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

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Species-level networks emerge as the combination of interactions spanning multiple individuals, and their study has received considerable attention over the past 30 y. However, less is known about the structure of interaction configurations within species, even though individuals are the actual interacting units in nature. We compiled 46 empirical, individual-based, interaction networks on plant-animal seed dispersal mutualisms, comprising 1,037 plant individuals across 29 species from various regions. We compared the structure of individual-based networks to that of species-based networks and, by extending the niche concept to interaction assemblages, we explored individual plant specialization. Using a Bayesian framework to account for uncertainty derived from sampling, we examined how plant individuals "explore" the interaction niche of their populations. Both individual-based and species-based networks exhibited high variability in network properties, lacking remarkable structural and topological differences between them. Within populations, frugivores' interaction allocation among plant individuals was highly heterogeneous, with one to three frugivore species dominating interactions. Regardless of species or bioregion, plant individuals displayed a variety of interaction profiles across populations, with a consistently-small percentage of individuals playing a central role and exhibiting high diversity in their interaction assemblage. Plant populations showed variable mid to low levels of niche specialization; and individuals' interaction niche "breadth" accounted for 70% of the population interaction diversity, on average. Our results highlight how downscaling from species to individual-based networks helps understanding the structuring of interactions within ecological communities and provide an empirical basis for the extension of niche theory to complex mutualistic networks.

complex networks | seed dispersal | mutualism | individual niche | frugivory

Significance

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

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. Network ecology based on graph theory has emerged as a useful framework to study these multispecies interactions simultaneously and assess the complexity of natural ecosystems (1–3). Starting with food webs (4), network theory expanded its versatility to other ecological interaction modes such as mutualisms (5, 6). Since then, abundant literature has revealed emergent and global properties of ecological networks, highlighting surprisingly similar architecture in the way they are assembled (7, 8). Among ecological networks, mutualistic networks represent mutually beneficial interactions, and their structure and topology have been extensively explored (9). 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 proper subsets of the species with which generalists interact), leading to asymmetric dependences among species (9, 10). Yet, it is not clear to what extent these properties emerge from networks at lower levels of organization, such as those composed of between-individual interactions.

Although interaction patterns are usually summarized at the species level, ecological interactions actually occur as encounters between individuals rather than species (11). For instance, while we say blackbirds (*Turdus merula*) consume fruits and disperse raspberry (*Rubus idaeus*) seeds, it is actually individual plants and birds interacting within a local population. By missing this individual-level resolution we miss two important opportunities: 1) the ability to effectively link individual trait variation with interaction outcomes (fitness effects) and thus connect ecological and evolutionary perspectives; and 2) to bridge the gap between niche theory and complex interaction networks, i.e., to assess how individual-based interactions scale up into complex interaction networks.

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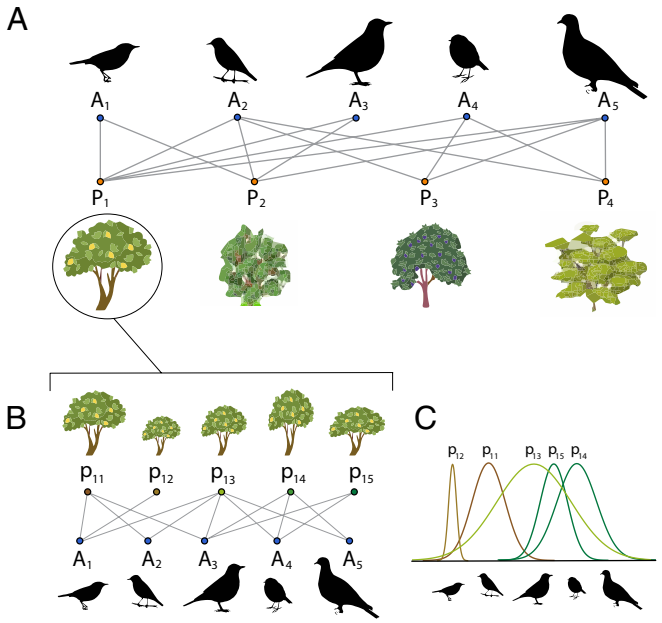

Fig. 1. (*A*) Schematic example of a species-based interaction network between four ornithochorous plant species (P_1 to P_4) and their frugivore assemblage with five animal species (A_1 to A_5) (*Top*). (*B*) A zoom-in on the individual-based network of plant species P_1 depicting the interactions of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

Classic studies of animal-mediated seed dispersal interactions have been plant-focused (e.g., ref. 12), and provide a useful framework to zoom-in into the interactions established between a particular plant species and a set of animal frugivores. By considering individual-based networks, in which one set of nodes is composed of plant individuals, and the other set is composed of animal species, we can examine individual variation in "interactions build-up," as well as its subsequent implications, in e.g., fitness (13–15). This is helpful not just for building a proper bridge between interaction ecology and demographic consequences (e.g., ref. 16), but also for bridging network ecology with evolutionary consequences (17, 18).

Network structure may not be consistent across hierarchical scales of organization (19, 20). 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 (21), discouraging major forbidden interactions (but see refs. 22 and 23) and likely increasing overall network connectance. Thus, we might expect individual-based networks to exhibit architectural and structural properties different to those found in species-based networks; yet, this remains an underexplored question.

Downscaling the study of interactions to individuals allows us to observe how the variation among individuals in their partner use is distributed in the population (Fig. 1 *A* and *B*). Since its origins, the niche concept has provided an ideal framework for studying individual variation in resource use (24–26). Even so, most previous work has focused on antagonistic interactions such as predator–prey trophic niches (24, 27–29). It was only very recently that niche theory was applied for understanding individual variation in mutualistic interactions (19, 30–34). However, the study on how a plant individual's interaction niche is distributed within a population remains largely unexplored, even less has been compared across different ecological systems. For this study, we rely on the concept of "interaction niche" as the space defined by the set of species with which a population, or a plant individual, can interact (Fig. 1*C*) (35).

Interaction probabilities between plant individuals and animal species (i.e., probability of interspecific encounter, PIE; 36, 37) are influenced by a myriad of factors such as population abundances, accessibility of resources, individual preferences, or physiological needs (e.g., optimal foraging theory) as well as required matching in traits and phenology (38). Intraspecific trait variability, neighborhood attributes, and spatiotemporal context drive animal preferences for certain plant individuals, which will govern the establishment of interactions between plant individuals and their mutualistic partner species (39–41). In mutualistic systems such as pollination or seed dispersal, variation in the patterns of interaction or exploitation of niches (available partners) can play a determining role, as mutualists directly affect the reproductive outcome of individuals, influencing fitness variation and trait selection, which act as raw material for coevolution (42), as well as population dynamics and community assembly (31, 43).

Quantifying individual variation in interaction niche, and particularly 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 and intraspecific competition and how partner diversity is promoted, determining, e.g., degree distributions in interaction networks (44). 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. Thus, this approach can prove useful to predict niche-shifts or interaction niche expansion (45, 46). The levels of individual specialization in individual-based networks can be estimated as the proportion of the total niche width in the population (TNW; total partner diversity) due to within-individual variation (WIC; average partner diversity of individuals). Thus, the distribution of frugivore–partner species richness and interaction allocation among plant individuals can be highly variable in local populations (e.g., refs. 16 and 47–50). By studying plant individual specialization and how frugivores distribute interactions among plants, we aim to understand variation in mutualistic interactions within plant populations (Fig. 1). Examining how interaction niches are partitioned globally can expand the concept of niche variation to mutualistic interactions and pave the way for future hypotheses.

A variety of node-level metrics for complex networks can provide insight into an individual's strategy within its population (51, 52). 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., refs. 14, 15, 31, 39, 47, 53, and 54). However, most of these studies have used a single or several metrics separately to understand the interaction profile of individuals and for single populations. By using a combination of node-level metrics, we aim to characterize interaction profiles of plant individuals with frugivore species and the distribution and frequencies of roles among and within populations in different geographic regions. Given contrasted differences in e.g., frugivore diversity and life histories across biogeographic realms, we could expect plant individuals from certain regions to exhibit similar interaction profiles, markedly different from those of individuals from other species and/or regions. Conversely, if life history or context-dependent effects were not determinant in structuring interactions between plant individuals and their frugivore partners, we could expect consistent individual interaction profiles across populations, irrespective of geographic location or biome type.

Obtaining an insightful picture of a mutualistic network structure from field data is a challenging task. When sampling is limited, the inferred network structure can be noisy, even biased, and thus subject to sampling fluctuations. This issue becomes particularly relevant when comparing networks from different studies (55). Here, we build upon Young et al. (56). Bayesian framework for reconstructing mutualistic networks to infer each pairwise interaction in individual-based networks, accounting for sampling completeness and the inherent stochasticity of field observation data. We then propagate the uncertainty of all pairwise interactions down through niche specialization and network interaction profiles.

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

Results

Structure of Individual-Based versus Species-Based Networks. We assembled a total of 46 individual-based plant–frugivore networks and compared them with 59 species-based networks using six network metrics (connectance, nestedness, modularity, assortativity, centralization, and interaction evenness). Networks showed a remarkable overlap in all metrics at both resolution scales (Fig. 2*A* and *SI Appendix*, Fig. S4 and Table S3). Species-based and individual-based networks presented wide variation in their structure. Overall, when controlled by network relative size and interaction abundances, networks were less connected, nested and even, and more modular, assortative, and central than their corresponding null models, although some of these differences were very subtle and consistent for networks at the two scales (Fig. 2*B* and *SI Appendix*, Fig. S4). Comparing across scales, individual-based networks were slightly less connected and less modular than species-based networks relative to random expectations. However, these differences remained subtle and highly overlapping (e.g., 0.05 average difference in connectance and 0.04 in modularity; *SI Appendix*, Table S3).

