sp		Brazil	24	7	168	50		Mist-netting	Passos, F.C., Silva, W.R., Pedro, W.A. & Bonin, M.R. (2003). Frugivoria em morcegos (Mammalia, Chiroptera) no Parque Estadual Intervales, sudeste do Brasil. Revista Brasileira de Zoologia, 20, 511-517.

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
100	sp		Brazil	13	7	91	30		Mist-netting	Pedro, W.A. (1992). Estrutura de uma taxocenose de morcegos da reserva do Panga (Uberlandia, MG), com enfase nas relações troficas em Phyllostomidae (Mammalia: Chiroptera). MSC thesis. Universidade Estadual de Campinas Campinas, SP, Brazil.
101	sp		Panama	17	20	340	86		Mist-netting	Poulin, B., Wright, S.J., Lefebvre, G. & Calderon, O. (1999). Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. Journal of Tropical Ecology, 15, 213-227.
102	sp		Brazil	56	20	1120	104		Mist-netting	Sarmento, R., Alves-Costa, C.i.P., Ayub, A. & Mello, M.A.R. (2014). Partitioning of seed dispersal services between birds and bats in a fragment of the Brazilian Atlantic Forest. Zoologia (Curitiba, Impresso), 31, 245-255.
103	sp		Germany	30	31	930	189		Focal observations	Stiebel, H. & Bairlein, F. (2008). Frugivorie mitteleuropäischer Vögel I: Nahrung und Nahrungserwerb. Vogelwarte, 46, 1-23.
104	sp		Bolivia	36	41	1476	127	Forest edge	Focal observations	Saavedra, F., Hensen, I., Beck, S. G., Böhning-Gaese, K., Lippok, D., Töpfer, T., & Schleuning, M. (2014). Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. Oecologia, 176, 837-848.
105	sp		Bolivia	20	23	460	52	Forest interior	Focal observations	

1232 **Table S2.** Sampling coverage in individual-based networks with lower- and upper-confidence limits

1233 of sample coverage (95%) (SC LCL, SC UCL, respectively).

Net no.	Focal plant species	Sampling coverage	SC LCL	SC UCL
1	*Pistacia lentiscus*	0.99	0.99	1.00
2	*Pistacia lentiscus*	0.96	0.93	0.99
3	*Juniperus phoenicea*	0.99	0.97	1.00
4	*Juniperus phoenicea*	0.99	0.98	1.00
5	*Juniperus phoenicea*	1.00	0.99	1.00
6	*Lithraea molleoides*	0.87	0.78	0.96
7	*Lithraea molleoides*	0.94	0.85	1.00
8	*Lithraea molleoides*	0.92	0.86	0.98
9	*Lithraea molleoides*	0.91	0.82	1.00
10	*Lithraea molleoides*	0.87	0.74	1.00
11	*Lithraea molleoides*	0.93	0.82	1.00
12	*Laurus nobilis*	0.98	0.95	1.00
13	*Prunus mahaleb*	1.00	0.99	1.00
14	*Euterpe edulis*	0.91	0.80	1.00
15	*Euterpe edulis*	0.89	0.79	0.99
16	*Euterpe edulis*	0.96	0.92	1.00
17	*Cecropia glaziovii*	0.88	0.84	0.93
18	*Heynea trijuga*	0.96	0.91	1.00
19	*Myristica dactyloides*	0.98	0.94	1.00
20	*Persea macrantha*	0.98	0.96	1.00
21	*Henriettea succosa*	0.87	0.81	0.93
22	*Prestoea decurrens*	0.98	0.97	1.00
23	*Corema album*	0.98	0.95	1.00
24	*Bursera penicillata*	0.94	0.87	1.00
25	*Erythroxylum monogynum*	0.97	0.91	1.00
26	*Flacourtia indica*	1.00	0.97	1.00
27	*Flueggea leucopyrus*	0.84	0.72	0.95
28	*Canthium coromandelicum*	0.91	0.82	1.00
29	*Santalum album*	0.88	0.79	0.96
30	*Ziziphus oenopolia*	0.97	0.94	1.00
31	*Chamaerops humilis*	1.00	0.99	1.00
32	*Chamaerops humilis*	1.00	0.99	1.00
33	*Miconia irwinii*	1.00	0.98	1.00
34	*Juniperus macrocarpa*	0.97	0.94	1.00
35	*Prosopis flexuosa*	1.00	0.98	1.00
36	*Prosopis flexuosa*	0.97	0.93	1.00
37	*Prosopis flexuosa*	0.97	0.95	0.99
38	*Prosopis flexuosa*	0.95	0.92	0.99
39	*Prosopis flexuosa*	0.99	0.97	1.00
40	*Schinus terebinthifolia*	0.96	0.92	0.99
41	*Phillyrea angustifolia*	0.95	0.90	0.99
42	*Phillyrea angustifolia*	0.94	0.88	1.00
43	*Marcgravia longifolia*	0.82	0.75	0.88
44	*Osyris lanceolata*	0.90	0.84	0.97
45	*Naringi crenulata*	0.96	0.90	1.00
46	*Ziziphus oenopolia*	0.93	0.87	1.00

Comparison of networks at different resolution scales

To compare networks focused at the population level (individual-based) and the community level (species-based) we calculated several network descriptors. We then used these descriptors to build a PCA-derived multivariate space defined by their correlation structure, so that the location of each network is defined by a combination of both topological (e.g., degree, connectance) and structural (e.g., nestedness, modularity) descriptors. In this way, networks closely located in this multivariate space would have more similarities in the combination of metrics (and thus topology and structure) than networks located in different parts of the space.

