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

Elena Quintero[1,2]*, Blanca Arroyo-Correa[1], Jorge Isla[1], Francisco Rodríguez-Sánchez[2], Pedro Jordano[1,2]

[1] Integrative Ecology Group, Estación Biológica de Doñana, EBD-CSIC, Av. Américo Vespucio 26, E-41092 Sevilla, Spain.

[2] Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla, Av. Reina Mercedes, E-41012 Sevilla, Spain.

*Corresponding author: Elena Quintero (elenaquintero.qb@gmail.com)

Author Contributions:

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

Competing Interest Statement: The authors declare no competing interest.

Keywords: individual-based networks, interaction niche, frugivory, mutualism.

Abstract

The study of mutualistic interactions among species has received considerable attention over the past 30 years. However, less is known about the structure of individual interaction configurations within species. Recently, individual-based networks have begun to garner more attention, as they represent the fundamental scale at which ecological interactions are assembled.

We compiled 44 empirical individual-based networks on plant-animal seed dispersal mutualism, encompassing 995 plant individuals across 28 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 levels of individual plant specialization. We examine how individual variation influences network structure and how plant individuals "explore" the interaction niche of the population.

Both individual-based and species-based networks exhibited high variability in network properties, leading to a lack of marked structural and topological differences between them. Our results reveal low to medium specialization, with European populations exhibiting higher generality compared to American and Asian populations. Within populations, frugivores' interaction allocation among plant individuals was highly heterogeneous, with one to three frugivore species dominating interactions in most populations.

Regardless of plant species or geographical region, plant individuals displayed similar interaction profiles across populations, with only a few individuals playing a central role and exhibiting high diversity in the interaction assemblage.

Our results emphasize the importance of downscaling from species-based to individual-based networks to understand the structuring of any given ecological community and provide an empirical basis for the extension of niche theory to complex interaction 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 individual plants "build" their interaction profiles with animal frugivores. Surprisingly, the structure of networks composed of individuals was indistinguishable from networks composed of species. Independently of species or region, interaction frequencies among frugivore partners was highly skewed, with a small subset of species providing most interactions. Additionally, 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.

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. For instance, while we may say that blackbirds consume and disperse raspberries (*Turdus merula-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 webs.

Classical studies of frugivory interactions for animal-mediated seed dispersal have been plant-focused (e.g., Snow & Snow 1988), and provide a most useful framework to zoom-in into species interactions of particular plant species and the coterie of animal frugivores they interact with. Thus, 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 (Siefer et al. 2015), discouraging major forbidden interactions (but see Albert et al. 2010, González-Varo & Traveset 2016). Thus, we might expect networks composed of individuals to exhibit architectural and structural properties different to those found in species 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). For this study, we rely on the concept of 'interaction niche 'as the space defined by the set of species with which a population can interact (Fig. 1C) (Ponisio et al. 2019).

Interaction probabilities between plant individuals plants 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 concept) as well as required matching in traits and phenology (Guimarães 2020). It was Darwin's idea that individual variation acts as the necessary raw material for natural selection (Bolnick et al. 2011). 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). These differences among plant individuals in interactions will be ultimately translated into outcome variations, acting as raw material for coevolution (Thompson 1999). In mutualistic systems such as pollination or seed dispersal, variation in the patterns of interaction or exploitation of niches (partners) can play a determining role, as mutualists directly affect the reproductive outcome of individuals, influencing fitness variation, population dynamics and trait selection.

Quantifying variation in individual interaction niche-partitioning can shed light on the coexistence and stability of mutualistic communities. 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 the 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).

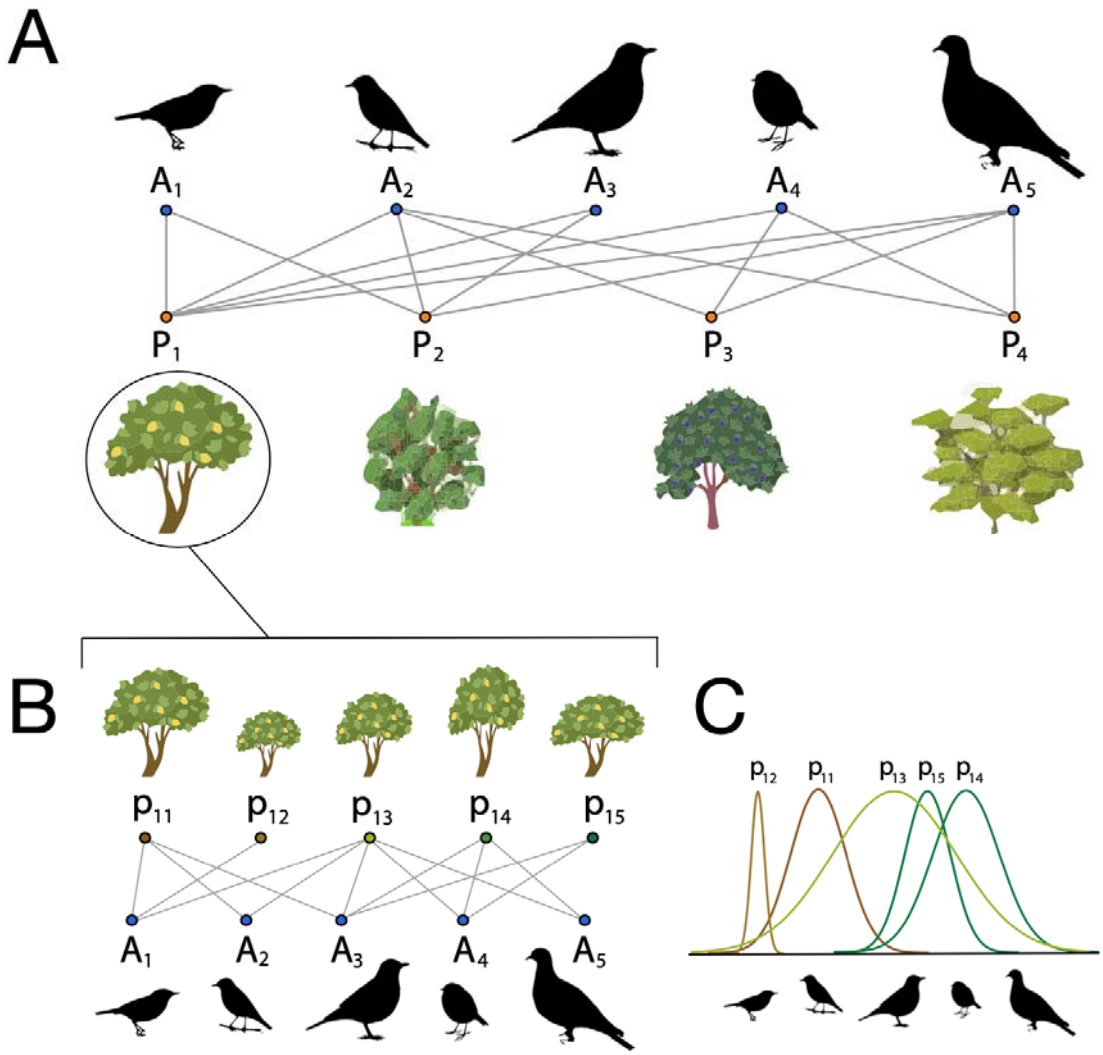

Figure 1. A) Schematic graph of an example, species-based, interaction network between four ornithochorous plant species (P_1 - P_4) and the frugivore assemblage with five animal species (A_1 - A_5) (top). B) A zoom in on the individual-based network of plant species P_1 depicting the interactions of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

The patterns we observe when species interact arise from the way in which their individuals interact (Guimarães 2020). 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 selection of node-level metrics combined, 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. If plant individuals from different populations across biome types and geographic regions present modes of interaction associated with their life-history, we could expect their individuals to exhibit similar interaction profiles, markedly different from those of individuals of other species and/or regions. Conversely, if phylogeny or context-dependent effects were not determinant in the way plant individuals interact with their frugivore partners, we could expect a consistency in individual interaction profiles distributions for all populations, irrespectively of geographic location or biome type.

The overarching goal of this study is to investigate the role played by individuals in the assembly of complex ecological networks of species interactions, determining their structuring and functioning. To do so, we combine network theory and niche theory to characterize the interaction profile of plant individuals in mutualistic seed dispersal systems across different geographic regions (Europe, Asia and America). We outline three main objectives: 1) to examine whether networks composed of individuals exhibit different architectural and structural properties than those found in species-based networks, 2) to understand how variation in frugivory interactions takes place at the plant population level by quantifying individual niche-partitioning and frugivore interaction allocation, and 3) to characterize interaction profiles of plant individuals with frugivore species and assess the distribution and frequencies of roles among the population.

Methods

Dataset acquisition and curation

We compiled studies on frugivory ecological networks with publicly-available data, both at the species and the individual plant levels. Species-based networks were gathered from 41 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 20 different study systems. Some of the studies selected presented more than one network from different communities (in species-based studies) or populations (in individual-based studies). These datasets document interactions between plant species and animal frugivore species (in species-based studies) or interactions between plant individuals of a single species and animal frugivore species (in individual-based studies). Data are provided as adjacency matrices, where rows represent plant species (or individuals) and columns represent animal species, with matrix elements a_{ij} indicating interaction frequency (visitation frequency to plants). In order to ensure networks sufficiently sampled to robustly characterize their structure and interaction profiles, we only kept those that were reasonably complete. We checked for sampling coverage of individual-based networks using iNext R package (Hsieh et al. 2016) (Table S2). To do so, we converted matrix data to an incidence frequency-data and considered plant individuals as sampling units and the number of frugivore species detected at each plant (species richness; $q = 0$). We discarded networks in which the number of interacting nodes (plants and frugivore species) was less than 15 (n = 11 networks). Our final dataset consisted of 105 networks with an average size of 380 potential links or cells (range = 55 - 2904) and 90 unique interactions (range = 21 - 419). Forty-four were individual-based networks and 61 were species-based networks (Table S1).