Plant Individuals' Specialization in Interaction Niche. The 46 populations included a total of 1,037 plant individuals: 373 individuals (from 9 species) from the Mediterranean (Iberian Peninsula), 389 (17 species) from Tropical regions in Asia and America, and 275 (3 species) from Southern Temperate regions (Southern Brazil and Argentina). Our aim in the compilation of individual-based networks was to showcase the diversity of environments and their associated variations; this analysis revealed major gaps in data coverage on the African continent and in the Australasian region (*SI Appendix*, Table S1), so a proper comparison among biogeographic areas awaits more complete data. Most plant populations studied presented low to medium levels of individual specialization (mean WIC/TNW = 0.68; 90% CI = 0.32 to 0.95). Individual-based networks from the Mediterranean region showed a higher proportion of generalized plant individuals (Fig. 3; mean WIC/TNW = 0.82), whereas Southern Temperate and Tropical populations presented higher levels of individual specialization (mean WIC/TNW = 0.56 and 0.65 respectively, P-value < 0.01). Plant populations interacting with higher numbers of frugivore species had a wider interaction niche (TNW, i.e., Shannon diversity index, r = 0.53, $P < 0.01$), but not necessarily higher levels of individual specialization (WIC/TNW) (*SI Appendix*, Fig. S5). The degree of individual specialization did not increase as TNW increased, because WIC increased in the same proportion as TNW

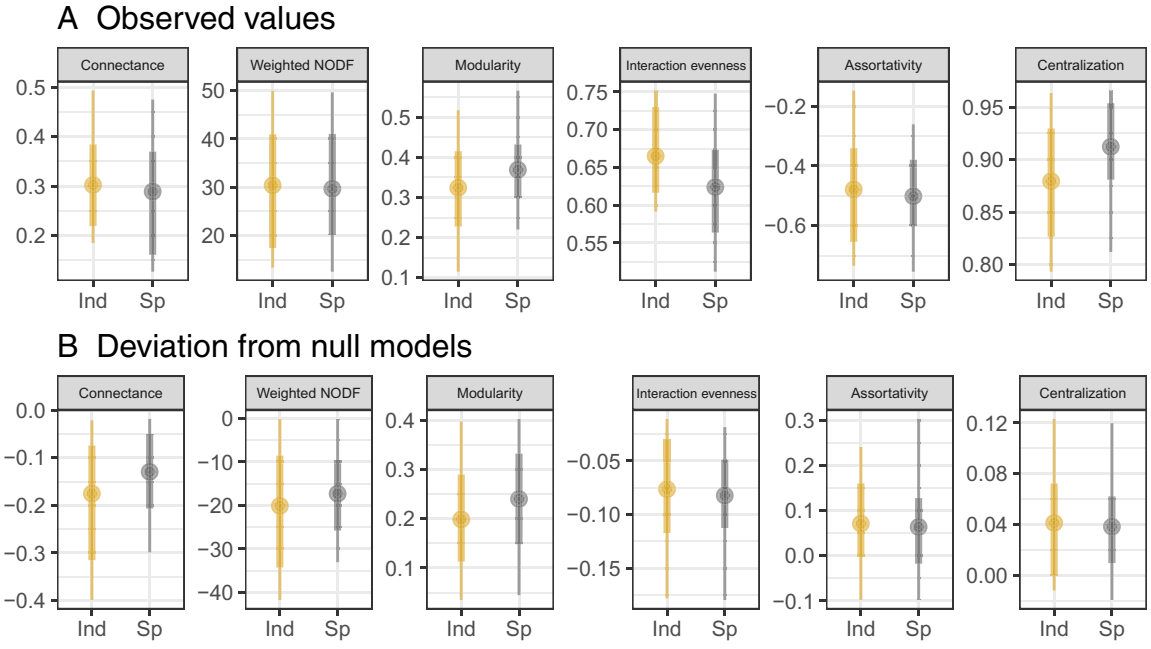

Fig. 2. Network metrics comparison across network scales (Ind = individual-based, n = 46; and Sp = species-based networks, n = 59). Panel (*A*) shows observed network-level metrics and panel (*B*) deviation of observed metric values from their corresponding null model, which represents a network of the same size and relative abundances (generated using Patefield's algorithm). Points represent the mean and thick and thin lines represent 0.6 and 0.9 CI respectively. For each network metric, deviation from null models represents the difference between the observed value and the null expectation.

(slope of log–log model = 1.000, SE = 0.005). That is, differences in the level of individual specialization between bioregions were achieved via changes in both the BIC and the WIC components.

Frugivore Interactions within Plant Populations. Across all plant populations and regions, we found that just a reduced subset of frugivore species (generally between one and three) usually accumulated most of the interactions, while the rest of frugivore species contributed a minor proportion. On average, more than half of these interactions were contributed by less than 20% of frugivore species (SD = 8.2%), regardless of the total number of frugivore species in the plant population (*SI Appendix*, Fig. S6). The frugivores that contributed most interactions also tended to interact with a higher number of plant individuals (Spearman's rho = 0.81, Fig. 4). Remarkably, frugivore species with smaller contributions interacted with a variable proportion of plant individuals, such proportion being higher in Mediterranean networks and lower in Southern Temperate networks (Fig. 4). Frugivores' body mass was not correlated with interaction contribution (rho = −0.08) nor with the proportion of plant individuals they interacted with (rho = −0.13).

Plant Individuals' Interaction Profiles. The multidimensional principal component analysis space occupied by all plant individuals and defined by node-level metrics (normalized degree, strength, specificity, overlap, and weighted closeness) did not produce distinct clusters by bioregion or population. Instead, individuals from different populations spread across the multidimensional space, suggesting ample within-population heterogeneity in plant individuals' interaction profiles (Fig. 5 and *SI Appendix*, Fig. S8). The first principal component (PC1), explaining more than half of the variation (51%), was mainly related to interaction degree and specificity, thus capturing individual variation in frugivore richness and composition of the plant individual's assemblages. The second component (PC2) explained 24% of the variation and was correlated with niche overlap and interaction strength; these metrics are related to plant individuals' interaction patterns in relation to their conspecifics and affected by interaction frequency (link weight). Plant individuals with more unique frugivore assemblages were positioned in the upper area of the PCA space, while many plants with highly overlapping frugivore assemblages within their populations were positioned toward the bottom area. The third component (PC3; 10% variation explained; *SI Appendix*, Table S4) was strongly related to weighted closeness, a measure of how strongly and well connected (i.e., central) individuals are within the network.

Few plants were highly central in the interaction network (high weighted closeness) and important for frugivore dependence (high node strength) (i.e., points in the upper-left area of the multivariate space). Most plant individuals showed uneven dependencies on frugivore species and/or medium-high frugivore overlap with other plants in the population. Yet plants with strong dependencies on one or few frugivore species tended to show lower overlap with

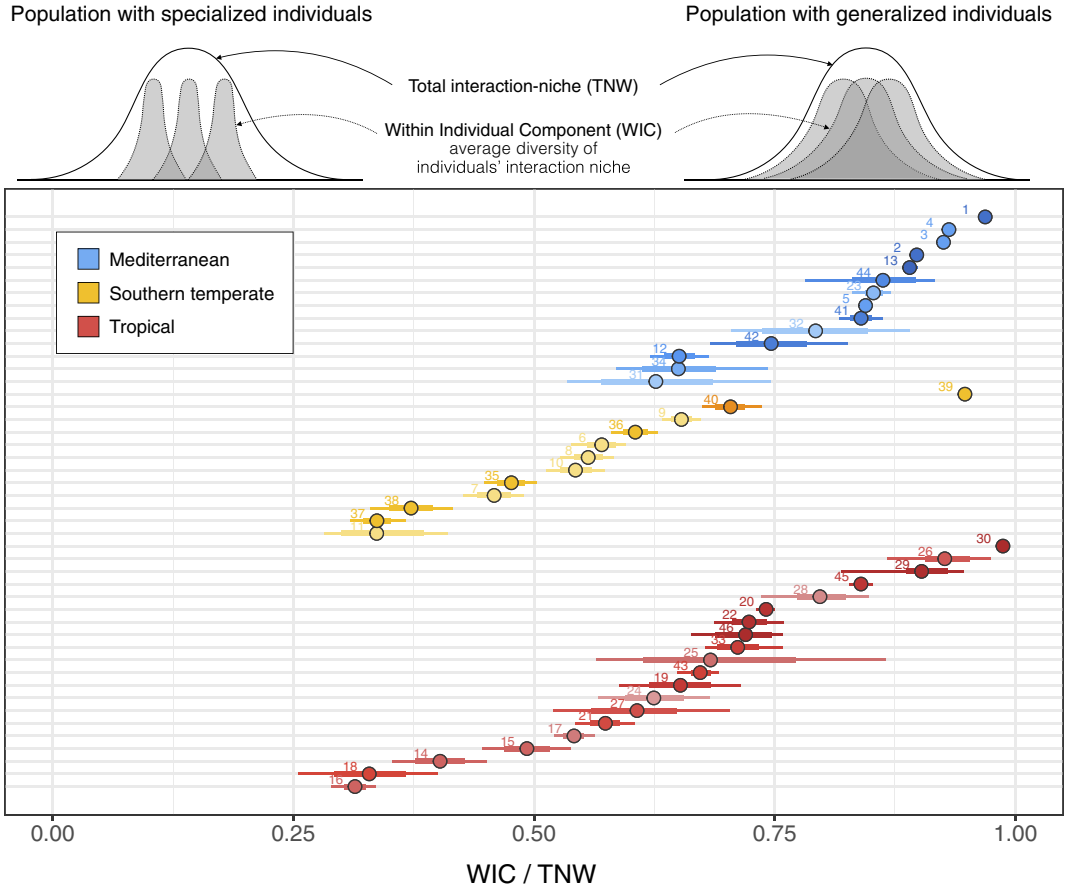

Fig. 3. A schematic representation of two plant populations (*Top*): the one on the left presents a population composed of highly specialized individuals (low WIC; low WIC/TNW) and the one on the right presents a population composed of highly generalized individuals (high WIC; high WIC/TNW). Values of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