Network-level metrics

With the aim of visualizing families of metrics that describe similar aspects of the bipartite networks, we computed an agglomerative hierarchical clustering (HC) analysis for all the metrics (function hclust in `stats` R package, R Core Team 2023).

We selected metrics indicative of biological properties of the networks, aiming to reduce redundancy in their meaning and avoiding high correlation with network size. Since we aim at finding structural differences among networks with different resolution scales we tried to avoid metrics strongly affected by sampling design, species diversity and study region characteristics (e.g., tropical vs. temperate regions), such as web asymmetry, Shannon diversity or links per species. Both the cluster analysis and the correlation analysis help us select network-level metrics that are interpretable in biological terms while trying to avoid highly correlated metrics. The selected network-level metrics allow us to discern differences in the topological properties of individual-based and species-based networks.

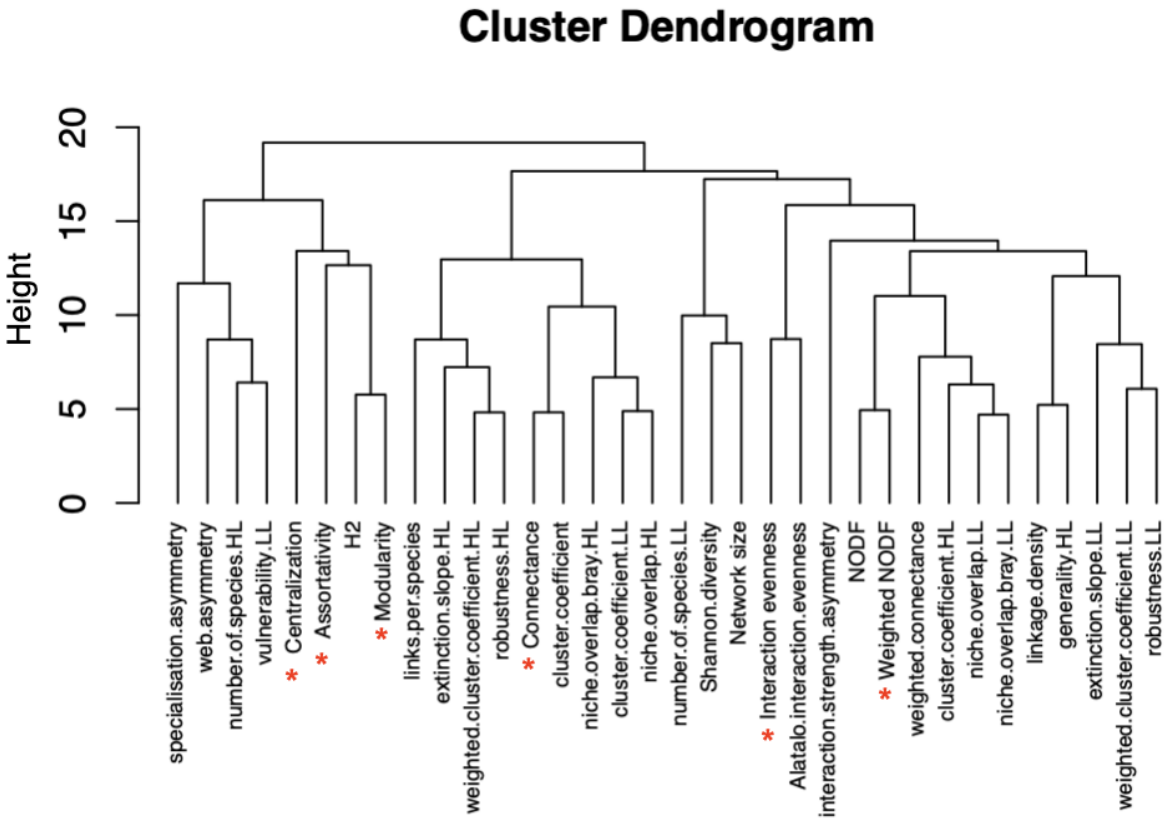


Figure S1. Hierarchical clustering analysis results for all the network metrics calculated. Metrics with * are the selected ones.

We checked for Pearson's correlation among the selected metrics and with network size (Fig. S2). We did not find strong effects of correlation with network size (medium/low correlation). The highest correlations were between centralization and interaction evenness, and weighted NODF and modularity. All variables have a VIF of 2.52 (VIF < 3).

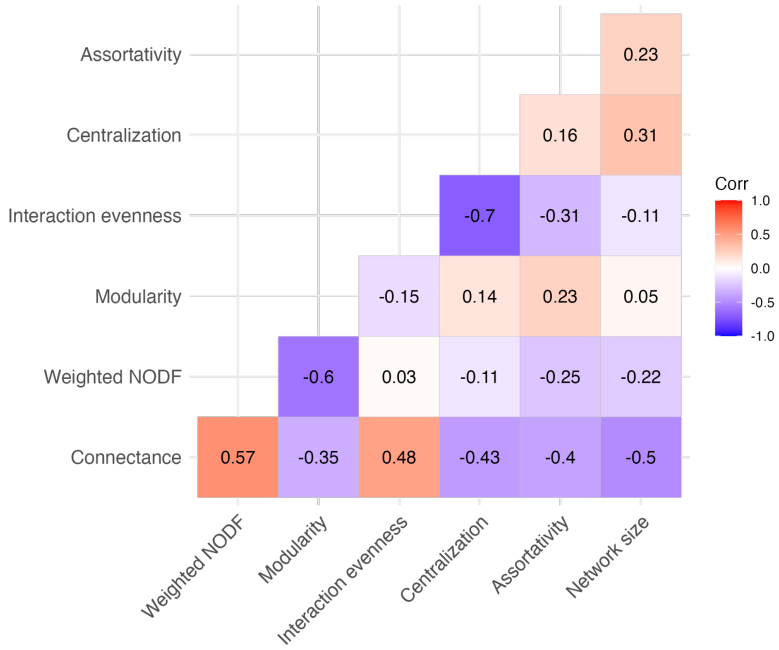


Figure S2. Correlation plot between selected network-level metrics for PCA analysis. Numbers denote Pearson correlation coefficients (r) and the color its magnitude and direction.