Individual-based networks were carefully curated and standardized by sampling effort on plant individuals(time and/or area). To do that, we divided the observed interaction intensity (e.g.

number of visits) by the amount of time observed and/or the area sampled. When possible we referred the interaction value to the coarsest level, that is, frugivore visitation events, otherwise number of fruits consumed. Once all individual-based networks were standardized by sampling effort, 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.

Network-level metrics

For both the individual and species-based networks, we calculated several network-level metrics, using R packages bipartite (Dormann et al. 2008) and igraph (Csárdi & Nepusz 2006). We selected a representative set of metrics that had suitable biological interpretation and were not highly correlated (Variance Inflation Factor < 3) and/or strongly affected by the number of species/individuals sampled or overall network size (Fig. S1, Fig. 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 nodes from other modules (Bascompte & Jordano 2014). Ranges from 0 (no clusters) in distinct clusters, where nodes within a module interact more among them than with to 1 (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. Alatalo interaction evenness *(interaction diversity)*. A metric to measure evenness in interaction distribution (Alatalo 1981, Müller et al. 1999). This metric is based on Hill

numbers (Hill 1973) and it is calculated as the modified Hill's ratio: $({}^{2}D - 1)/({}^{1}D - 1)$. It uses the diversity (D) of order 1 in the denominator (q = 1; exponential of Shannon index; expH') and diversity of order 2 in the numerator (q = 2; inverse Simpson's index). We chose this metric over traditional measure of interaction evenness (Pielou's or Shannon's evenness) because it was less correlated with connectance, also, being based on Hill numbers, gives a better description of interaction diversity (see Fig. A2). Its correlation with Pielou's interaction evenness was r = 0.66, p >0.01.

Niche specialization

We estimated populations 'niche specialization using the Shannon approximation of the WIC/TNW index for discrete data (Roughgarden 1972, 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. 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 study was present as a random factor (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). Again, 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. S6, Fig. S7).

Selected node-level metrics were:

7. Normalized degree *(interaction diversity).* Represents the richness of partners for a given node and is scaled relative to the rest of nodes in the network. 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).* 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. Normalized species strength *(interaction intensity).* Quantifies the dependence of the community on a given node (Dormann 2011). 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.

Data analysis for network metrics

In order to determine variation distribution in network structuring and topology we performed two principal component analyses (PCA), one at network-level and other at node-level. Previous studies have used PCA for comparing network metrics (e.g., Sazima et al. 2010, Mora et al. 2018, Medeiros et al. 2018, Burin et al. 2021, Acevedo-Quintero et al 2023). For comparing network metrics at two resolution scales (species-based and individual-based) we performed a PCA including both groups of networks and their values for selected network-level metrics. This procedure resulted in an ordination of both species-level and individual-based networks in relation to the multivariate space defined by network-level metrics. For comparing the plant individuals' interaction profiles, the second PCA was performed using the set of node-level metrics estimated for plant individuals within their population (i.e. individual-based networks). This resulted in an ordination of elements (plant individuals) in relation to the multivariate space defined by node-level metrics. Thus, such PCAs provide an exploratory analysis of how networks (species-based and individual-based

networks; first PCA analysis) or plant individuals (individual-based networks; second PCA analysis) span the multivariate space of network metrics: in such ordination, the location of each network or individual characterizes its structural properties or interaction profiles, respectively. We calculated 95% confidence data ellipses for different network types in both PCAs (individual-based vs. species-based in the first PCA, and for different geographical regions in the second PCA). For the second PCA we also calculated an overall 95% data ellipse for normal distributed data using all individual plants and quantified the number of outlying plant individuals relative to their own network (i.e., population).

Results

Structure of individual versus species-based networks

We assembled a total of 44 individual-based plant-frugivore networks and compared them with 61 species-based networks using six network metrics (connectance, nestedness, modularity, assortativity, centralization and interaction evenness, see Methods). Networks at different resolution scales presented similar structural properties, overlapping across the multivariate PCA space (Fig. 2). All metrics varied considerably, with a remarkable overlap at both resolution scales (see Fig. S3). Noticeably, interaction evenness was higher in individual-based networks than in species-based networks (average interaction evenness: ind-based = 0.67, sp-based = 0.59; Fig. S3).

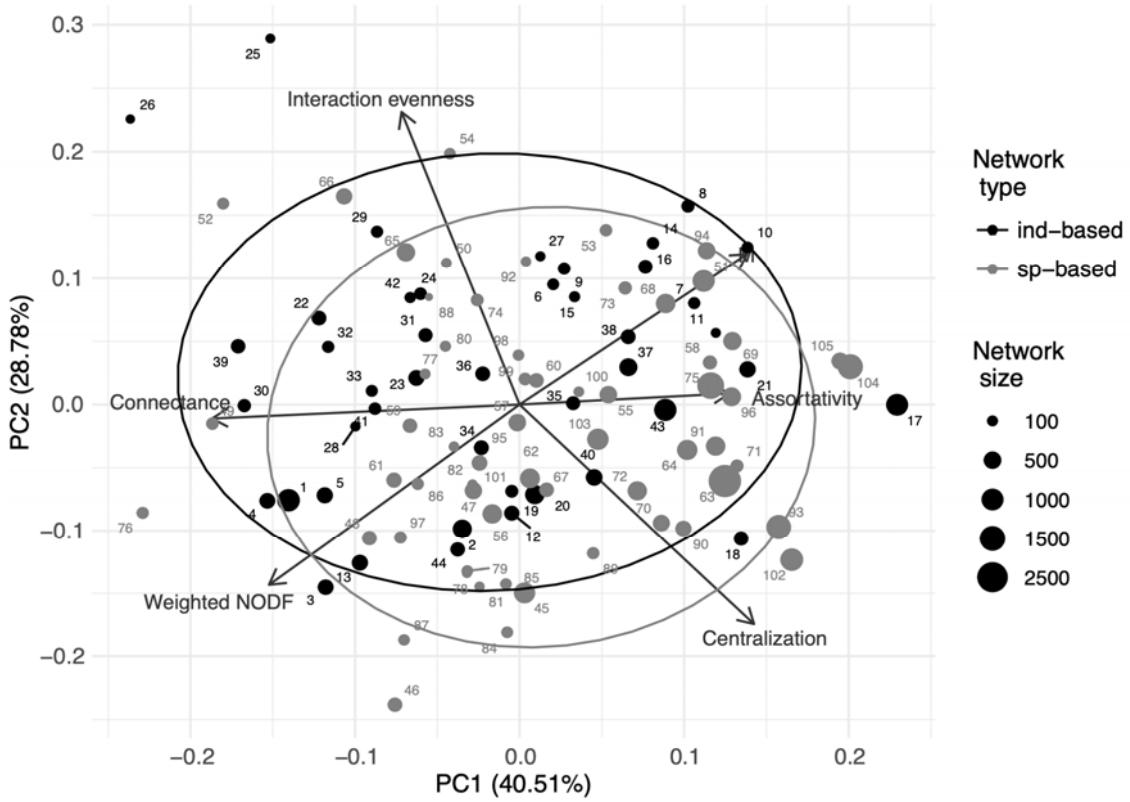

Figure 2. Principal Component Analysis of individual and species-based frugivory networks based on six different networks metrics. Each point represents a plant-frugivore network and the number indicates study identification (see Table S1). The dot size is proportional to network size (number of cells in the interaction matrix) and the color represents the resolution scale of the network. Ellipses of 95% confidence for normal data distribution are depicted for each network type.

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

Most plant populations studied presented slight to medium levels of individual specialization (mean WIC/TNW = 0.61; range = 0.28 - 0.90). Individual-based networks from America and Asia (India) showed a higher proportion of more specialized plant individuals, whereas European/Mediterranean populations presented higher levels of individual generalization (Fig. 3; difference Europe-America = 0.23, p-value >0.01). Plant populations interacting with higher

numbers of frugivore species had a wider interaction niche (TNW, i.e. Shannon diversity index), but not necessarily higher levels of individual specialization (WIC/TNW) (Fig S4).

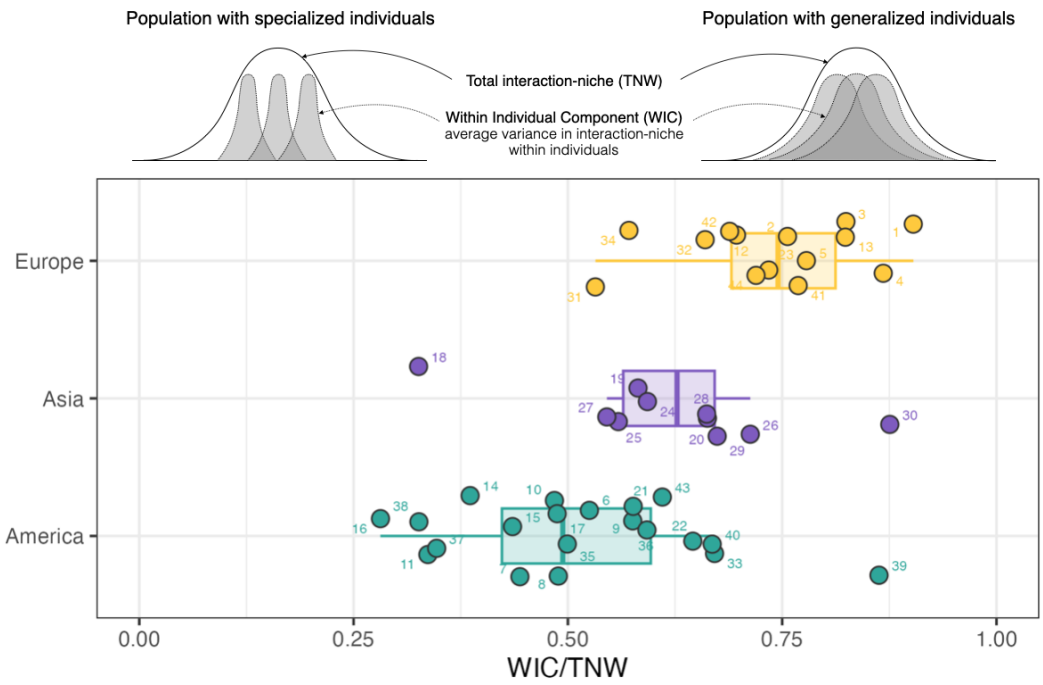

Figure 3. Values of population specialization (WIC/TNW) for all plant individual-focused studies (n = 44 networks). The total niche width (TNW) refers to the interaction niche of the population (i.e., interactions with frugivore species) and the within-individual component (WIC) is the average variation in the use of this interaction niche found within individual plants. Each point in the graph represents an individual-based network (see Table S1 for each network metadata) and colors represent the continent of the study site. At the top of the graph, a schematic representation of two plant populations: 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).