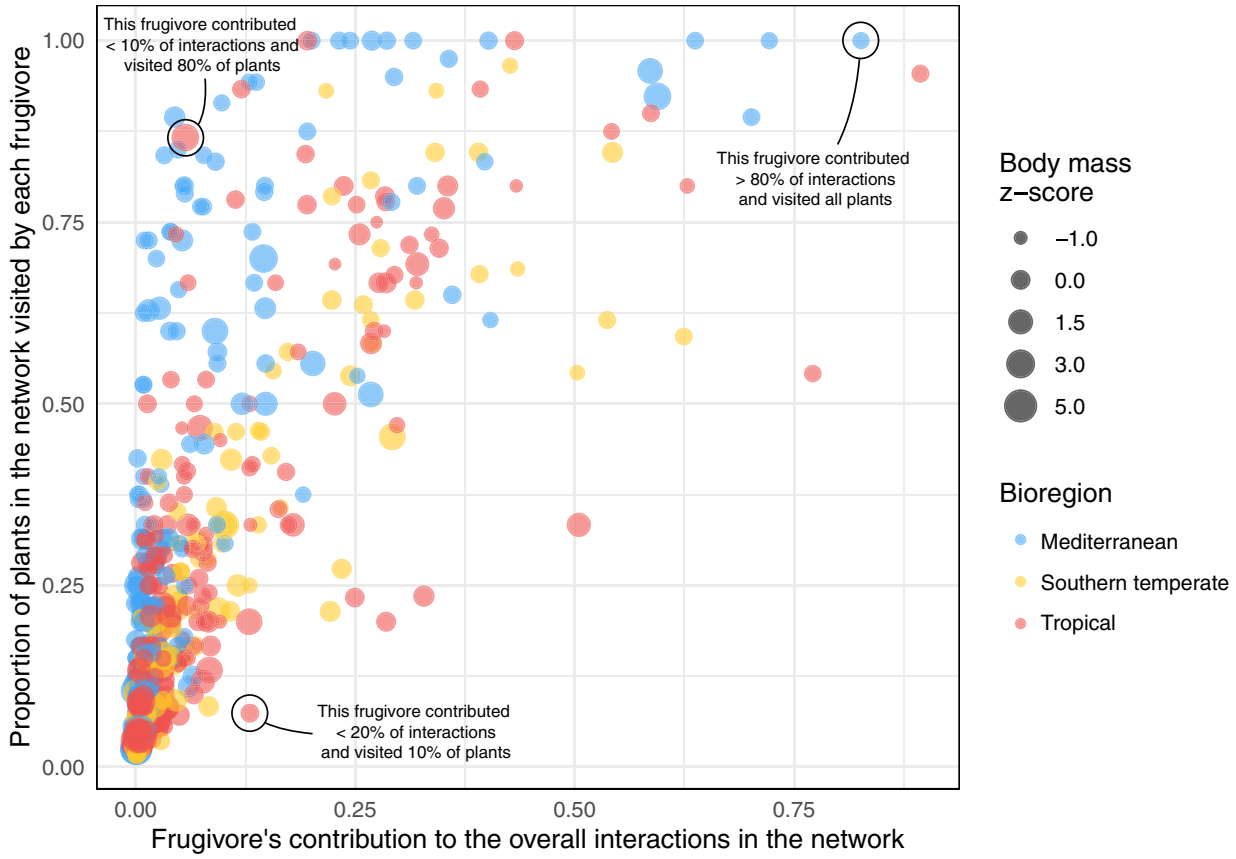

Fig. 4. Relationship between the overall contribution to the total number of interactions by each frugivore species (i.e., link weights in the individual-based networks) and the proportion of plant individuals with which they interacted (i.e., animal degree). Each point represents a frugivore species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

other individuals in the frugivore assemblage, suggesting a trade-off between partner specialization and partner sharing (lower-right Fig. 5). Overall, plant individuals from the Mediterranean tended to have more similar frugivore assemblages (higher niche overlap), while plant individuals from Southern Temperate regions presented less overlapping and more specialized frugivore assemblages (*SI Appendix*, Fig. S9).

A cluster analysis further revealed consistent interaction profiles within plant populations, regardless of bioregion or species. All networks presented a variable but substantial proportion (mean = 42%; 90% CI = 8 to 77%) of plant individuals with "neutral" interaction profiles, which did not excel in any node-level metric (Fig. 5 and *SI Appendix*, Fig. S9). The clusters "specialized" (mean = 28%; 90% CI = 0 to 67%) and "overlapping" (mean = 22%; 90% CI = 0 to 86%) included a variable but substantial proportion of plants, most likely reflecting either distinct frugivore assemblages (e.g., in the tropical biomes) or more overlapping in composition (mostly nontropical), respectively. Notably, in most populations (36 out of 46), we detected a low proportion (mean = 8%, 90% CI = 0 to 24%) of "keystone" individuals showing high strength and weighted closeness. We termed these plant individuals as keystone since they accounted for a high proportion of interactions within their respective populations, playing a central role in plant–frugivore interaction structuring.

Discussion

Our study highlights how downscaling from species to individuals uncovers consistent network structures across biological levels, mutualistic partner allocation among plants globally, and interaction profile similarities within populations, regardless of species or ecological context. This reveals aspects of ecological interactions and network assembly at the individual level.

Effects of Downscaling Resolution on Network Structure. The structure of plant–animal mutualistic networks revealed fundamental heterogeneity across networks and resolution scales. We did not find major deviations in the assembly patterns of interactions as we zoomed in from species to an individual-based scale. Previous research exploring the consequences of downscaling on network architecture found significant shifts in the structure of pollination networks (19, 20): Individual-based networks were less connected and individuals were more specialized than species. These studies examined one community using a single methodology. Our approach, however, involved diverse communities and populations from different regions with varying methodologies, capturing broader interaction patterns. Surprisingly, we found no significant differences in network connectance across scales, contrary to our initial expectations. The slightly larger connectance of individual networks after Bayesian modeling (average connectance = 0.4 ± 0.2 versus 0.3 ± 0.1 in raw networks) suggests that undersampled interaction matrices could be missing interactions. On the other hand, the slightly lower modularity in individual-based networks could stem from a decrease in the number of forbidden links as frugivores can potentially interact with virtually all the plant individuals within populations (see ref. 23). In contrast, species-based networks involve much more heterogeneous sets of plant species. The addition of new species or individuals with new traits provides new link possibilities in a network, yet in the case of species, potential interactions must undergo stronger trait and