Table S3. Average metric values and standard deviation (SD) for species-based (sp) and individual-based (ind) networks. Null networks were generated using Patefield's null model algorithm that maintains network size (number of rows and columns) and interaction abundances (marginal totals).

Metric	Type	Observed mean ± SD	Nulls mean ± SD	Average difference ± SD
Assortativity	ind	-0.48 ± 0.17	-0.52 ± 0.04	0.04 ± 0.12
	sp	-0.5 ± 0.15	-0.57 ± 0.03	0.06 ± 0.11
Centralization	ind	0.88 ± 0.07	0.82 ± 0.02	0.06 ± 0.06
	sp	0.91 ± 0.05	0.87 ± 0.01	0.04 ± 0.04
Connectance	ind	0.3 ± 0.1	0.43 ± 0.01	-0.12 ± 0.17
	sp	0.29 ± 0.13	0.42 ± 0.01	-0.13 ± 0.1
Interaction evenness	ind	0.67 ± 0.07	0.74 ± 0.01	-0.08 ± 0.06
	sp	0.62 ± 0.07	0.71 ± 0	-0.08 ± 0.04
Modularity	ind	0.33 ± 0.12	0.2 ± 0.02	0.13 ± 0.17
	sp	0.37 ± 0.1	0.13 ± 0.01	0.24 ± 0.11
Weighted NODF	ind	30.52 ± 12.26	37.89 ± 3.43	-7.37 ± 24.77
	sp	29.66 ± 11.53	46.94 ± 3.57	-17.27 ± 9.29

Population specialization (TNW ~ WIC)

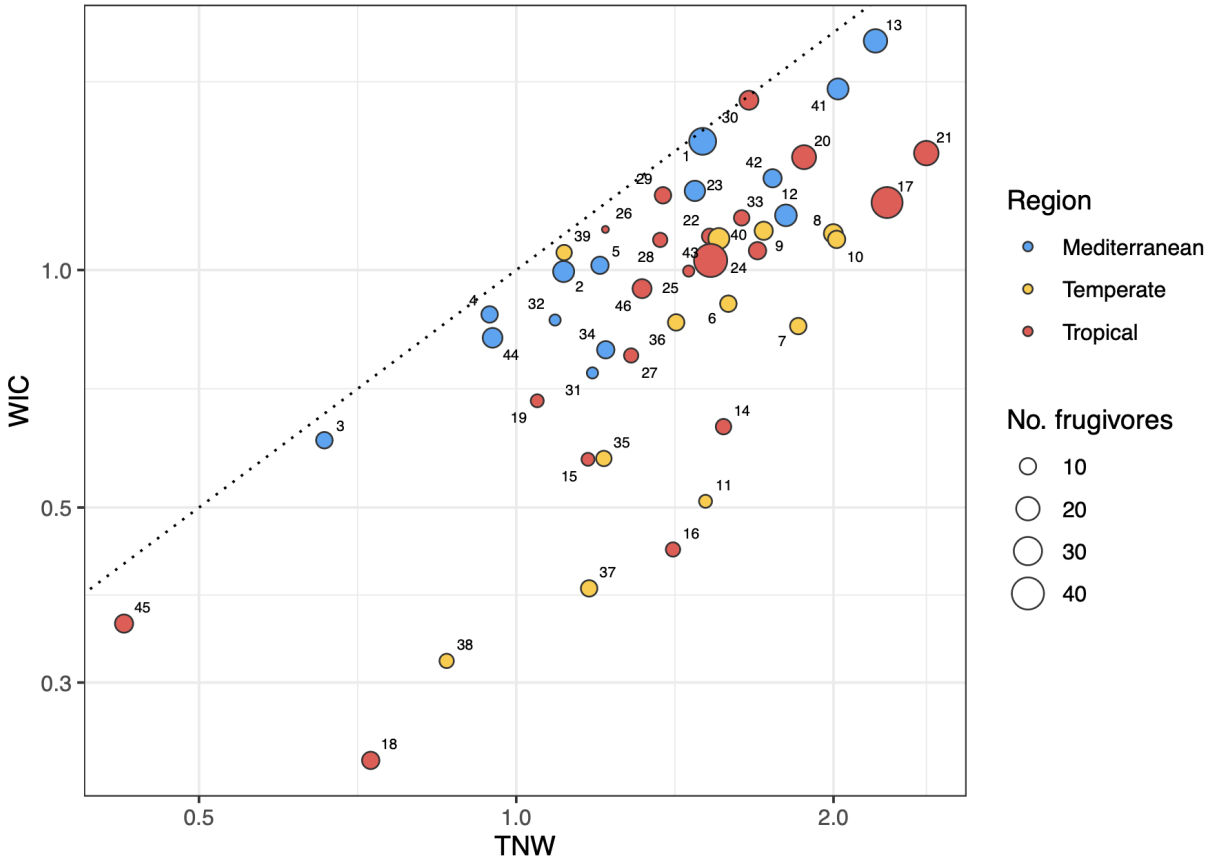
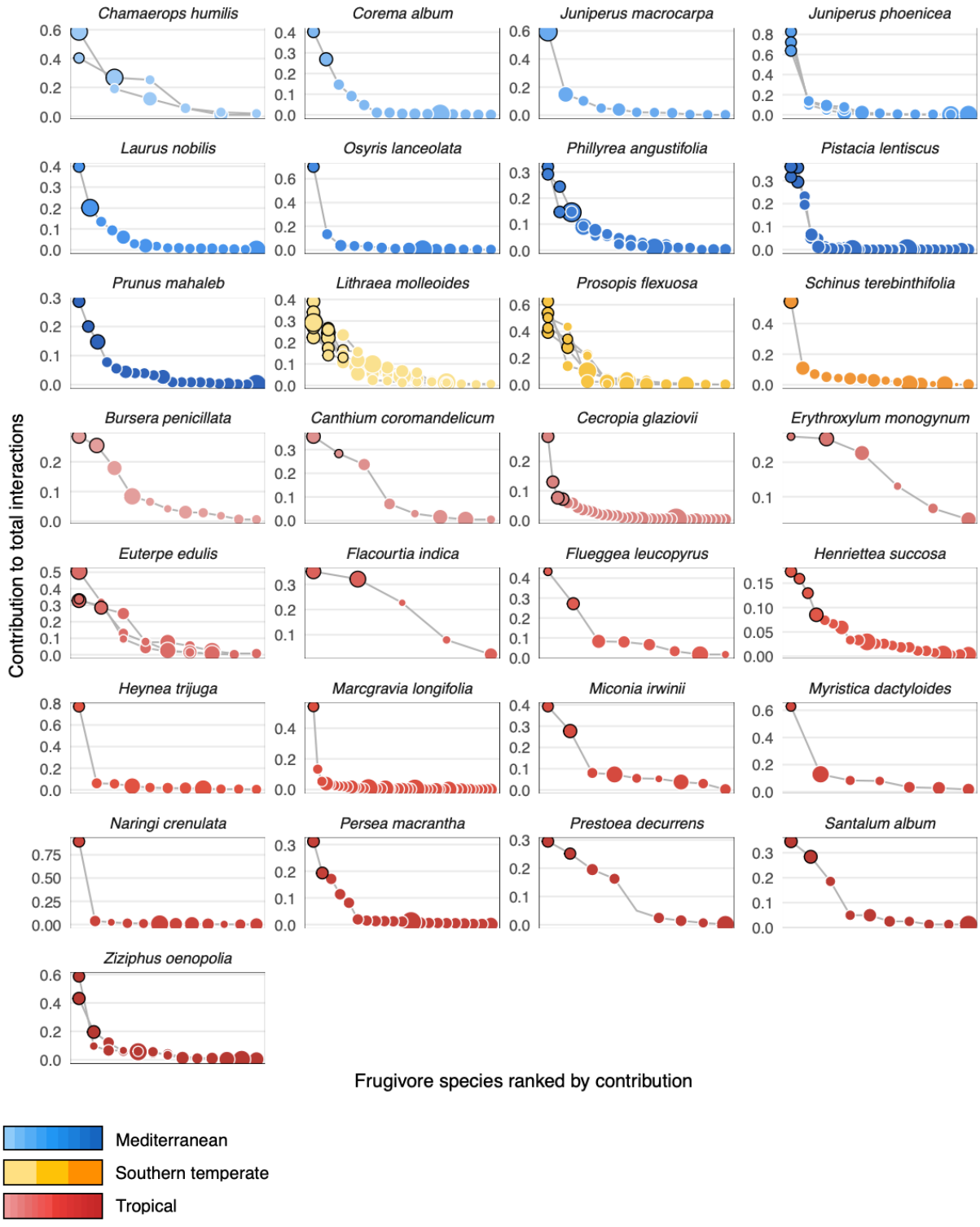