Frugivore interactions within plant populations

Notably, just a reduced subset of frugivore species in most networks (generally between one and three) usually accumulated most of the interactions, while the rest of frugivore species contributed a minor proportion. On average less than 20% of frugivores contributed more than half of the interactions, regardless of the total number of frugivore species in the population (SD = 9.6%, Fig. S5). The frugivores that contributed most interactions also tended to interact with a higher number of plant individuals (Spearman s rho = 0.81, p-value < 0.01, Fig. 4). Remarkably, frugivore species with smaller contributions interacted with a variable proportion of plant individuals, such proportion being higher in European networks and lower in American networks (Fig. 4). Frugivores' body mass was not correlated with interaction contribution (rho = -0.05) nor with the proportion of plant individuals interacted (rho = -0.11).

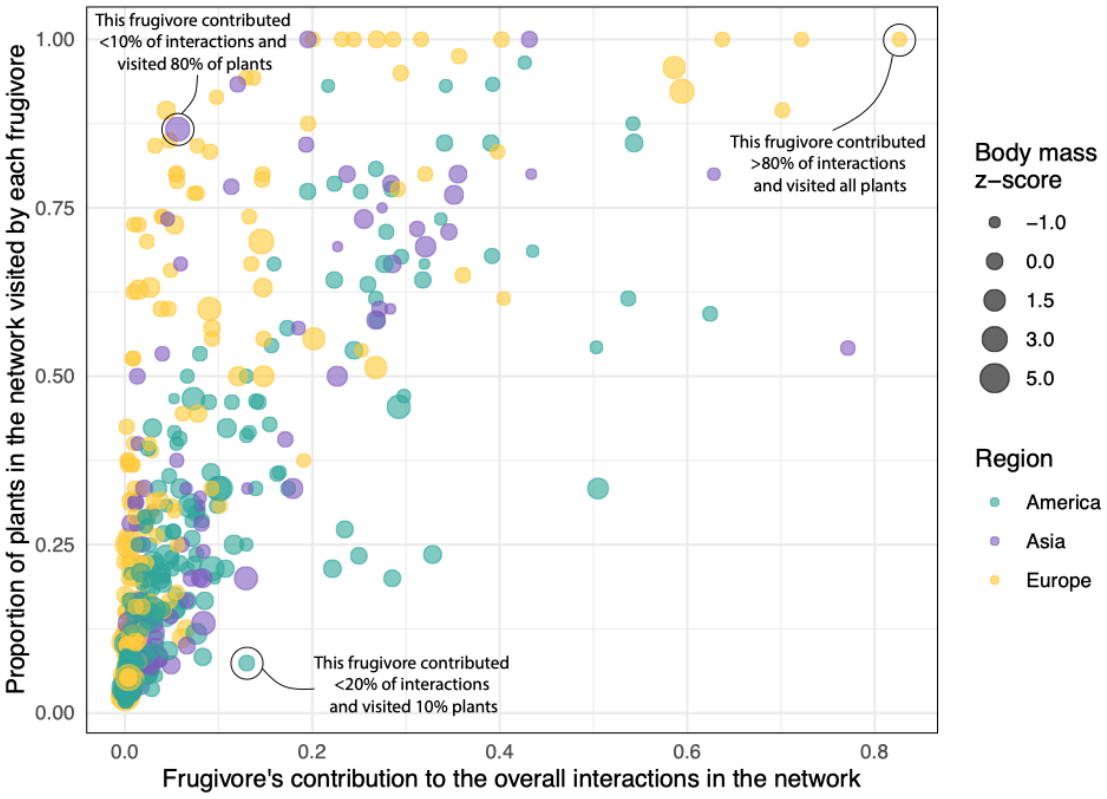

Figure 4. Relationship between the overall contribution to the total number of interactions by each frugivore species (i.e., link weights in the individual-based networks) and the proportion of plant

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 geographic region and point size represents the frugivore's body mass relative to its population (z-score).

Plant individuals' interaction profiles

The 44 individual-based networks included a total of 995 plant individuals: 452 (from 9 species) from America, 170 (10 species) from Asia and 373 (9 species) from Europe. The principal component analysis based on all the individual´s interaction profiles did not produce distinct clusters by region or population. Instead, individuals from different populations (i.e. individual-based networks) spread across the multidimensional space, suggesting ample within-population heterogeneity in plant individuals 'interaction profiles (Fig. 5). The first principal component (PC1), explaining more than half of the variation, was mainly related to interaction degree and specialization index, thus capturing individual variation in frugivore richness and composition. The second component (PC2) explained 22% 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). The PC2 distinguished plant individuals based on their frugivore assemblage composition, where plant individuals with more unique frugivore assemblages were positioned in the bottom area of the PCA , while many plants with highly-overlapping frugivore assemblages within their populations were positioned towards the upper area. The third component (PC3; 14% variation explained; Table A4) was strongly related to weighted closeness, a measure of how strongly and well connected individuals are within the network (i.e. central).

Overall, individual plants from Europe tended to have more similar frugivore assemblages (higher niche overlap), while plants from America presented less overlapping and more specialized individual assemblages (Fig. 5). 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 bottom-left area of the multivariate space). Most individual plants 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 (upper-right Fig. 5).

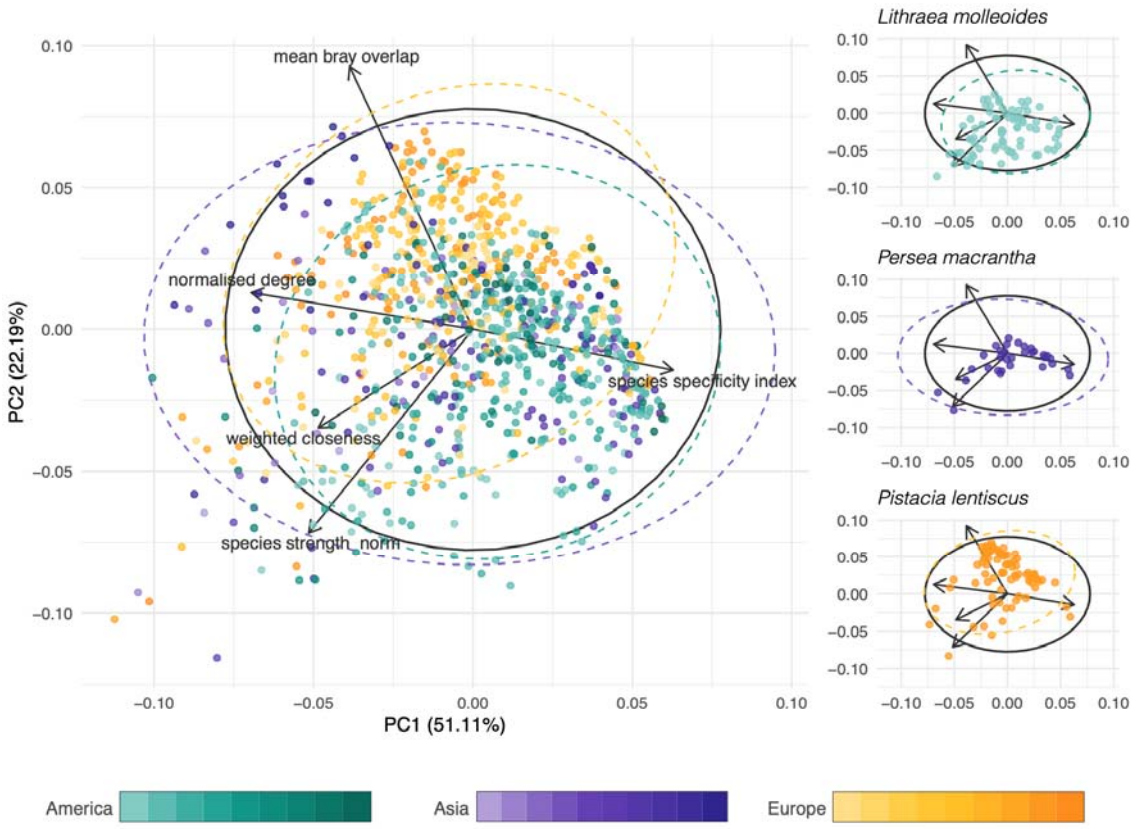

Figure 5. PCA for node-level metrics. Each point represents an individual plant. Point color indicates the geographic region and different shades to refer to different plant species within each region. Ellipses represent 95% CI for all individual plants (in black) and each continent (in color) (see Fig. S9 for a 3D visualization of PCA results). Panels on the right are a subset of PCA for three plant species.