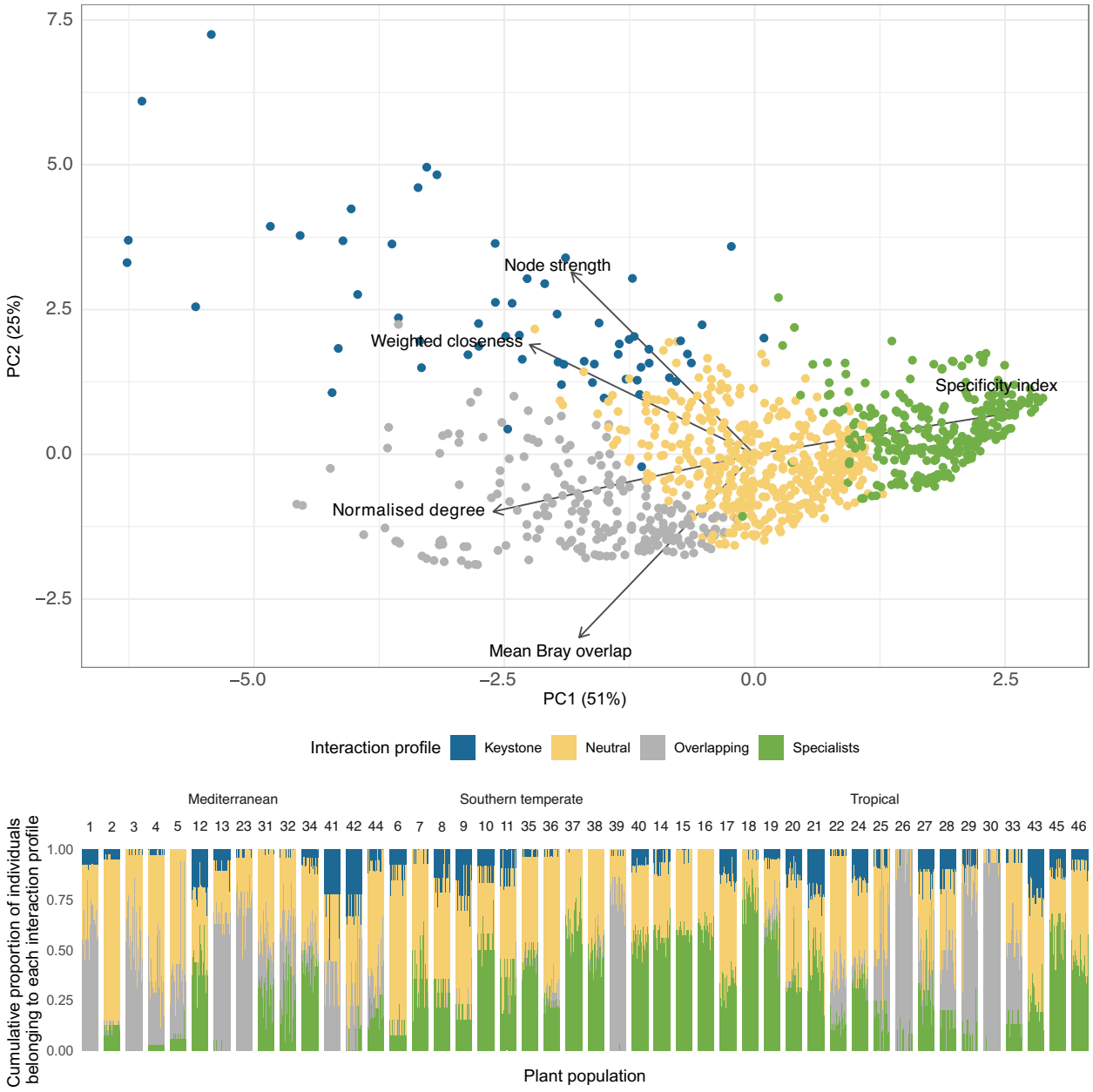

Fig. 5. Principal component analysis for node-level metrics of plant individuals in all plant populations with the most common cluster attribution for each individual depicted in color. Each plant individual (points) is represented by the centroid of its 1,000 node-metric values calculated with the full posterior distribution (*SI Appendix*, Fig. S8). The panel below shows different plant populations as bars with a number code above (*SI Appendix*, Table S1). Each stacked bar is composed of 1,000 thinner stacked bars that represent the cumulative proportion of individuals attributed to each cluster or interaction profile originated from the 1,000 reanalysis using the posterior samples.

phenological matching filters than in individual-based networks (57). 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 taxonomically diverse available plant species in a community. The former set imposes less constraints to interactions by including much more homogenous conspecific partners. In this way, downscaling from species to individuals fundamentally alters the probabilistic distribution of interactions among partners (58).

Aside from minor differences in certain network metrics, the overall topology and structure of frugivory networks at different resolution scales were not sufficient to make clear distinctions. This convergence in network structure may be driven by factors like the probability distribution of interspecific encounters (PIEs), influencing network configurations consistently across scales. We argue that numerical effects are likely at the base of these emergent properties, governing interactions distribution across nodes and asymmetric interactions (5, 38, 59, 60). These numerical effects can be caused by varied organism abundances in the case of species, or traits and genotypes in the case of individuals, that modulate the attractiveness of plants to frugivores, such as crop size, plant height, or phenology (41).

Individual Specialization in the Interaction Niche. Individuals' interaction niches were narrower than those of their populations, supporting that individual specialization is substantial and common in nature (24), even in mutualisms. Plant individuals' specialization levels were similar to levels reported in other animal taxa (27). Interestingly, the degree of individual specialization varied across biogeographic regions, yet most plant species showed WIC/TNW ratios >50%, which indicates moderate generalization among plant individuals. Broader and more overlapping frugivore

assemblages in Mediterranean regions versus higher specialization and variability in Southern Temperate and Tropical networks could not be attributed to differences in frugivore taxonomic diversity as all regions presented similar TNW (*SI Appendix*, Fig. S5). Instead, plant individuals in Southern Temperate regions presented smaller relative niches. Tropical populations consisted of frugivore assemblages of variable diversity and highly variable individual specialization, yet limited area coverage of the available individual-based networks hindered comparisons. No significant niche breadth differences were found across bioregions, aligning with studies of terrestrial food webs, challenging the latitude-niche breadth hypothesis that predicts narrower niches in tropical regions (61, although see ref. 62). The large variation in individual specialization within bioregions may be pointing to the role of fine-scale factors such as the local habitat, neighborhood effects, or the influences of individual phenological variation. Further research is needed to evaluate the ecological correlates of plant individual interaction niche utilization and its consequences.

Different levels of individual specialization can have implications for population stability (63) and niche expansion (26). According to the niche variation hypothesis, populations experiencing niche expansion achieve it through increasing their inter-individual variation (45). By diversifying its resources, plant individuals would be able to exploit novel and underutilized frugivores escaping competition from conspecifics. Niche shifts and expansion have become exceptionally important for adaptation to changing climate conditions (64) as well as changes in frugivore assemblages and fluctuating abundances (65). Therefore, the variation we found among populations in frugivore assemblage specialization will likely have an impact on the adaptation of plant–frugivore mutualistic interaction niche in current and future scenarios of global change.

In all plant populations just a few frugivore species, even within diversified assemblages, consistently perform most of the mutualistic interactions (*SI Appendix*, Fig. S6; 39, 47, 66–68). Although frugivore body mass did not prove to be a good indicator of their contribution to interactions (although see ref. 69), 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 (12, 70). These highly uneven interaction patterns will result in asymmetric dependencies between plant individuals and frugivore species, where the main frugivore shows low specificity for specific plants, while most plant individuals rely mostly on the main frugivores' service (16). Asymmetric dependency between partners also emerges at species–species interaction level (5, 71, 72); further downscaling into individual–individual interactions would help elucidate whether asymmetry remains consistent across scales. Finally, our analysis reveals a consistent trend for frugivory and seed dispersal service in a given plant population (estimated from the proportion of plant individuals with which a frugivore species interacts) to increase with the overall contribution to the total number of interactions by each frugivore species (i.e., link weights in the individual-based networks, Fig. 4). Thus, central frugivores interact with a wide range of plant individuals, most likely an emergent result of the interaction asymmetry discussed above.

Consistency of Plant Individuals' Interaction Profiles across Regions and Populations. Plant individuals' interaction profiles were not explained by bioregion or species, pointing to 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 (5, 30, 38, 73). Remarkably, we found a consistent distribution of plant interaction profiles within populations, with most individuals acting in an average manner, a variable fraction standing out for their specialization or redundancy and only very few individuals having a central role, high diversity of interactions, and strong frugivores' dependence on them ("keystone" plant individuals). Similar results are reported in food webs, where a core group of species shares ecological roles, while peripheral species have unique interaction profiles (8). 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 (39, 41).

Although some of the plant species considered in this study were generalists within their community, individuals in their populations showed variable interaction niche breadths (47), with populations consisting of both generalist and specialist individuals (31, 45). This mix creates species that appear broadly interactive but actually include individuals with varied interaction patterns, from wide generalization to specific partner preferences. This highlights the complexity of species' ecological roles within communities (38).

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 individual-based network included a similar representation of individual interaction profiles, evidencing a common backbone in the way interactions are organized (8). Conducting future analyses on interaction types or motifs of individual-based networks may provide us with additional insights, as these approaches have proven effective in distinguishing networks between and within ecological systems (8, 74, 75).

Intraspecific variation appears as a central ingredient in the configuration of complex networks of mutualistic interactions, driven by the widespread interaction profiles of frugivore species with plant individuals. High levels of intraspecific variation have been shown to confer greater stability to mutualistic systems (31). By zooming in on ecological interactions this study provides valuable insights into how mutualistic interactions are similarly structured at the individual level and reveal underlying, consistent, patterns of role assignment within populations and across bioregions.

Methods

Dataset Acquisition. We compiled frugivory ecological networks, both at the species and the plant individual level. Species-based networks were gathered from 40 published studies at the community scale (12, 59, 76–113; see *SI Appendix*, 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 gathered data for 21 different study systems (16, 39, 47–50, 53, 54, 68, 114–124; see *SI Appendix*, Table S1), including datasets from our own field studies with different Mediterranean species (n = 9). Some of the studies selected presented more than one network from different communities (in species-based studies) or populations (in individual-based studies). These datasets document interactions between plant species and animal frugivore species (in species-based studies) or interactions between plant individuals of a single species that coexist in a local population and animal frugivore species (in individual-based studies). None of the datasets collected are nested, that is, individual-based networks are not sampled within the same study as a species-based network, which prevents a direct structure dependence between the two scales of the datasets. Data were entered 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 were 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 (125) (*SI Appendix*, Table S2). To do so, we converted the adjacency matrix data to an incidence frequency-data and considered plant individuals as sampling units and the number of frugivore species detected at each plant as species richness. We discarded networks in which the number of interacting nodes (plants and frugivore species) was less than 15 or plants were less than six (n = 13 networks). Our final dataset consisted of 105 networks with an average size of 384 potential links or cells (range = 65 to 2,904) and 90 unique interactions (range = 22 to 419). Forty-six were individual-based networks and 59 were species-based networks (*SI Appendix*, Table S1). When possible, we referred the interaction value to the coarsest level, that is, frugivore visitation events, otherwise number of fruits consumed.