Figure S3. Total niche width (TNW) versus Within Individual Component (WIC) for individual-based frugivory networks. Point size is proportional to the number of observed frugivore species in the network, point color indicates the geographic region and number the network id (see Table S1). Note the log-scale in both axes. The dotted line represents a 1:1 ratio, in which the WIC would be equal to the TNW indicating individual niche widths that encompass the whole population niche width. The closer the networks are to the line, the higher WIC/TWN (i.e., lower individual specialization). Networks including many frugivore species tend to have a wider interaction niche (TNW), but not necessarily higher levels of individual specialization (WIC/TNW, i.e., far from the 1:1 line).

1284 **Interaction curves by frugivores**



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1287 **Figure S4.** Relative contribution of each frugivore species (dots) to the total interactions of each

1288 plant species. Frugivores are ranked by decreasing contribution. Plant species with more than one

1289 population/network present several curves. Colors for each species correspond with different

bioregions and different color shades differentiate plant species. Dots size represents frugivore body mass relative to the population (z-score) and black outlines in dots indicate those frugivore species whose aggregate contributions account for at least 50% of the interactions.

Plant individuals' interaction profiles.

Node-level metrics

Same as with network-level metrics, we tried to select node-level metrics that were not strongly correlated. All variables had a maximum VIF of 2.16 (VIF < 3).