The 95% CI ellipse for all individuals (black line ellipse in Fig. 5) illustrates a broad overlap among species, irrespective of biome or frugivore assemblage composition, i.e., points for individual plants broadly admixed relative to the multivariate network metrics space. Notably, highly central plants,

that account for a high proportion of interactions within their populations, represent outliers in their networks and most networks presented one or few individuals with these network role (i.e., outside the overall 95%CI ellipse; median = 1 individual per network, min-max range = 0-5 individuals per network); this represented an average of the 7% of the individuals within populations (range min-max = 0% and 33%). Out of 44 networks (i.e., plant populations), 36 had outlier individuals and out of 28 plant species, 26 had outlier individuals (see Fig. S8). These outlying individuals displayed a notable association with high scores in weighted closeness (see 3D representation in Fig. S9).

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 in different populations around the world, as well as the similarity in the interaction profiles within populations regardless the species or context we observe.

Downscaling in ecological resolution

The structure of plant-animal mutualistic networks revealed fundamental heterogeneity in structure across networks and scales. We did not reveal major deviations in the assembly patterns of interactions as we zoomed in the scale of resolution- from the hierarchically higher species scale to a lower, individual-based scale. Previous efforts to explore network architecture when downscaling the ecological resolution, found shifts in the structuring of pollination networks (Tur el al. 2014, Wang et al. 2021). Both studies observed that individual-based networks were less connected and that individuals were more specialized than species. Their approach for testing the effect of scale change in network structure is however different from the one we use, as these studies focused on a specific community at a specific time and used the same methodology for

sampling both resolution scales. In contrast, our approach considers communities and populations from different parts of the world at different times and sampled with different methodologies, capturing as much variation as possible to examine differences and similarities in general interaction patterns. We only observed slight differences across scales in interaction evennes. The resulting higher overall interaction evenness in individual-based networks can be explained by a lack of major forbidden links, which allows frugivores to potentially interact with most individual plants and distribute their interactions more homogeneously when compared to interactions established with a more heterogeneous set of species partners. We argue that the addition of new species or individuals with new traits to a network provides new link possibilities, yet in the case of species-based networks these potential interactions will need to undergo stronger trait and phenological matching filters than 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 between our study and those of Tur el al. 2014 and Wang et al. 2021, we also look at different mutualistic systems. The specialization levels of pollination and frugivory systems likely differ due to the nature of both ecological interactions (Wheelwright & Orians 1982, Jordano 1987). For instance, structural limitations such as morphological adjustment between the corolla and mouthparts in pollination systems usually require stronger morphological coupling and are perhaps more favored (to avoid hybridization) than the adjustment between fruits and the mouthparts of the consumers 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 was not sufficient to make clear distinctions. The absence of discriminatory patterns to determine the scale could indicate the existence of underlying effects that control ecological network configurations. We argue that numerical effects (i.e., organism abundances) are likely at the base of these emergent properties, governing interaction strength distribution across nodes and asymmetric interactions (Vázquez et al. 2007, Schleuning et al. 2011, Guimarães 2020).

Exploitation of the interaction niche

Individuals 'interaction niches were narrower than that of their populations, supporting that individual specialization in mutualisms is substantial and common in nature (Bolnick et al. 2003). Plant individuals' specialization levels were similar to specialization levels reported in other animal taxa (Araujo et al. 2011). Interestingly, the degree of individual specialization markedly varied across regions, with European populations being more generalized than South American populations, yet with most plant species showing WIC/TNW ratios >50 %, which indicates moderate generalization among individual plants. Furthermore, frugivores 'interaction allocation among individual plants also varied among regions. Broader and more overlapping frugivore assemblages in Mediterranean regions versus higher specialization and variability in tropical and subtropical networks (higher frequency of study cases with WIC/TNW ratios <50 %) can be attributed to differences both in taxonomic diversity and redundancy levels in seed dispersal service, with frugivore assemblages being substantially more diversified and complementary as we descend in the latitudinal gradient (Fleming 1987, Willig et al. 2003). Although the latitude–niche breadth hypothesis does hold for food webs in terrestrial systems (Cirtwill et al. 2015), it could be influencing specialization patterns of mutualistic plant-animal in frugivory systems. The degree of fruit dependence in the animal's diet may influence individual specialization; tropical birds are more likely to be obligate frugivores, heavily relying on fruits, while temperate birds present more generalized diets with less dependency on fruits as their primary food source (Dalsgraad et al. 2017). Species range size may also be behind differences encountered across regions, as it has been

demonstrated to increase populations 'niche breadth (Galiana et al. 2023). Different levels of individual specialization can have implications for population stability and niche expansion (Van Valen 1965). According to the niche variation hypothesis, populations with higher levels of individual specialization will be more prone to niche expansion (Araujo et al. 2011). Niche shifts and expansion have become exceptionally important for 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 geographical regions 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.

Differential contribution by frugivores to plant consumption was widespread in all populations, supporting previous studies and providing more evidence on how just a few species, even within diversified assemblages, 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). These 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 just 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, 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).

Individual plants ’interaction profile

Individual plants showed widespread interaction patterns, regardless of the population or species, as revealed by a rather homogeneous multivariate structure of interaction metrics, lacking distinct groupings in the multivariate space. This resulted in a heterogeneous positioning of individual plants across the multivariate space, pointing to the existence of fundamental architectural patterns in the assemblage of mutualistic interactions that are not strongly constrained by phylogeny or geographic location but rather by the interplay between traits and numerical effects (Jordano 1987, Carnicer et al. 2009, Albrecht et al. 2018, Guimarães 2020). We observed a consistent distribution of plant roles within populations, in which a large majority of individuals act in an average manner, a smaller number of individuals stand out for their specialization and only very few individuals stand out for their high diversity, frugivores ’dependence and central role in interactions. This pattern reinforces previous findings in food webs, which revealed the presence of a core group of species fulfilling similar ecological roles, alongside peripheral species exhibiting idiosyncratic profiles (Mora et al. 2018). It is likely that within frugivory networks these key individuals present unique phenotypic traits, such as abundant fruit crops or advantageous locations that make them reliable to many frugivores (Snell et al. 2019, Isla et al. 2023).

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

Concluding remarks

We found consistent patterns of interaction assembly across biological scales using a set of 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 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. 2021, 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 mutualism interactions are structured at the individual level and reveal underlying patterns of role assignment within populations and across geographical regions.

Acknowledgments

We are grateful to Miguel Jácome, Gemma Calvo, Pablo Homet, Pablo Villaba and Juan Miguel Arroyo, for support in data collection and processing with some of the individual networks which was fundamental for this manuscript, as well as, discussion and comments for improving the quality of this work. We are also grateful to Daniel Stouffer for his help and discussion on the network centralization metric. We thank the logistic and facilities support form ICTS-RBD Doñana and the Doñana National Park for the access authorizations to collect data from many of the individual networks here presented. Funding from LIFEWATCH-2019-09-CSIC-13 project and PID2022-136812NB-I00, Spanish Ministry of Science and Innovation, as well as funding from the VI Plan

Propio de Investigación of the Universidad de Sevilla (VI PPIT-US) supported this research (PJ). EQ was supported by "la Caixa" Foundation fellowship LCF/BQ/DE18/1167000. FRS was supported by VI PPIT-US and grants US-1381388 from Universidad de Sevilla/Junta de Andalucía/FEDER-UE and grant CNS2022-135839 from Ministerio de Ciencia e Innovación.

Author Contributions:

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

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. 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

15. 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

16. 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.

17. 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

18. 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

19. 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

20. 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

21. 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

22. 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

23. Cohen, J. E. (1978). *Food webs and niche space*. Princeton University Press. https://press.princeton.edu/books/paperback/9780691082028/food-webs-and-niche-space-mpb-11-volume-11

24. 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

25. 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

26. 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

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

28. Dalsgaard, B., Schleuning, M., Maruyama, P. K., Dehling, D. M., Sonne, J., Vizentin-Bugoni, J., Zanata, T. B., Fjeldså, J., Böhning-Gaese, K., & Rahbek, C. (2017). Opposed latitudinal patterns of network-derived and dietary specialization in avian plant–frugivore interaction systems. *Ecography*, *40*(12), 1395–1401. https://doi.org/10.1111/ecog.02604

29. 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

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

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

32. 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

33. Fleming, T. H., Breitwisch, R., & Whitesides, G. H. (1987). Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics*, *1*, 91–109.

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. Galiana, N., Lurgi, M., Montoya, J. M., Araújo, M. B., & Galbraith, E. D. (2023). Climate or diet? The importance of biotic interactions in determining species range size. *Global Ecology and Biogeography*, *32*, 1178–1188. https://doi.org/10.1111/geb.13686

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. 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

53. 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

54. 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

55. 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

56. 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

57. 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

58. 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

59. 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

60. 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

61. 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

62. 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

63. 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

64. 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

65. 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

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

67. 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

68. 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

69. 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

70. 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

71. 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

72. 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

73. 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

74. 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

75. 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

76. 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

77. 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

78. 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

79. 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

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

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

82. 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

83. 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

84. 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

85. 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

86. 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

87. 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

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

89. 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

90. 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

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

92. 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

93. 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

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

95. 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

96. 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

97. 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

98. 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

99. 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.

100. Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 273–309. https://doi.org/10.1146/annurev.ecolsys.34.012103.144032

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. 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

8. 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

9. 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

10. 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

11. 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

12. 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

13. 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

14. 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.

15. 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

16. 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

17. 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

18. 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. Kantak, G. E. (1979). Observations on some fruit-eating birds in Mexico. *The Auk*, *96*(1), 183–186. https://doi.org/10.1093/auk/96.1.183

22. 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

23. 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

24. 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

25. 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

26. 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

27. 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

28. 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.

29. 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.

30. 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

31. 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

32. Robinson, V. (2015). *Índice de importância de diferentes espécies de plantas na atração de aves para uma área reflorestada em Piracicaba*. Universidade Estadual Paulista.

33. 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.

34. 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

35. 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

36. 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

37. 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.