Network-Level Metrics. For both the individual and species-based networks, we calculated several network-level metrics, using R packages bipartite (126) and igraph (127). All network metrics were calculated using standardized matrices to minimize the impact of differences in sampling effort and study-site characteristics. Specifically, for all those individual-based networks where sampling effort across plant individuals was heterogeneous within the population (21 out of 46 networks), we divided plant visits by the amount of time observed and/or the area sampled in each plant, so that interaction counts were comparable. Subsequently, all networks (individual and species-based) were scaled by dividing the weight of each pairwise interaction by the total number of interactions in the matrix (grand total standardization; 128). In this way, 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.

We selected a representative set of metrics that had suitable biological interpretation and were not highly correlated (Variance Inflation Factor < 3) and/or not strongly affected by the number of species/individuals sampled or overall network size (*SI Appendix*, Figs. S1–S3).
Selected network-level metrics were the following:

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) (129).
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 (130). Values of 0 indicate nonnestedness, those of 100 perfect nesting (131).
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) (132, 133).
4. Modularity (*structure–clustering*). It reflects the tendency of a network to be organized in distinct clusters or modules (44). This metric ranges from 0 (no clusters) to 1, where nodes within a module interact more among them than with nodes from other modules (highly compartmentalized network; 134).
5. Eigenvector centralization (*centrality*). This metric quantifies how centralized or decentralized the distribution of eigenvector centrality scores is across all nodes in a network (135). 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 (136). The network-level eigenvector centralization provides a measure of the extent to which a few nodes dominate the network in terms of influence. In a network with low centralization, the centrality scores are relatively evenly distributed among the nodes, suggesting a more decentralized structure where many nodes contribute to the overall connectivity of the network, and therefore to the interaction services. On the other hand, a network with high centralization indicates that only a small number of nodes have a higher centrality, suggesting a more centralized structure where a few nodes play a crucial role in the network's overall connectivity. We normalized this measure to ensure that the centralization value is relative to the maximum centralization for a network of a given size.
6. Interaction evenness (*interaction diversity*). Also known as Pielou's evenness, it quantifies how balanced the distribution of interactions is across nodes (137). This metric considers all links as species, and their weight as a measure of their abundance. It quantifies link diversity using the Shannon index and divides it by the theoretical maximum richness of all possible links (i.e., logarithm of the number of cells in the matrix). It ranges from 0 to 1, where low values indicate high unevenness and high values approach perfect evenness in interaction distribution.

Comparison across Network Scales. We used the aforementioned metrics to compare the structure and assemblage of species-based versus individual-based networks. Additionally, to account for network size and inherent characteristics of each study, we assessed metric deviations against 1,000 randomizations using null models. We use a Patefield algorithm (138, 139) that maintains network marginal totals. For each network and metric, we calculated the difference between the observed values and the randomizations. This difference indicates both the magnitude and direction in which observed values deviate from what could be expected at random.

Bayesian Modeling of Individual-Based Network Structure. Reconstructing mutualistic network structure from field data is a challenging task. Interaction data are hard to collect and typically require large sampling efforts, particularly to characterize infrequent interactions. Inferred network structure is highly sensitive to sampling design, effort, and completeness (140). Comparing networks from different studies without accounting for these sampling effects may lead to mistaken inferences (55). Here, we build upon (56) Bayesian framework for reconstructing mutualistic networks to infer the posterior probability of each pairwise interaction in individual-based networks, accounting for sampling completeness and the inherent stochasticity of field observation data.

Following (56), pairwise interaction counts between plants and animals can be modeled as following a Poisson distribution whose mean (μ_{ij}) is determined by the sampling effort spent on each plant (C_i), the relative interaction abundance of each plant and animal in the population (σ_i and τ_j), the (inferred) existence of an interaction link among both partners (B_{ij}), and the "preference" parameter r which represents the difference in the average number of visits or interactions when there is a connection between mutualistic partners (i.e., when a frugivory preferentially interacts with a given plant, $B_{ij} = 1$) compared to when there is no connection ($B_{ij} = 0$). Thus,

$$\mu_{ij} = C_i \sigma_i \tau_j (1 + r B_{ij}).$$

The preference parameter r accommodates the expectation that the number of interactions will be higher when a frugivore prefers a given plant. When there is no preference the number of interactions can still be higher than zero, but lower in principle. Here, we adapted the model proposed by ref. 56 to allow for varying preferences (i.e., interaction counts) among different frugivore species, so that some frugivores may bring many more visits than other mutualists. Rather than having a single preference parameter r for all species, each frugivore has its own preference r_j which is drawn from an exponential distribution with rate parameter beta = 0.01. In order to facilitate modeling and incorporate these modifications, we developed an R package called "BayesianWebs" (141) which relies on Stan (142) and cmdstanr (143) for parameter estimation, and contains functions to facilitate modeling of bipartite mutualistic networks including data preparation, model fitting, checking, and visualization. Using this package, we fitted a Bayesian model to each individual-based network. As model output, we obtained 1,000 posterior samples of the expected count for each pairwise interaction. Posterior predictive checks showed the expected increase of uncertainty in networks with limited sampling, and overall confirmed the good match between the observed data and predicted counts.

To ensure comparability across networks, posterior interaction counts were rounded to integer values and then standardized following the same procedure explained above. Networks with heterogeneous sampling effort across plant individuals were adjusted by dividing the posterior counts by the individual relative observation time or sampled area. Subsequently, all networks were standardized dividing each interaction value by the total number of interactions (grand total standardization, 128), so that matrix cell values reflected the relative frequency of each interaction within the population.

The resulting distributions of pairwise interaction counts generated by the Bayesian model for each network (1,000 matrices for each network or population) were then propagated all the way down to niche specialization and individual node-level metrics (see below).

Niche Specialization. We estimated populations' niche specialization using the Shannon approximation of the WIC/TNW index for discrete data (144, 145) implemented in the "network.tools" R package (146). 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 TNW explained by within-individual variation (WIC). TNW is calculated as the total diversity of frugivore species visiting the plant population, using the Shannon index,

$$TNW = -\sum_j q_j ln(q_j),$$

where j represents an animal species, and q_j is the proportion of interactions contributed by frugivore species j to the total number of interactions in the plant population.

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,

$$\text{WIC} = \sum_i p_i \left(-\sum_j p_{ij} ln(p_{ij}) \right),$$

where i presents a plant individual, p_i is the proportion of interactions contributed by plant i to the total number of interactions in the population, and p_{ij} the proportion of interactions that animal species j contributed to plant individual i.

Finally, WIC is divided by TNW. Values closer to 1 indicate a population composed of generalist individuals that are using most of the niche available to the population. On the contrary, values closer to 0 indicate a population of specialist individuals using small subsets of the population niche, with large differences in resource-use among them. WIC and TNW estimates were calculated for each of the posterior counts (n = 1,000) generated from Bayesian models for each network, rendering a credibility interval of individual specialization for each plant population. To test differences in individual specialization (i.e., WIC/TNW) between different bioregions (n = 3) we fitted a mixed-effects linear model with a normal distribution where the network and study were present as random factors (147).

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 (126). Additionally, we calculated average niche overlap using the Bray–Curtis dissimilarity index. We computed these metrics using the full posterior distribution of each individual-based network. That is, for each of the 1,000 posterior matrices generated for each network we calculated node-level metrics, therefore we obtained 1,000 values for each plant individual and metric. We selected a representative set of metrics that had suitable biological interpretation for assessing the individuals' interaction profiles and were not highly correlated nor affected by the number of individuals sampled (*SI Appendix*, Fig. S7).

Selected node-level metrics were the following:

1. Normalized degree (*interaction diversity*). It represents the richness of partners for a given node and is scaled relative to the rest of nodes in the network. This metric ranges from 0 to 1, where a plant individual would score 1 if it interacts with all the frugivore species available (51).
2. Specificity index (*interaction diversity*). This metric informs about the variation in the distribution of interactions with frugivore species partners. It is estimated as a coefficient of variation of interactions for each plant individual, normalized to range between 0 and 1 (52, 148). 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.
3. Node strength (*interaction intensity*). It quantifies the dependence of the community on a given node (51), in this case, the frugivores represent the community and the plant individuals the nodes. It is calculated as the sum of the dependencies of each frugivore species (i.e., the fraction of all visits to a given plant individual coming from a particular frugivore species) (71).
4. 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 (149). 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, with links between plant individuals representing the number of frugivore interactions shared. 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. Individuals with higher values of weighted closeness are strongly connected with more plant individuals in the population through shared frugivore species.
5. Mean interaction overlap using the 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., ref. 150). 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.

Comparison across Individual-Based Networks. In order to determine variation distribution in interaction structuring and node topology we performed a principal component analysis (PCA). Previous studies have used PCA for comparing network metrics (e.g., refs. 8 and 151–154). In order to compare plant individuals' interaction profiles, we performed a PCA using the full set of node-level metric distributions estimated for plant individuals within their population (i.e., individual node metrics derived from the full Bayesian posterior of each individual). This resulted in an ordination of elements (1,000 points per each plant individual, single values sampled from the full posterior distributions of each individual-based network) in relation to the multivariate space defined by node-level metrics. Thus, such PCA provides an exploratory analysis of how plant individuals span the multivariate space of network metrics, where the location of each individual characterizes its interaction profile.