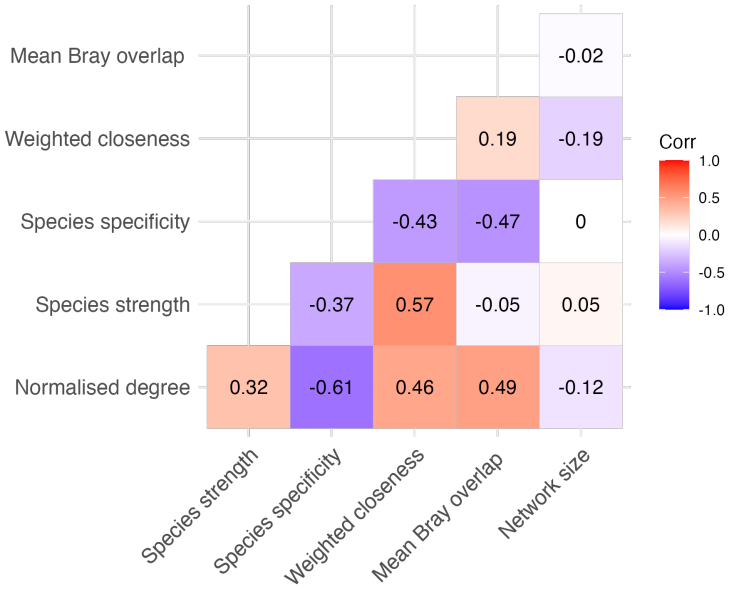

Figure S5. Correlation plot between selected node-level metrics. Numbers denote Pearson correlation coefficients (r) and the color its magnitude and direction.

1302

1303 *PCA analysis for comparing plant individuals' interaction profiles*

1304 **Table S4.** Principal Component Analysis results node-level metrics.

	PC1	PC2	PC3	PC4	PC5
Importance of components:					
Eigenvalue	1.60	1.11	0.71	0.59	0.58
Proportion of Variance	0.51	0.25	0.10	0.07	0.07
Cumulative Proportion	0.51	0.76	0.86	0.93	1.00
PC loadings:					
Normalised degree	-0.52	-0.20	-0.23	-0.72	-0.34
Species strength	-0.37	0.63	-0.20	0.40	-0.51
Species specificity index	0.51	0.15	0.5	-0.28	-0.61
Weighted closeness	-0.45	0.38	0.7	-0.17	0.36
Mean Bray-Curtis overlap	-0.35	-0.63	0.40	0.46	-0.33

1305

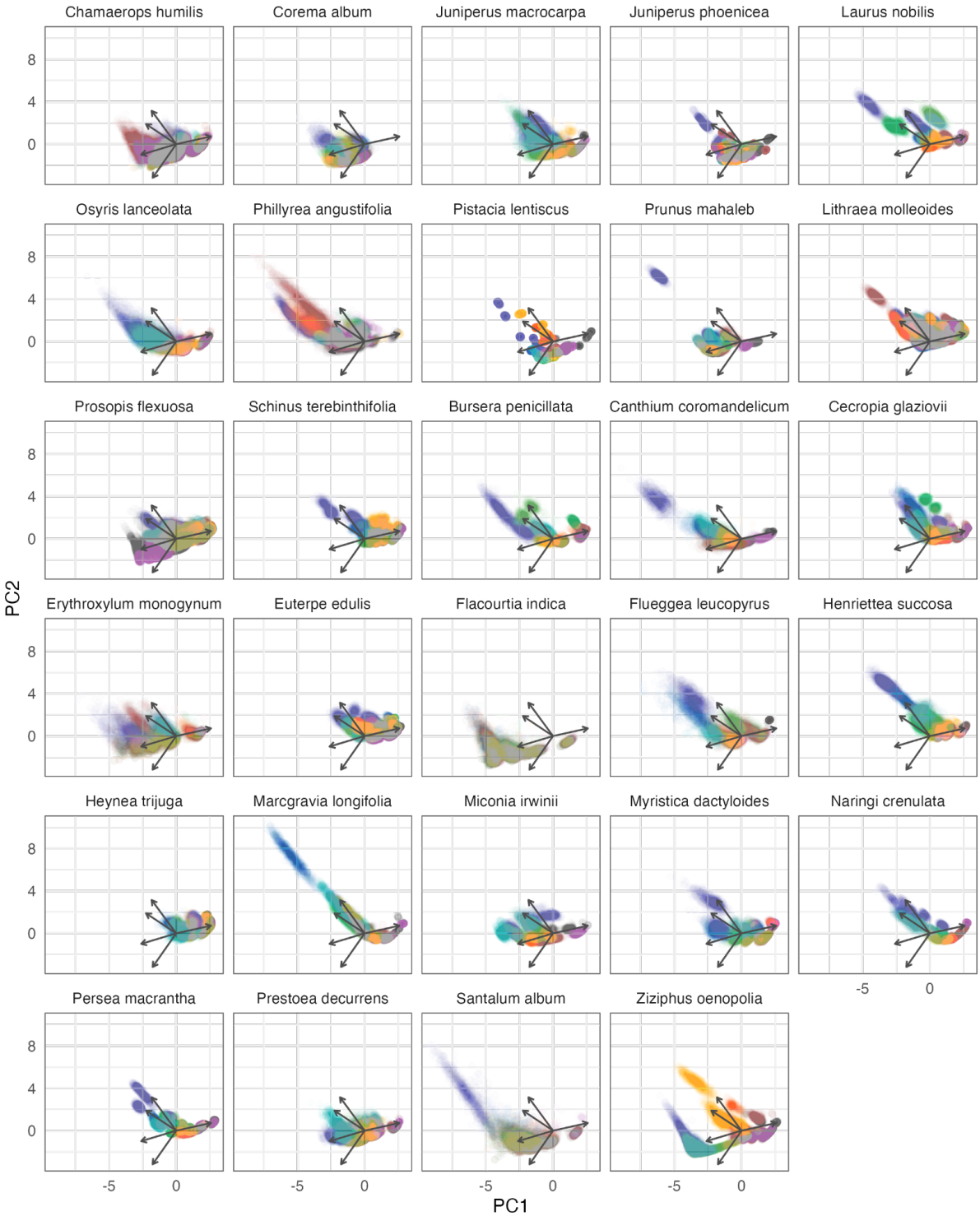

Figure S6. Principal Component Analysis for node-level metrics of individual plants in their respective networks. PCA multivariate space is faceted by plant species to facilitate display of plant individuals distribution in the multivariate space and the identification of outlying individuals. Note that some species present more than one population (i.e., more than one network, see Table S1). Each individual plant is represented by a point cloud with a different color and its node-level metrics

1312 were estimated using the full network posterior distribution (n = 1000 points per individual). It is
1313 visible how some individuals have well delimited point clouds, while some other individuals have
1314 much more uncertainty due to lower sampling coverage. See Fig. 5 for information on what node-
1315 level metric represents each of the five arrows.