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

39. 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

40. Stiebel, H., & Bairlein, F. (2008). Frugivorie mitteleuropäischer Vögel I: Nahrung und Nahrungserwerb. *Vogelwarte*, *46*, 1–23.

41. 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

Elena Quintero[1]*, Blanca Arroyo-Correa[1], Jorge Isla[1], Francisco Rodríguez-Sánchez[2], Pedro Jordano[1,2]

[1] Integrative Ecology Group, Estación Biológica de Doñana, EBD-CSIC, Av. Américo Vespucio 26, E-41092 Sevilla, Spain.

[2] Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla, Av. Reina Mercedes, E-41012 Sevilla, Spain.

**corresponding author: elenaquintero.qb@gmail.com*

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, the number of plants and number of frugivores present in the network, the network size (potential interactions), the 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

1088

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	
10	ind	*Lithraea molleoides* (Anacardiaceae)	Argentina	12	11	132	29	Las Rabonas	Focal observations	

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
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 size differentially influence frugivory of select rainforest tree species in Western Ghats, India. Biotropica, 52(5), 871-883.
19	ind	*Myristica dactyloides* (Myristicaceae)	India	25	7	175	45		Focal observations	

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
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	
28	ind	*Canthium coromandelicum* (Rubiaceae)	India	10	8	80	30		Focal observations	

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
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	
37	ind	*Prosopis flexuosa* (Fabaceae)	Argentina	54	10	540	112	El Doménico	Camera traps	

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
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
45	sp		Spain	25	36	900	228	Cazorla	Focal observations	Olesen JM, Bascompte J, Dupont YL, Elberling H,

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
46	sp		Spain	16	17	272	120	Hato Ratón	Mist-netting	Rasmussen C, Jordano P. (2011). Missing and forbidden links in mutualistic networks. Proceedings of the Royal Society B-Biological Sciences 278: 725-732.
47	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.
48	sp		Papua New Guinea	31	9	279	119		Focal observations	Beehler B. (1983) Frugivory and polygamy in birds of paradise. Auk, 100, 1-11.
49	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.
50	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.
51	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.
52	sp		Mexico	5	27	135	86		Focal observations	Kantak, G.E. (1979). Observations on some fruit-eating birds in Mexico. Auk, 96, 183-186.
53	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.

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
54	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.
55	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.
56	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.
57	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.
58	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.
59	sp		Kenya	7	38	266	104	Edge little disturbed	Focal observations	
60	sp		Kenya	8	34	272	88	Interior highly disturbed	Focal observations	
61	sp		Kenya	8	39	312	115	Edge highly disturbed	Focal observations	
62	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
63	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.
64	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.
65	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.
66	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.
67	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.
68	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
69	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.
70	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.
71	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.
72	sp		Brazil	23	29	667	129	25-year-old restored plot	Focal observations	
73	sp		Brazil	14	14	196	35	57-year-old restored plot	Focal observations	
74	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.
75	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.
76	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.
77	sp		Poland	8	12	96	38	site_11	Focal observations	Albrecht, J., Bohle, V., Berens, D. G., Jaroszewicz, B.,

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
78	sp		Poland	7	11	77	32	site_13	Focal observations	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.
79	sp		Poland	9	13	117	42	site_15	Focal observations	
80	sp		Poland	8	13	104	36	site_30	Focal observations	
81	sp		Poland	8	10	80	29	site_35	Focal observations	
82	sp		Poland	8	10	80	30	site_36	Focal observations	
83	sp		Poland	8	11	88	33	site_102	Focal observations	
84	sp		Poland	10	13	130	42	site_111	Focal observations	
85	sp		Poland	8	15	120	57	site_112	Focal observations	
86	sp		Poland	9	16	144	41	site_203	Focal observations	
87	sp		Poland	6	20	120	43	site_301	Focal observations	
88	sp		Poland	5	11	55	21	site_314	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	

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

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.

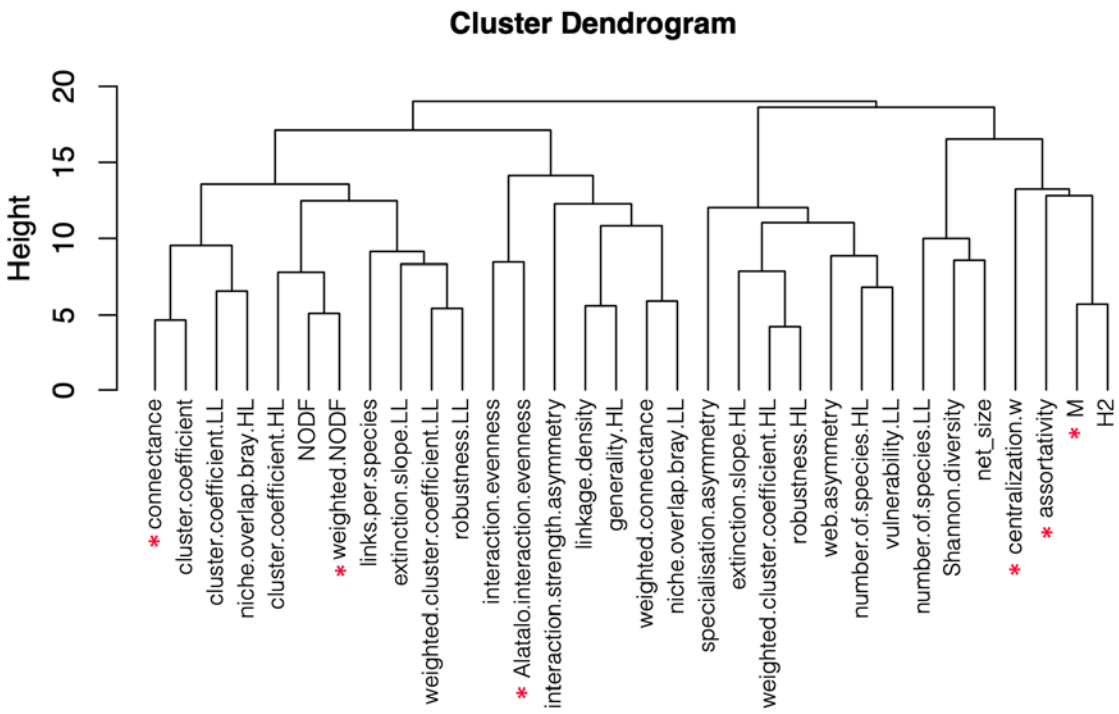

Figure S1. Hierarchical clustering analysis results for all the network metrics calculated. Metrics with * are the selected ones.

We checked for 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<3.15.

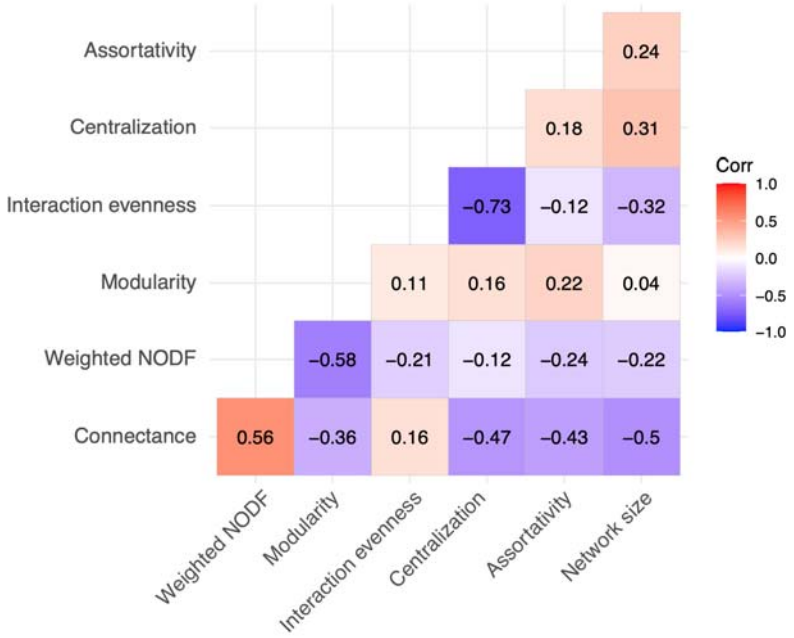

Figure S2. Correlation plot between selected network-level metrics for PCA analysis.

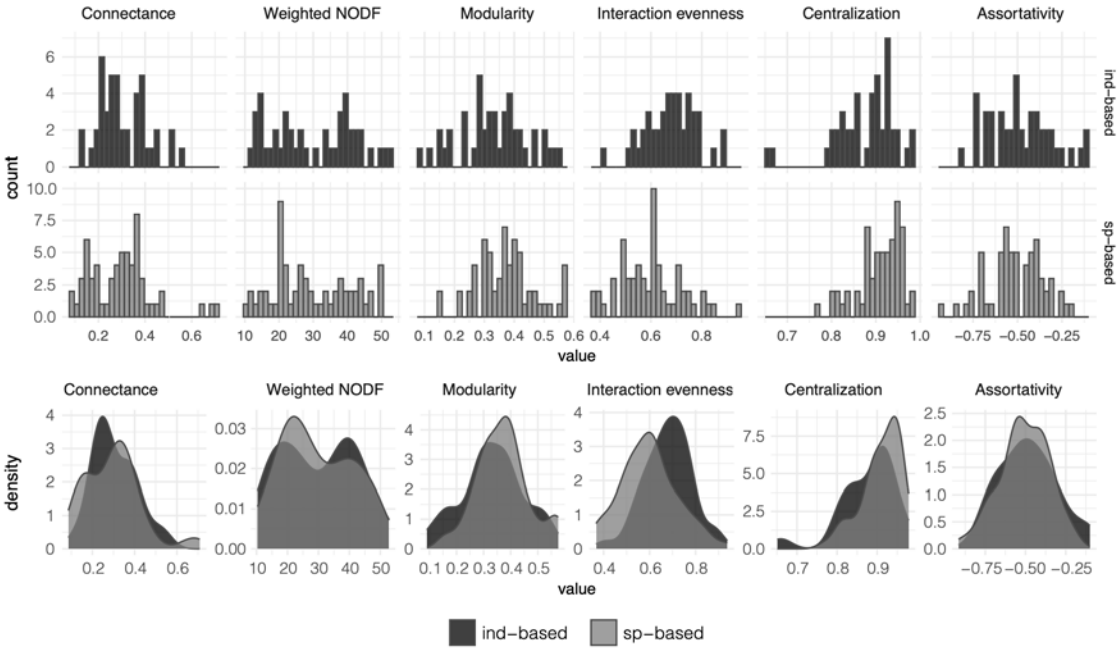

Figure S3. Distribution of network-level metrics of frugivory networks at different scales of resolution. Species-based networks are represented in gray (n = 61) and individual-based networks in black (n = 44). Upper two rows show histograms for each network type, and the lower row shows density plot for both network types facilitating comparison.