With the aim of identifying distinct plant individual profiles we performed a discriminant analysis of principal components (DAPC) using the adegenet R package (155). We performed 1,000 DAPCs using node-level metrics derived from the 1,000 posterior samples of the individual-based networks. We selected four groups or clusters as the minimal number that would facilitate interpretation of each plant individual performance given its position in the network. In each of the 1,000 analysis runs, plant individuals were assigned to one of the four groups given the highest probability provided by the DAPC. This analysis was based on the variation captured by the first 3 PCs which together explained 86% of the variance, with eigenvalues >0.7. Cluster groups were named post hoc according to plants' relative position in the PCA into "Keystone," "Overlapping," "Specialist," and "Neutral" interaction profile types. We subsequently quantified the percentage of individuals assigned to these four groups for each plant population in each of the 1,000 repetitions.

Data, Materials, and Software Availability. All datasets and code used to generate this study are available for download in Zenodo (https://doi.org/10.5281/zenodo.14591621; 124) and GitHub repository (https://github.com/PJordano-Lab/MS_individual-based_networks) (156). Previously published data were used in this work. A list of bibliographic references for all R packages used in the data analyses is included in the *SI Appendix*.

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

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Supporting information for

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

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Network characteristics and sampling effort

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

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

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

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
19	ind	*Myristica dactyloides* (Myristicaceae)	India	25	7	175	45		Focal observations	size differentially influence frugivory of select rainforest tree species in Western Ghats, India. Biotropica, 52(5), 871-883.
20	ind	*Persea macrantha* (Lauraceae)	India	32	21	672	186		Focal observations	
21	ind	*Henriettea succosa* (Melastomataceae)	Brazil	18	22	396	77		Focal observations	Crestani, A. C., Mello, M. A. R., & Cazetta, E. (2019). Interindividual variations in plant and fruit traits affect the structure of a plant-frugivore network. Acta Oecologica, 95, 120-127.
22	ind	*Prestoea decurrens* (Arecaceae)	Ecuador	31	9	279	100		Camera traps	Lamperty, T., Karubian, J., & Dunham, A. E. (2021). Ecological drivers of intraspecific variation in seed dispersal services of a common neotropical palm. Biotropica, 53(4), 1226–1237.
23	ind	*Corema album* (Ericaceae)	Spain	24	15	360	129		Camera traps	Villalva, P., Arroyo-Correa, B., Calvo, G., Homet, P., Isla, J., Mendoza, I., Moracho, E., Quintero, E., Rodríguez-Sánchez, F., & Jordano, P. (2024). FRUGIVORY CAMTRAP: A dataset of plant-animal interactions recorded with camera traps. Ecology 105(11): e4424. https://doi.org/10.1002/ecy.4424
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	

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
27	ind	*Flueggea leucopyrus* (Phyllanthaceae)	India	10	8	80	22		Focal observations	
28	ind	*Canthium coromandelicum* (Rubiaceae)	India	10	8	80	30		Focal observations	
29	ind	*Santalum album* (Santalaceae)	India	14	10	140	38		Focal observations	
30	ind	*Ziziphus oenopolia* (Rhamnaceae)	India	15	13	195	102		Focal observations	
31	ind	*Chamaerops humilis* (Arecaceae)	Spain	39	6	234	76	Matasgordas	Footprint traps	Jácome-Flores, M. E. et al. 2020. Interaction motifs variability in a Mediterranean palm under environmental disturbances: the mutualism–antagonism continuum. Oikos 129: 367–379.
32	ind	*Chamaerops humilis* (Arecaceae)	Spain	24	6	144	57	Martinazo	Footprint traps	
33	ind	*Miconia irwinii* (Melastomataceae)	Brazil	15	9	135	59		Focal observations	Guerra, T. J. et al. 2017. Intraspecific variation in fruit–frugivore interactions: effects of fruiting neighborhood and consequences for seed dispersal. Oecologia 185: 233–243.
34	ind	*Juniperus macrocarpa* (Cupressaceae)	Spain	26	11	286	72		Camera traps	Villalva, P., Arroyo-Correa, B., Calvo, G., Homet, P., Isla, J., Mendoza, I., Moracho, E., Quintero, E., Rodríguez-Sánchez, F., & Jordano, P. (2024). FRUGIVORY CAMTRAP: A dataset of plant-animal interactions recorded with camera traps. Ecology 105(11): e4424. https://doi.org/10.1002/ecy.4424
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

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
36	ind	*Prosopis flexuosa* (Fabaceae)	Argentina	28	10	280	84	El Bonito	Camera traps	anthropogenic effects on individual plant–frugivore networks. Oikos, 127: 1045-1059.
37	ind	*Prosopis flexuosa* (Fabaceae)	Argentina	54	10	540	112	El Doménico	Camera traps	
38	ind	*Prosopis flexuosa* (Fabaceae)	Argentina	35	8	280	61	MaB Ñacuñán Reserve Protected 1	Camera traps	
39	ind	*Prosopis flexuosa* (Fabaceae)	Argentina	29	9	261	99	MaB Ñacuñán Reserve Protected 2	Camera traps	
40	ind	*Schinus terebinthifolia* (Anacardiaceae)	Brazil	26	16	416	93		Focal observations	Vissoto, M., Vizentin-Bugoni, J., Sendoya, S. F., Gomes, G. C., & Dias, R. A. (2022). Plant height and spatial context influence individual connectivity and specialization on seed dispersers in a tree population. Oecologia, 198(3): 721-731.
41	ind	*Phillyrea angustifolia* (Oleaceae)	Spain	10	16	160	72	El Puntal	DNA-barcoding	Quintero, E., Arroyo-Correa, B., Isla, J., Rodriguez-Sánchez, F., & Jordano, P. (2024). Data and code from Downscaling mutualistic networks from species to individuals reveals consistent interaction niches and roles within plant populations. https://doi.org/10.5281/zenodo.14591621
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

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
44	ind	*Osyris lanceolata* (Santalaceae)	Spain	19	14	266	62		DNA-barcoding	Quintero, E., Arroyo-Correa, B., Isla, J., Rodriguez-Sánchez, F., & Jordano, P. (2024). Data and code from Downscaling mutualistic networks from species to individuals reveals consistent interaction niches and roles within plant populations. https://doi.org/10.5281/zenodo.14591621
45	ind	*Naringi crenulata* (Rutaceae)	India	22	12	264	62		Focal observations	Jayanth, A., Isvaran, K., & Naniwadekar, R. (2024). Drivers of intraspecific variation in seed dispersal can differ across two species of fleshy-fruited savanna plants. Biotropica, 56(3), e13322. https://doi.org/10.1111/btp.13322
46	ind	*Ziziphus oenopolia* (Rhamnaceae)	India	20	13	260	57		Focal observations and mist-netting	
47	sp		Spain	25	36	900	228	Cazorla	Focal observations	Olesen JM, Bascompte J, Dupont YL, Elberling H, Rasmussen C, Jordano P. (2011). Missing and forbidden links in mutualistic networks. Proceedings of the Royal Society B-Biological Sciences 278: 725-732.
48	sp		Spain	16	17	272	120	Hato Ratón	Mist-netting	
49	sp		Spain	17	28	476	130	Spain	Focal observations	García-Castaño, J.L. (2001). Consecuencias demográficas de la dispersión de semillas por aves y mamíferos frugívoros en la vegetación mediterránea de montaña. PhD Thesis. Universidad de Sevilla, Spain.
50	sp		Papua New Guinea	31	9	279	119		Focal observations	Beehler B. (1983) Frugivory and polygamy in birds of paradise. Auk, 100, 1-11.
51	sp		South Africa	16	10	160	110		Focal observations	Frost P.G.H. (1980) Fruit-frugivore interactions in a South African coastal dune forest. In: Acta XVII Congressus Internationalis Ornithologici (ed. Noring R), pp. 1179-1184. Deutsche Ornithologische Ges., Berlin, Germany.

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
52	sp		Spain	12	7	84	40		Mist-netting	Guitián J. (1983) Relaciones entre los frutos y los passeriformes en un bosque montano de la cordillera Cantabrica occidental. PhD Thesis. Universidad de Santiago, Spain.
53	sp		Brazil	35	29	1015	146		Focal observations	Galetti M. & Pizo M.A. (1996) Fruit eating birds in a forest fragment in southeastern Brazil. Ararajuba, Rev. Brasil. Ornitol., 4, 71-79.
54	sp		England	11	14	154	47		Focal observations	Snow, B.K. & Snow, D.W. (1988). Birds and berries. T. and A.D. Poyser, Calton, England.
55	sp		Japan	15	8	120	38		Focal observations	Noma, N. & Yumoto, T. (1997). Fruiting phenology of animal-dispersed plants in response to winter migration of frugivores in a warm temperate forest on Yakushima Island, Japan. Ecological Research, 12, 119-129.
56	sp		Australia	71	7	497	142		Focal observations	Crome, F. H.J. (1975). The ecology of fruit pigeons in tropical Northern Queensland. Aust Wildl Res, 2, 155-185.
57	sp		Trinidad and Tobago	50	14	700	234		Focal observations	Snow B.K. & Snow D.W. (1971) The feeding ecology of tanagers and honeycreepers in Trinidad. Auk, 88, 291-322.
58	sp		United States	7	21	147	50		Focal observations	Baird, J.W. (1980). The selection and use of fruit by birds in an Eastern forest. Wilson Bulletin, 92, 63-73.
59	sp		Kenya	8	30	240	69	Interior little disturbed	Focal observations	Menke, S., Böhning-Gaese, K. & Schleuning, M. (2012). Plant-frugivore networks are less specialized and more robust at forest-farmland edges than in the interior of a tropical forest. Oikos, 121, 1553-1566.
60	sp		Kenya	7	38	266	104	Edge little disturbed	Focal observations	
61	sp		Kenya	8	34	272	88	Interior highly disturbed	Focal observations	