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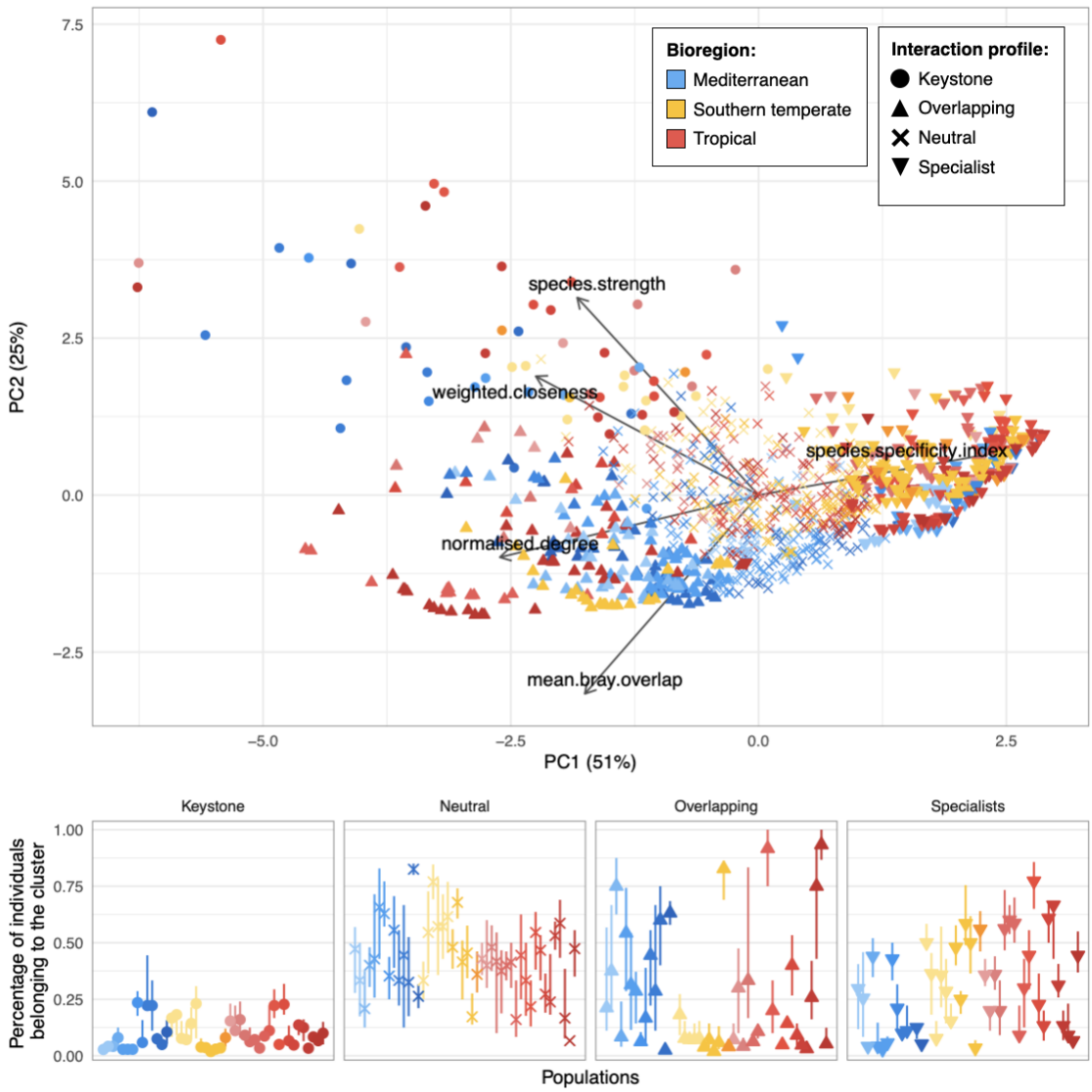

1317

1318 **Figure S7.** PCA for node-level metrics in all plant populations. Each point represents an individual
1319 plant. For each plant individual we have represented the centroid of its posterior distribution node-
1320 metric values, see Fig. S6. The shape of the points represent the most common categorization into
1321 one of the four different interaction profiles of each plant individual. The panel below shows the
1322 proportion of individuals within each population that fall into one of these clusters or interaction

profiles. The interval of each point represents the 90% confidence interval for the 1000 cluster analysis repetitions. Colors indicate the bioregion and different shades refer to different plant species within each bioregion.