Table S3. Principal Component Analysis results for network-level metrics.

	PC1	PC2	PC3	PC4	PC5	PC6
Importance of components:						
Eigenvalue	1.56	1.31	0.91	0.74	0.54	0.42
Proportion of Variance	0.41	0.29	0.14	0.09	0.05	0.03
Cumulative Proportion	0.41	0.69	0.83	0.92	0.97	1
PC loadings:						
Connectance	-0.54	-0.03	0.1	-0.56	0.56	-0.26
Weighted NODF	-0.44	-0.42	-0.23	-0.27	-0.71	-0.05
Modularity	0.4	0.35	0.36	-0.69	-0.31	0.1
Alatalo interaction evenness	-0.21	0.67	-0.1	0.19	-0.25	-0.63
Centralization	0.41	-0.51	0.25	0.01	0.01	-0.71
Assortativity	0.37	0.03	-0.86	-0.3	0.15	-0.11

Population specialization (TNW ~ WIC)

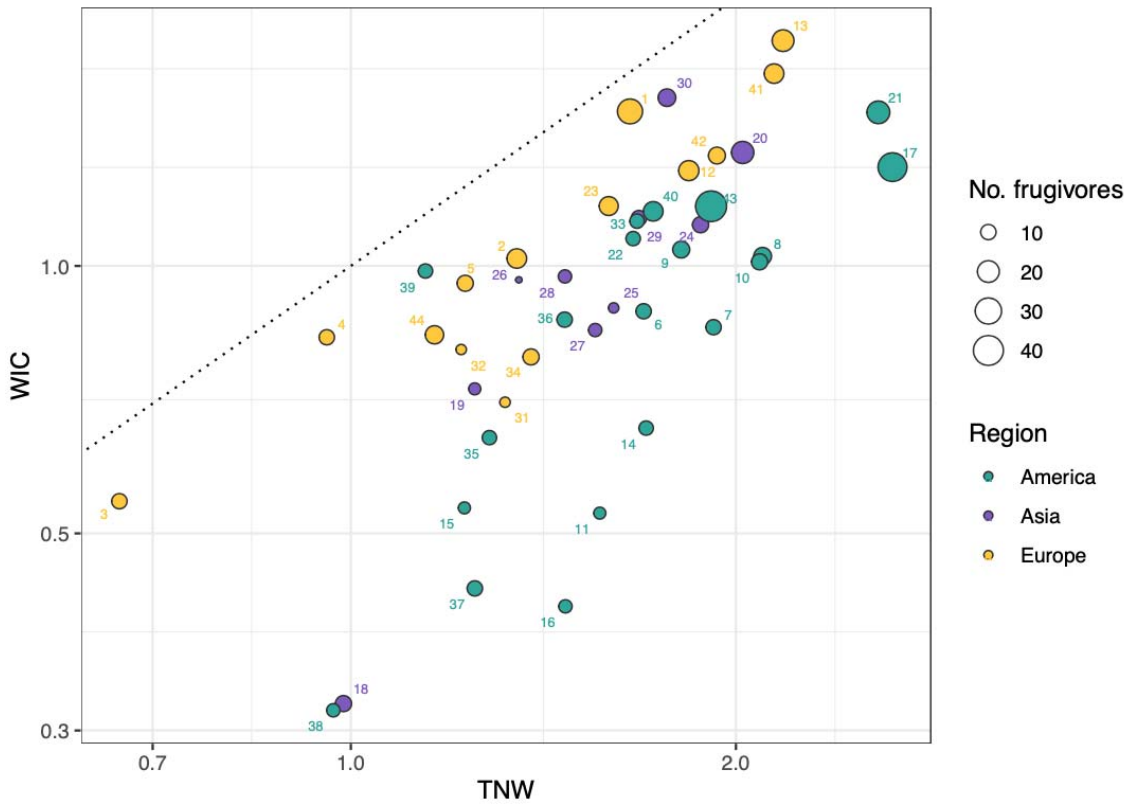

Figure S4. Total niche width (TNW) versus Within Individual Component (WIC) for individual-based frugivory networks. Point size is proportional to the number of frugivore species in the network, point color indicates the geographic region and number the network id (see Table S1). Note the log-scale in 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).

Interaction curves by frugivores

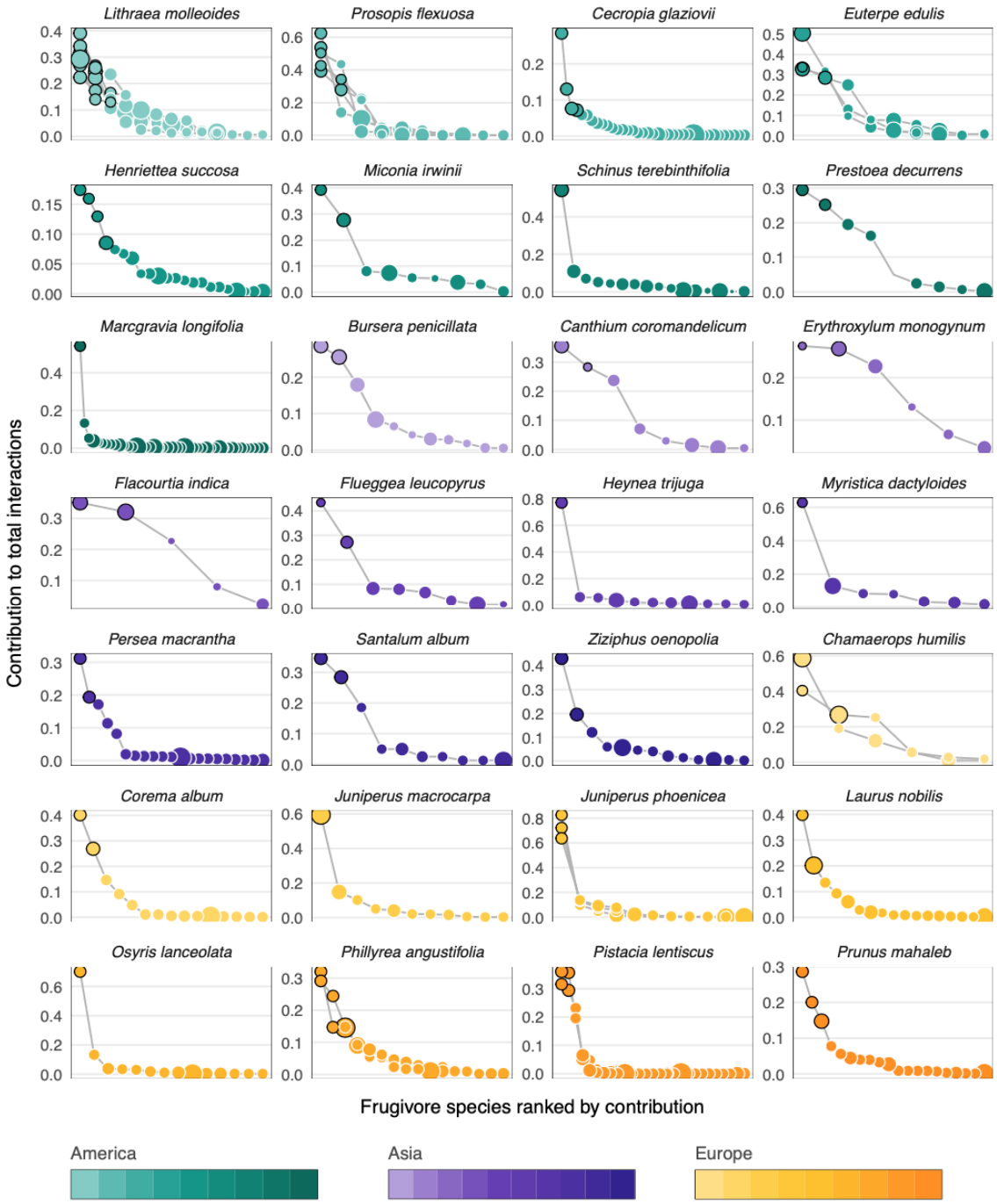

Figure S5. Relative contribution of each frugivore species (dots) to the total interactions of each plant species. Frugivores are ordered by contribution ranking. Plant species with more than one population/network present several curves. Colors for each species correspond with different geographical regions (teal = America, purple = Asia, orange = Europe) and different color shades differentiate plant species, these correspond with colors

in the individual-based networks PCA plot (Fig. 5). 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 were not strongly correlated. All variables had a maximum VIF of 2.85 (VIF < 3).