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
62	sp		Kenya	8	39	312	115	Edge highly disturbed	Focal observations	
63	sp		Brazil	15	49	735	143		Focal observations	Pizo, M.A. (2004). Frugivory and habitat use by fruit-eating birds in a fragmented landscape of southeast Brazil. Ornitologia Neotropical, 15, 117-126.
64	sp		Kenya	33	88	2904	419		Focal observations	Schleuning M, Bluthgen N, Florchinger M, Braun J, Schaefer HM, Bohning-Gaese K. 2011. Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. Ecology 92: 26-36.
65	sp		Brazil	49	16	784	131		Focal observations	Castro, E.R.D. (2007). Fenologia reprodutiva do palmito Euterpe edulis (Erecaceae) e sua influência na abundância de aves frugívoras na floresta atlântica. PhD Thesis. Instituto de Biociencias. Universidade Estadual Paulista "Juio de Mesquita Filho" Rio Claro, SP, Brazil.
66	sp		Brazil	13	45	585	183		Focal observations	Correia, J.M.S. (1997). Utilização de espécies frutíferas de mata Atlântica na alimentação da avifauna da reserva biológica de Poço das Antas, RJ. MSc Thesis. Instituto de Biologia. UNB, Brazil.
67	sp		Brazil	13	30	390	145		Focal observations	Alves, K.J.F. (2008). Composição da avifauna e frugivoria por aves em um mosaico sucessional na mata Atlântica. MSc Thesis. Instituto de Biociencias. Universidade Estadual Paulista, Julio de Mesquita Filho, Rio Claro, SP, Brazil.
68	sp		Brazil	9	30	270	92		Focal observations	Athie, S. (2009). Composição da avifauna e frugivoria por aves em um mosaico de vegetação secundária em Rio Claro, região centro-leste do estado de São Paulo. MSc Thesis. Universidade Federal de São Carlos, Brazil.

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
69	sp		Brazil	25	28	700	90		Focal observations	Ferreira Fadini, R. & De Marco Jr., P. (2004). Interações entre aves frugívoras e plantas em um fragmento de mata atlântica de Minas Gerais. Ararajuba, 12, 97-103.
70	sp		Brazil	26	22	572	79		Focal observations and mist-netting	Hasui, Erica. (1994). O papel das aves frugivoras na dispersao de sementes em um fragmento de floresta semidecidua secundaria em Sao Paulo, SP. MSc thesis. USP Sao Paulo, Brazil.
71	sp		Brazil	22	20	440	67		Focal observations	Silva, R. F. d. M. (2011). Interações entre plantas e aves frugívoras no campus da Universidade Federal Rural do Rio de Janeiro. In: Instituto de Florestas. Universidade Federal do Rio de Janeiro Rio de Janeiro, Brazil.
72	sp		Brazil	12	15	180	32	15-year-old restored plot	Focal observations	Ribeiro da Silva, F., Montoya, D., Furtado, R., Memmott, J., Pizo, M.A. and Rodrigues, R.R. (2015), The restoration of tropical seed dispersal networks. Restor Ecol, 23: 852-860.
73	sp		Brazil	23	29	667	129	25-year-old restored plot	Focal observations	
74	sp		Brazil	14	14	196	35	57-year-old restored plot	Focal observations	
75	sp		Brazil	6	28	168	50		Focal observations	Robinson, V. (2015). Interações entre aves frugívoras e plantas em um fragmento de mata atlântica de Minas Gerais. In: Instituto de Biociencias. Universidade Estadual Paulista "Julio de Mesquita Filho" Rio Claro, SP, Brazil.
76	sp		Brazil	30	58	1740	240		Focal observations	Rodrigues, S. B. M. (2015). Rede de interações entre aves frugivoras e plantas em una área de mata Atlântica no sudeste do Brasil. Universidade Federal de Sao Carlos, Campus Sorocaba Sorocaba, SP, Brazil.

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
77	sp		New Zealand	18	8	144	102		Focal observations	Burns, K.C. (2013). What causes size coupling in fruit-frugivore interaction webs? Ecology, 94, 295-300.
78	sp		Poland	8	12	96	38	site_11	Focal observations	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.
79	sp		Poland	7	11	77	32	site_13	Focal observations	
80	sp		Poland	9	13	117	42	site_15	Focal observations	
81	sp		Poland	8	13	104	36	site_30	Focal observations	
82	sp		Poland	8	10	80	29	site_35	Focal observations	
83	sp		Poland	8	10	80	30	site_36	Focal observations	
84	sp		Poland	8	11	88	33	site_102	Focal observations	
85	sp		Poland	10	13	130	42	site_111	Focal observations	
86	sp		Poland	8	15	120	57	site_112	Focal observations	
87	sp		Poland	9	16	144	41	site_203	Focal observations	
88	sp		Poland	6	20	120	43	site_301	Focal observations	
89	sp		Poland	8	19	152	56	site_315	Focal observations	
90	sp		Brazil	22	17	374	78		Focal observations	Andrade, P., Mota, J. & Carvalho, A. (2011). Mutual interactions between frugivorous birds and plants in an urban fragment of Atlantic Forest, Salvador, BA. Revista Brasileira de Ornitologia, 19, 63-73.
91	sp		Puerto Rico	34	20	680	95		Focal observations	Yang, S., Albert, R. & Carlo, T.A. (2013). Transience and constancy of interactions in a plant-frugivore network. Ecosphere, 4(12): 147.

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
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.
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	

Net no.	Type	Focal plant species	Country	Plants	Frugivores	Net size	Unique interactions	Population site	Sampling method	Reference
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.
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
45	*Naringi crenulata*	0.96	0.90	1.00
46	*Ziziphus oenopolia*	0.93	0.87	1.00

Comparison of networks at different resolution scales

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

Network-level metrics

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

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

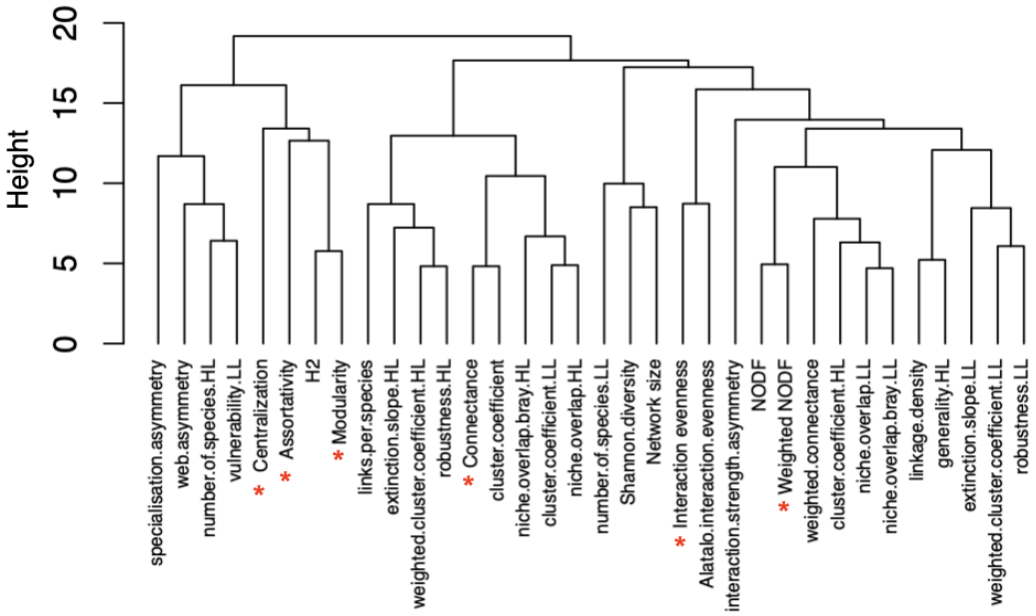


Figure S1. Hierarchical clustering analysis results for all the network metrics calculated. Metrics with * are the selected ones.

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

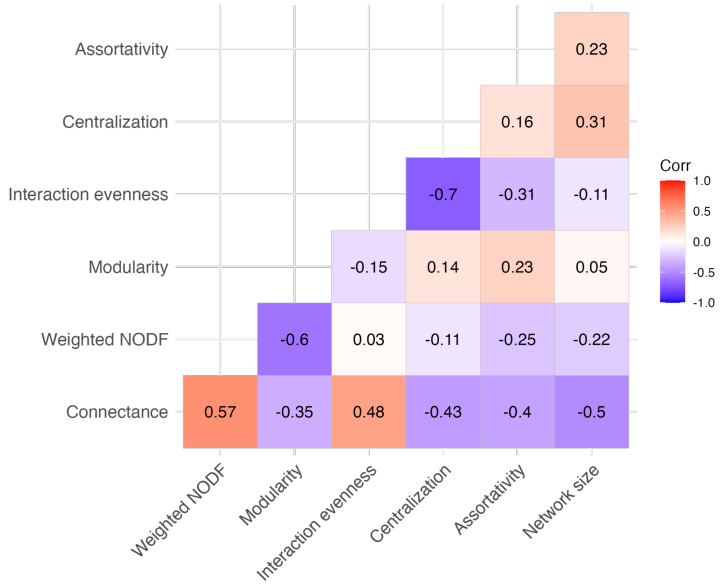


Figure S2. Correlation plot between selected network-level metrics for PCA analysis. Numbers denote Pearson correlation coefficients (r) and the color its magnitude and direction.