Software citations

We used R version 4.4.0 (R Core Team 2024) and the following R packages: adegenet v. 2.1.10 (Jombart 2008; Jombart and Ahmed 2011), BayesianNetworks v. 0.0.7 (Rodriguez-Sanchez and Young 2024), bayestestR v. 0.13.2 (Makowski, Ben-Shachar, and Lüdecke 2019), bipartite v. 2.19 (Dormann, Gruber, and Fruend 2008; Dormann et al. 2009; Dormann 2011), cluster v. 2.1.6 (Maechler et al. 2023), DHARMa v. 0.4.6 (Hartig 2022), fmsb v. 0.7.6 (Nakazawa 2024), GGally v. 2.2.1 (Schloerke et al. 2024), ggcorrplot v. 0.1.4.1 (Kassambara 2023), ggdist v. 3.3.2 (Kay 2024b, 2024a), ggfortify v. 0.4.17 (Tang, Horikoshi, and Li 2016; Horikoshi and Tang 2018), ggh4x v. 0.2.8 (van den Brand 2024), ggrepel v. 0.9.5 (Slowikowski 2024), ggridges v. 0.5.6 (Wilke 2024), grateful v. 0.1.11 (Rodríguez-Sánchez, Jackson, and Hutchins 2022), glmmTMB v. 1.1.9 (Brooks et al. 2017), gridExtra v. 2.3 (Auguie 2017), here v. 1.0.1 (Müller 2020), igraph v. 2.0.3 (Csardi and Nepusz 2006; Csárdi et al. 2024), iNEXT v. 3.0.1 (Chao et al. 2014; Hsieh, Ma, and Chao 2024), knitr v. 1.46 (Xie 2014, 2015, 2024), MetBrewer v. 0.2.0 (Mills 2022), modelbased v. 0.8.7 (Makowski et al. 2020), network.tools v. 0.0.4 (Rodriguez-Sanchez 2024), paletteer v. 1.6.0 (Hvitfeldt 2021), patchwork v. 1.2.0 (Pedersen 2024), psych v. 2.4.3 (William Revelle 2024), rcartocolor v. 2.1.1 (Nowosad 2018), renv v. 1.0.7 (Ushey and Wickham 2024), reshape2 v. 1.4.4 (Wickham 2007), rmarkdown v. 2.26 (Xie, Allaire, and Grolemund 2018; Xie, Dervieux, and Riederer 2020; Allaire et al. 2024), scales v. 1.3.0 (Wickham, Pedersen, and Seidel 2023), summarytools v. 1.0.1 (Comtois 2022), tidylog v. 1.0.2 (Elbers 2020), tidyverse v. 2.0.0 (Wickham et al. 2019), tnet v. 3.0.16 (Opsahl 2009).

References

Allaire, JJ, Yihui Xie, Christophe Dervieux, Jonathan McPherson, Javier Luraschi, Kevin Ushey, Aron Atkins, et al. 2024. rmarkdown: Dynamic Documents for r. https://github.com/rstudio/rmarkdown.

Auguie, Baptiste. 2017. gridExtra: Miscellaneous Functions for "Grid" Graphics. https://CRAN.R-project.org/package=gridExtra.

Brooks, Mollie E., Kasper Kristensen, Koen J. van Benthem, Arni Magnusson, Casper W. Berg, Anders Nielsen, Hans J. Skaug, Martin Maechler, and Benjamin M. Bolker. 2017. "glmmTMB Balances Speed and Flexibility Among Packages for Zero-Inflated Generalized Linear Mixed Modeling." The R Journal 9 (2): 378–400. https://doi.org/10.32614/RJ-2017-066.

Chao, Anne, Nicholas J. Gotelli, T. C. Hsieh, Elizabeth L. Sander, K. H. Ma, Robert K. Colwell, and Aaron M. Ellison. 2014. "Rarefaction and Extrapolation with Hill Numbers: A Framework for Sampling and Estimation in Species Diversity Studies." Ecological Monographs 84: 45–67.

Comtois, Dominic. 2022. summarytools: Tools to Quickly and Neatly Summarize Data. https://CRAN.R-project.org/package=summarytools.

Csardi, Gabor, and Tamas Nepusz. 2006. "The Igraph Software Package for Complex Network Research." InterJournal Complex Systems: 1695. https://igraph.org.

Csárdi, Gábor, Tamás Nepusz, Vincent Traag, Szabolcs Horvát, Fabio Zanini, Daniel Noom, and Kirill Müller. 2024. igraph: Network Analysis and Visualization in r. https://doi.org/10.5281/zenodo.7682609.

Dormann, Carsten F. 2011. "How to Be a Specialist? Quantifying Specialisation in Pollination Networks." Network Biology 1 (1): 1–20.

Dormann, Carsten F., Jochen Fruend, Nico Bluethgen, and Bernd Gruber. 2009. "Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks." The Open Ecology Journal 2: 7–24.

Dormann, Carsten F., Bernd Gruber, and Jochen Fruend. 2008. "Introducing the Bipartite Package: Analysing Ecological Networks." R News 8 (2): 8–11.

Elbers, Benjamin. 2020. tidylog: Logging for "dplyr" and "tidyr" Functions. https://CRAN.R-project.org/package=tidylog.

Hartig, Florian. 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. https://CRAN.R-project.org/package=DHARMa.

Horikoshi, Masaaki, and Yuan Tang. 2018. ggfortify: Data Visualization Tools for Statistical Analysis Results. https://CRAN.R-project.org/package=ggfortify.

Hsieh, T. C., K. H. Ma, and Anne Chao. 2024. iNEXT: Interpolation and Extrapolation for Species Diversity. http://chao.stat.nthu.edu.tw/wordpress/software_download/.

Hvitfeldt, Emil. 2021. paletteer: Comprehensive Collection of Color Palettes. https://github.com/EmilHvitfeldt/paletteer.

Jombart, T. 2008. "adegenet: A r Package for the Multivariate Analysis of Genetic Markers." Bioinformatics 24: 1403–5. https://doi.org/10.1093/bioinformatics/btn129.

Jombart, T., and I. Ahmed. 2011. "Adegenet 1.3-1: New Tools for the Analysis of Genome-Wide SNP Data." Bioinformatics.https://doi.org/10.1093/bioinformatics/btr521.

Kassambara, Alboukadel. 2023. ggcorrplot: Visualization of a Correlation Matrix Using "ggplot2". https://CRAN.R-project.org/package=ggcorrplot.