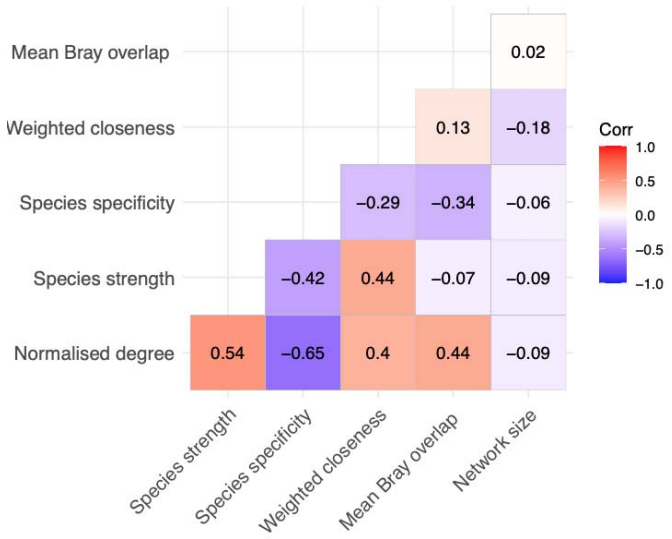

Figure S6. Correlation plot between selected node-level metrics.

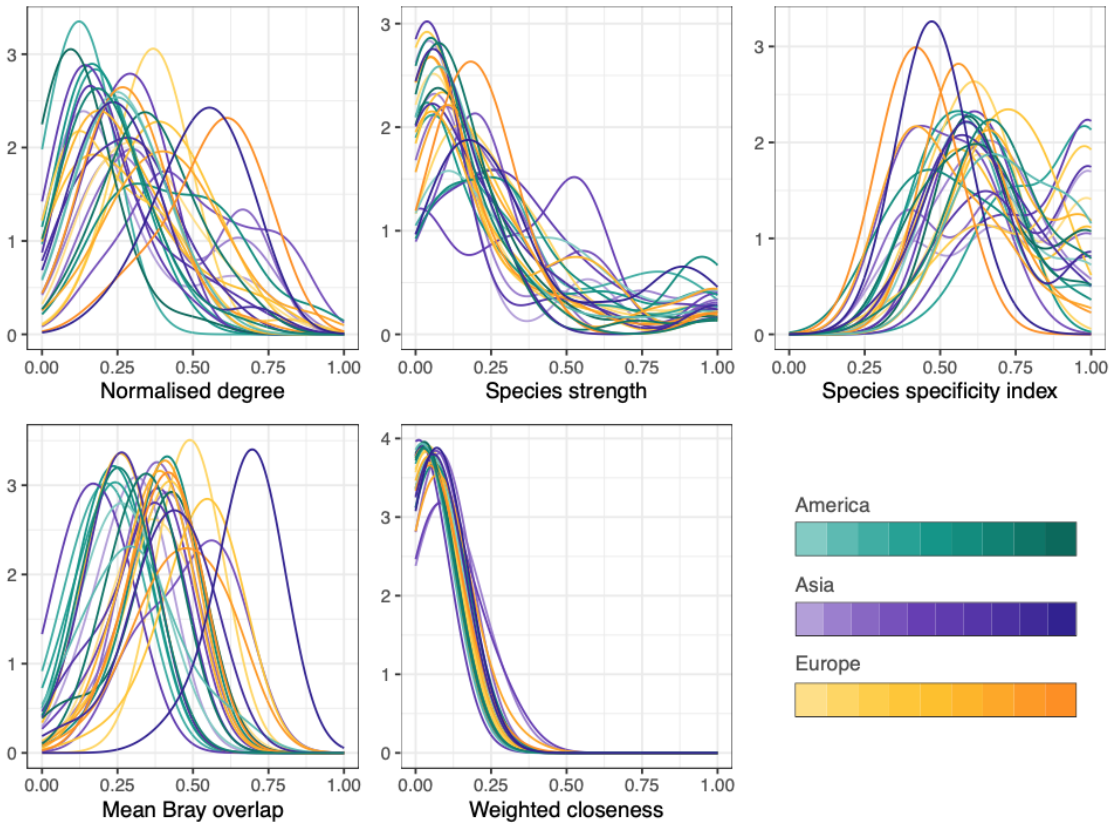

Figure S7. Density plots of selected node-level metrics estimated for plant individuals within their networks. Color indicates a different geographical region (teal = America, purple = Asia, orange = Europe) and different color shades differentiate plant species.

PCA analysis for comparing plant individuals' interaction profiles

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

	PC1	PC2	PC3	PC4	PC5
Importance of components:					
Eigenvalue	1.60	1.05	0.84	0.64	0.48
Proportion of Variance	0.51	0.22	0.14	0.08	0.05
Cumulative Proportion	0.51	0.73	0.87	0.95	1.00
PC loadings:					
normalised.degree	-0.56	0.10	-0.19	-0.21	0.77
species.strength.norm	-0.42	-0.58	-0.23	-0.51	-0.42
species.specificity.index	0.51	-0.12	0.39	-0.70	0.29
weighted.closeness	-0.39	-0.28	0.84	0.24	0.02
mean.bray.overlap	-0.31	0.75	0.22	-0.38	-0.38

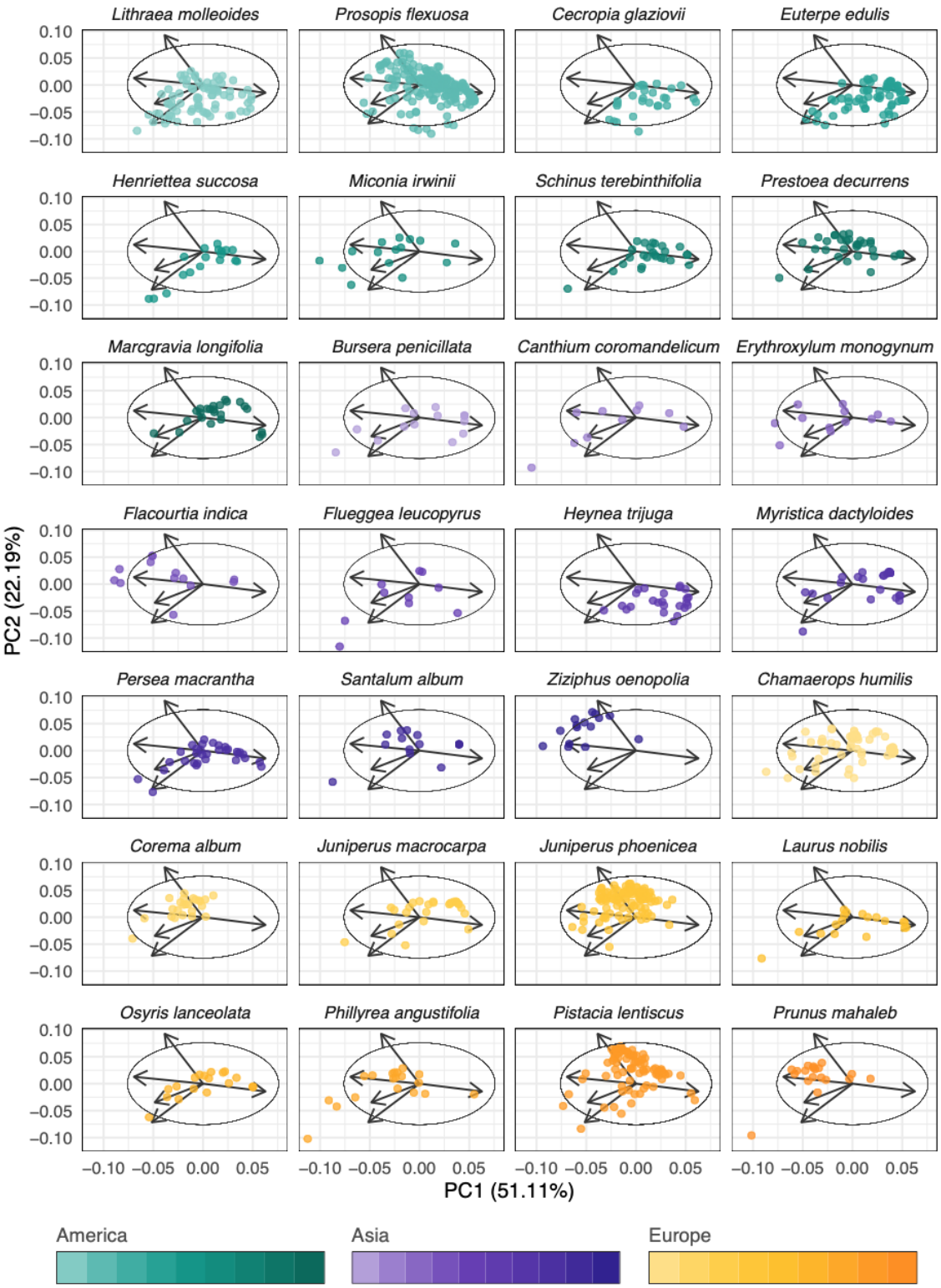

Figure S8. Principal Component Analysis for node-level metrics of individual plants in their respective networks. PCA multivariate space is faceted by plant species to facilitate display of plant individuals

distribution in the multivariate species and the identification of outlying individuals. Note that some species present more than one population (i.e. more than one network, see Table A1). Color indicates a different geographical region (teal = America, purple = Asia, orange = Europe) and different color shades differentiate plant species. See Fig. 5 for information on what node-level metric represents each of the five arrows.

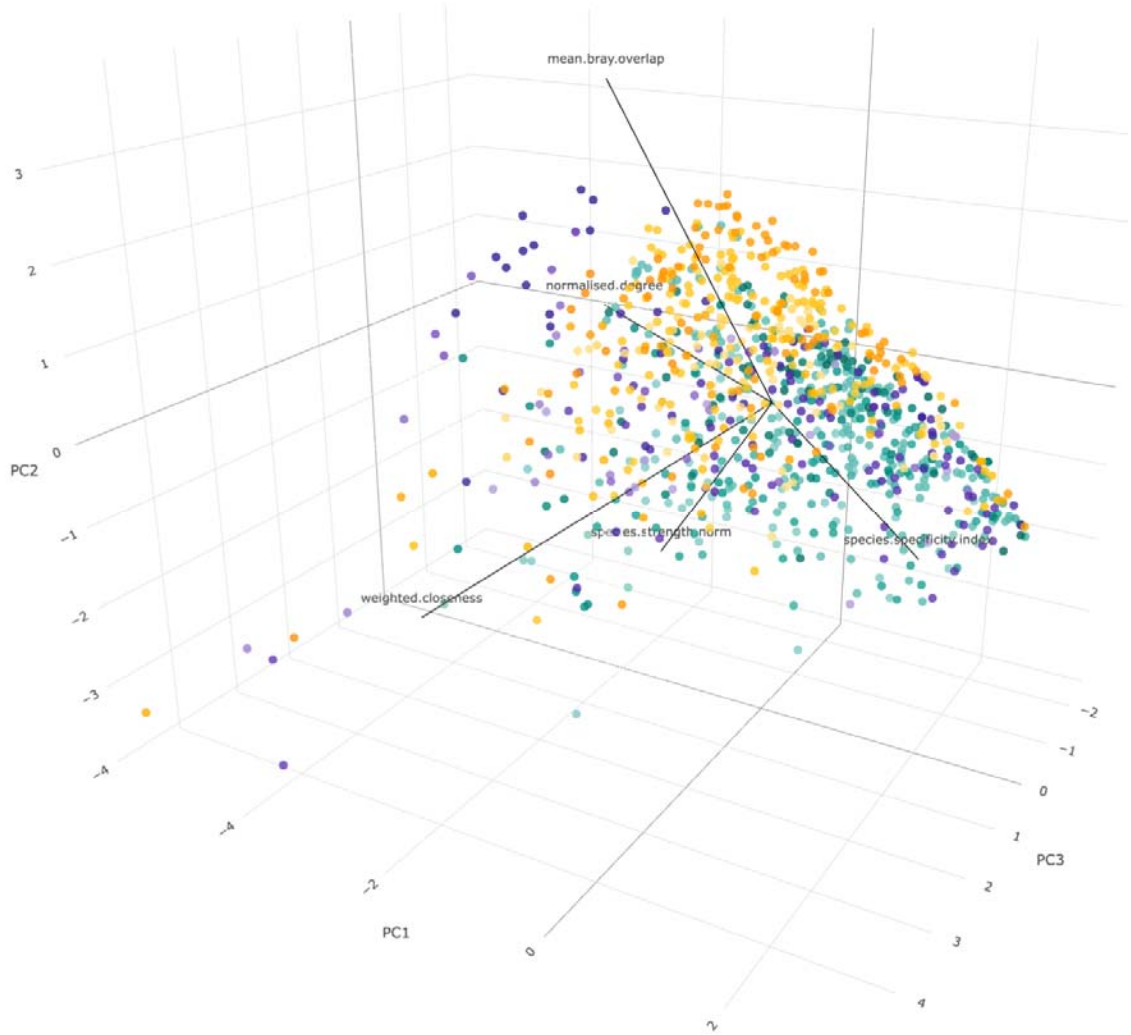

Figure S9. Three dimensional representation of Principal Component Analysis for node-level metrics of individual plants in their respective networks (Fig. 5) (interactive graph link: https://plotly.com/~elequinter/1/). This representation evidences how PC3 is primarily influenced by weighted closeness and how the outlying individuals in the two-dimensional point cloud, that exhibit idiosyncratic interaction profiles, are also strongly associated with PC3.

Software citations

We used R version 4.2.0 (R Core Team 2022) and the following R packages: bipartite v. 2.17 (Dormann, Gruber, and Fruend 2008; Dormann et al. 2009; Dormann 2011), car v. 3.1.0 (Fox and Weisberg 2019), cluster v. 2.1.3 (Maechler et al. 2022), DHARMa v. 0.4.5 (Hartig 2022), fmsb v. 0.7.3 (Nakazawa 2022), ggcorrplot v. 0.1.4 (Kassambara 2022), ggforce v. 0.3.3 (Pedersen 2021), ggfortify v. 0.4.16 (Tang, Horikoshi, and Li 2016; Horikoshi and Tang 2018), ggpubr v. 0.4.0 (Kassambara 2020), ggrepel v. 0.9.1 (Slowikowski 2021), ggsci v. 2.9 (Xiao 2018), gllvm v. 1.4.3 (Niku et al. 2019, 2021, 2023; van der Veen et al. 2021, 2022), glmmTMB v. 1.1.3 (Brooks et al. 2017), grateful v. 0.1.11 (Rodríguez-Sánchez, Jackson, and Hutchins 2022), gridExtra v. 2.3 (Auguie 2017), here v. 1.0.1 (Müller 2020), hillR v. 0.5.1 (Li 2018), igraph v. 1.3.2 (Csardi and Nepusz 2006), iNEXT v. 3.0.0 (Chao et al. 2014; Hsieh, Ma, and Chao 2022), knitr v. 1.39 (Xie 2014, 2015, 2022), lme4 v. 1.1.29 (Bates et al. 2015), MASS v. 7.3.56 (Venables and Ripley 2002), modelbased v. 0.8.5 (Makowski et al. 2020), patchwork v. 1.1.1 (Pedersen 2020), plotly v. 4.10.0 (Sievert 2020), rcartocolor v. 2.0.0 (Nowosad 2018), reshape2 v. 1.4.4 (Wickham 2007), RInSp v. 1.2.5 (Zaccarelli, Mancinelli, and Bolnick 2013), rmarkdown v. 2.14 (Xie, Allaire, and Grolemund 2018; Xie, Dervieux, and Riederer 2020; Allaire et al. 2022), scales v. 1.2.0 (Wickham and Seidel 2022), SIBER v. 2.1.8 (Jackson and Parnell 2023), tidylog v. 1.0.2 (Elbers 2020), tidyverse v. 1.3.1 (Wickham et al. 2019), tnet v. 3.0.16 (Opsahl 2009), vegan v. 2.6.2 (Oksanen et al. 2022).

References

Allaire, JJ, Yihui Xie, Jonathan McPherson, Javier Luraschi, Kevin Ushey, Aron Atkins, Hadley Wickham, Joe Cheng, Winston Chang, and Richard Iannone. 2022. *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.

Bates, Douglas, Martin Mächler, Ben Bolker, and Steve Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67 (1): 1–48. https://doi.org/10.18637/jss.v067.i01.

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://journal.r-project.org/archive/2017/RJ-2017-066/index.html.

Chao, Anne, Nicholas J. Gotelli, T. C. Hsieh, Elizabeth L. Sande, 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.

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

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

Dormann, C. F., J. Frueund, N. Bluethgen, and B. Gruber. 2009. "Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks." *The Open Ecology Journal* 2: 7–24.

Dormann, C. F., B. Gruber, and J. 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.

Fox, John, and Sanford Weisberg. 2019. *An R Companion to Applied Regression*. Third. Thousand Oaks CA: Sage.https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

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. 2022. *iNEXT: Interpolation and Extrapolation for Species Diversity*. http://chao.stat.nthu.edu.tw/wordpress/software_download/.

Jackson, Andrew, and Andrew Parnell. 2023. *SIBER: Stable Isotope Bayesian Ellipses in r*. https://CRAN.R-project.org/package=SIBER.

Kassambara, Alboukadel. 2020. *Ggpubr: "Ggplot2" Based Publication Ready Plots*. https://CRAN.R-project.org/package=ggpubr.

———. 2022. *Ggcorrplot: Visualization of a Correlation Matrix Using "Ggplot2"*. https://CRAN.R-project.org/package=ggcorrplot.

Maechler, Martin, Peter Rousseeuw, Anja Struyf, Mia Hubert, and Kurt Hornik. 2022. *Cluster: Cluster Analysis Basics and Extensions*.https://CRAN.R-project.org/package=cluster.

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.

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

Nakazawa, Minato. 2022. *Fmsb: Functions for Medical Statistics Book with Some Demographic Data*. https://CRAN.R-project.org/package=fmsb.

Oksanen, Jari, Gavin L. Simpson, F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, Peter R. Minchin, R. B. O'Hara, et al. 2022. *Vegan: Community Ecology Package*. https://CRAN.R-project.org/package=vegan.

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. 2020. *Patchwork: The Composer of Plots*. https://CRAN.R-project.org/package=patchwork.

———. 2021. *Ggforce: Accelerating "Ggplot2"*. https://CRAN.R-project.org/package=ggforce.

R Core Team. 2022. *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.

Sievert, Carson. 2020. *Interactive Web-Based Data Visualization with r, Plotly, and Shiny*. Chapman; Hall/CRC. https://plotly-r.com.

Slowikowski, Kamil. 2021. *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.

van der Veen, Bert, Francis K. C. Hui, Knut A. Hovstad, Erik B. Solbu, and Robert B. O'Hara. 2021. "Model-Based Ordination for Species with Unequal Niche Widths." *Methods in Ecology and Evolution* 12: 1288–1300.

Venables, W. N., and B. D. Ripley. 2002. *Modern Applied Statistics with s*. Fourth. New York: Springer. https://www.stats.ox.ac.uk/pub/MASS4/.

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, and Dana Seidel. 2022. *Scales: Scale Functions for Visualization*. https://CRAN.R-project.org/package=scales.

Xiao, Nan. 2018. *Ggsci: Scientific Journal and Sci-Fi Themed Color Palettes for 'Ggplot2'*. https://CRAN.R-project.org/package=ggsci.

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. http://www.crcpress.com/product/isbn/9781466561595.

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

———. 2022. *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.

Zaccarelli, Nicola, Giorgio Mancinelli, and Daniel I. Bolnick. 2013. "RInSp: An r Package for the Analysis of Individual Specialisation in Resource Use." *Methods in Ecology and Evolution* 4 (11): 1018–23. https://dx.doi.org/10.1111/2041-210X.12079.