Kay, Matthew. 2024a. ggdist: Visualizations of Distributions and Uncertainty. https://doi.org/10.5281/zenodo.3879620.

———. 2024b. "ggdist: Visualizations of Distributions and Uncertainty in the Grammar of Graphics." IEEE Transactions on Visualization and Computer Graphics 30 (1): 414–24. https://doi.org/10.1109/TVCG.2023.3327195.

Maechler, Martin, Peter Rousseeuw, Anja Struyf, Mia Hubert, and Kurt Hornik. 2023. cluster: Cluster Analysis Basics and Extensions. https://CRAN.R-project.org/package=cluster.

Makowski, Dominique, Mattan S. Ben-Shachar, and Daniel Lüdecke. 2019. "bayestestR: Describing Effects and Their Uncertainty, Existence and Significance Within the Bayesian Framework." Journal of Open Source Software 4 (40): 1541. https://doi.org/10.21105/joss.01541.

Makowski, Dominique, Mattan S. Ben-Shachar, Indrajeet Patil, and Daniel Lüdecke. 2020. "Estimation of Model-Based Predictions, Contrasts and Means." CRAN. https://github.com/easystats/modelbased.

Mills, Blake Robert. 2022. MetBrewer: Color Palettes Inspired by Works at the Metropolitan Museum of Art. https://CRAN.R-project.org/package=MetBrewer.

Müller, Kirill. 2020. here: A Simpler Way to Find Your Files. https://CRAN.R-project.org/package=here.

Nakazawa, Minato. 2024. fmsb: Functions for Medical Statistics Book with Some Demographic Data. https://CRAN.R-project.org/package=fmsb.

Nowosad, Jakub. 2018. "CARTOColors" Palettes. https://jakubnowosad.com/rcartocolor/.

Opsahl, Tore. 2009. Structure and Evolution of Weighted Networks. University of London (Queen Mary College), London, UK. http://toreopsahl.com/publications/thesis/.

Pedersen, Thomas Lin. 2024. patchwork: The Composer of Plots. https://CRAN.R-project.org/package=patchwork.

R Core Team. 2024. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Rodríguez-Sánchez, Francisco, Connor P. Jackson, and Shaurita D. Hutchins. 2022. Grateful: Facilitate Citation of r Packages. https://github.com/Pakillo/grateful.

Rodriguez-Sanchez, Francisco. 2024. network.tools: Tools to Analyse and Visualise Bipartite Networks. https://github.com/Pakillo/network.tools.

Rodriguez-Sanchez, Francisco, and Jean-Gabriel Young. 2024. BayesianNetworks: Bayesian Modelling of Bipartite Networks. https://github.com/Pakillo/BayesianNetworks.

Schloerke, Barret, Di Cook, Joseph Larmarange, Francois Briatte, Moritz Marbach, Edwin Thoen, Amos Elberg, and Jason Crowley. 2024. GGally: Extension to "ggplot2". https://CRAN.R-project.org/package=GGally.

Slowikowski, Kamil. 2024. ggrepel: Automatically Position Non-Overlapping Text Labels with "ggplot2". https://CRAN.R-project.org/package=ggrepel.

Tang, Yuan, Masaaki Horikoshi, and Wenxuan Li. 2016. "ggfortify: Unified Interface to Visualize Statistical Result of Popular r Packages." The R Journal 8 (2): 474–85. https://doi.org/10.32614/RJ-2016-060.

Ushey, Kevin, and Hadley Wickham. 2024. renv: Project Environments. https://CRAN.R-project.org/package=renv.

van den Brand, Teun. 2024. Ggh4x: Hacks for "ggplot2". https://CRAN.R-project.org/package=ggh4x.

Wickham, Hadley. 2007. “Reshaping Data with the reshape Package.” Journal of Statistical Software 21 (12): 1–20. http://www.jstatsoft.org/v21/i12/.

Wickham, Hadley, Mara Averick, Jennifer Bryan, Winston Chang, Lucy D’Agostino McGowan, Romain François, Garrett Grolemund, et al. 2019.“Welcome to the tidyverse.” Journal of Open Source Software 4 (43): 1686. https://doi.org/10.21105/joss.01686.

Wickham, Hadley, Thomas Lin Pedersen, and Dana Seidel. 2023. scales: Scale Functions for Visualization. https://CRAN.R-project.org/package=scales.

Wilke, Claus O. 2024. ggridges: Ridgeline Plots in “ggplot2”. https://CRAN.R-project.org/package=ggridges.

William Revelle. 2024. psych: Procedures for Psychological, Psychometric, and Personality Research. Evanston, Illinois: Northwestern University. https://CRAN.R-project.org/package=psych.

Xie, Yihui. 2014. “knitr: A Comprehensive Tool for Reproducible Research in R.” In Implementing Reproducible Computational Research, edited by Victoria Stodden, Friedrich Leisch, and Roger D. Peng. Chapman; Hall/CRC.

———. 2015. Dynamic Documents with R and Knitr. 2nd ed. Boca Raton, Florida: Chapman; Hall/CRC. https://yihui.org/knitr/.

———. 2024. knitr: A General-Purpose Package for Dynamic Report Generation in r. https://yihui.org/knitr/.

Xie, Yihui, J. J. Allaire, and Garrett Grolemund. 2018. R Markdown: The Definitive Guide. Boca Raton, Florida: Chapman; Hall/CRC. https://bookdown.org/yihui/rmarkdown.

Xie, Yihui, Christophe Dervieux, and Emily Riederer. 2020. R Markdown Cookbook. Boca Raton, Florida: Chapman; Hall/CRC. https://bookdown.org/yihui/rmarkdown-cookbook