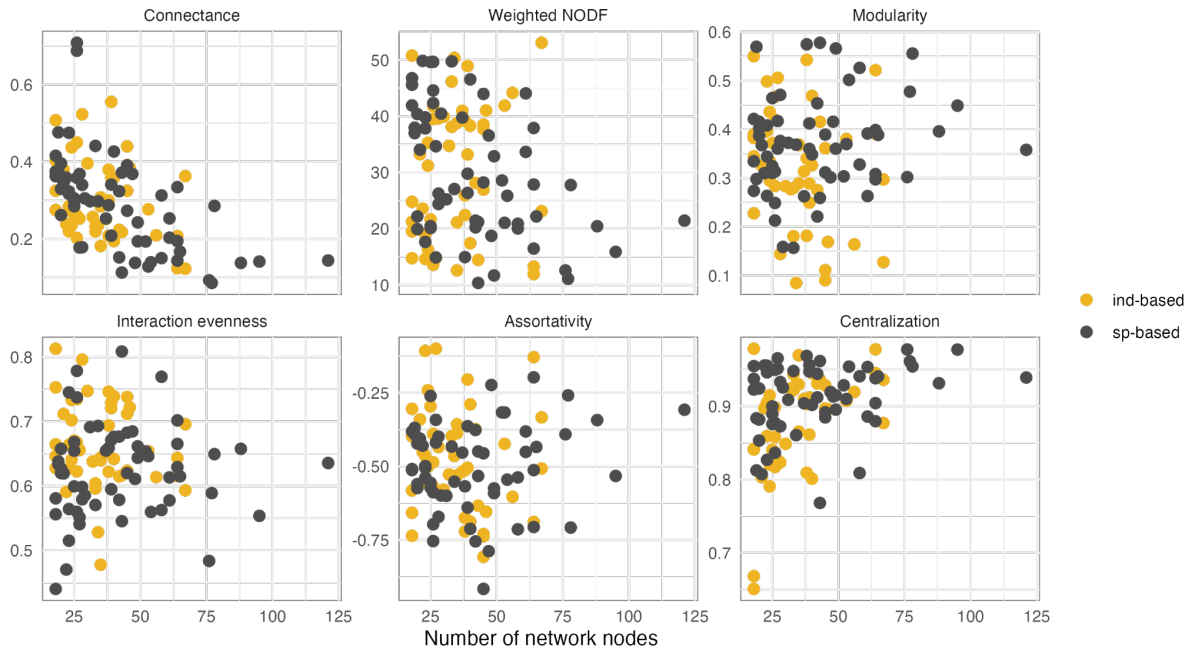
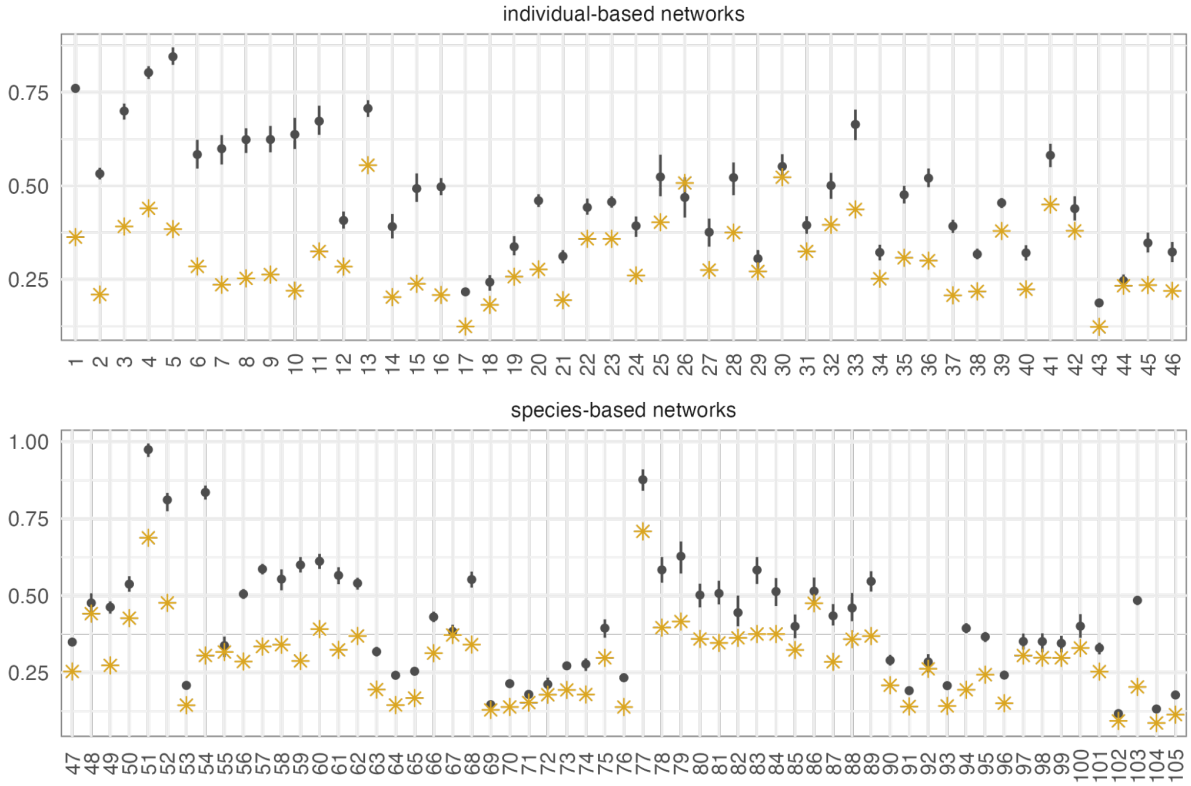
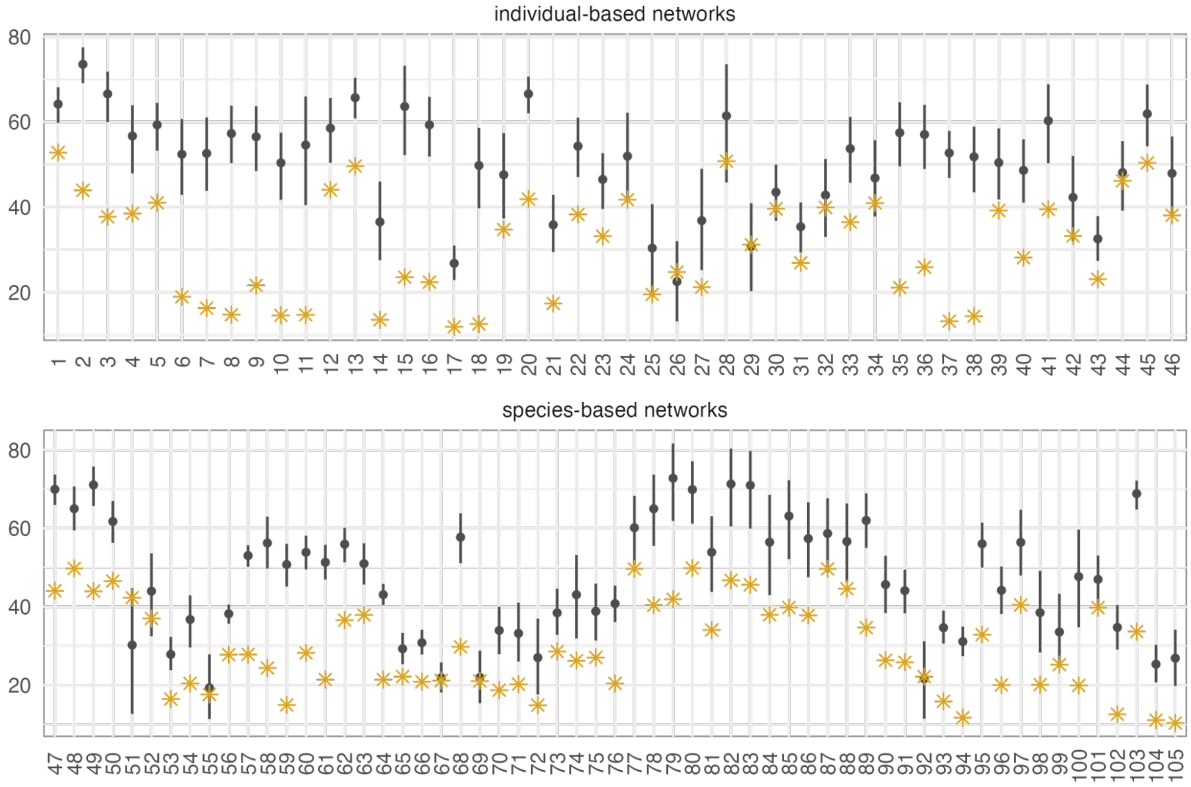


Figure S3. Correlation between selected network metrics and the number of nodes present in the network (species and/or individuals).

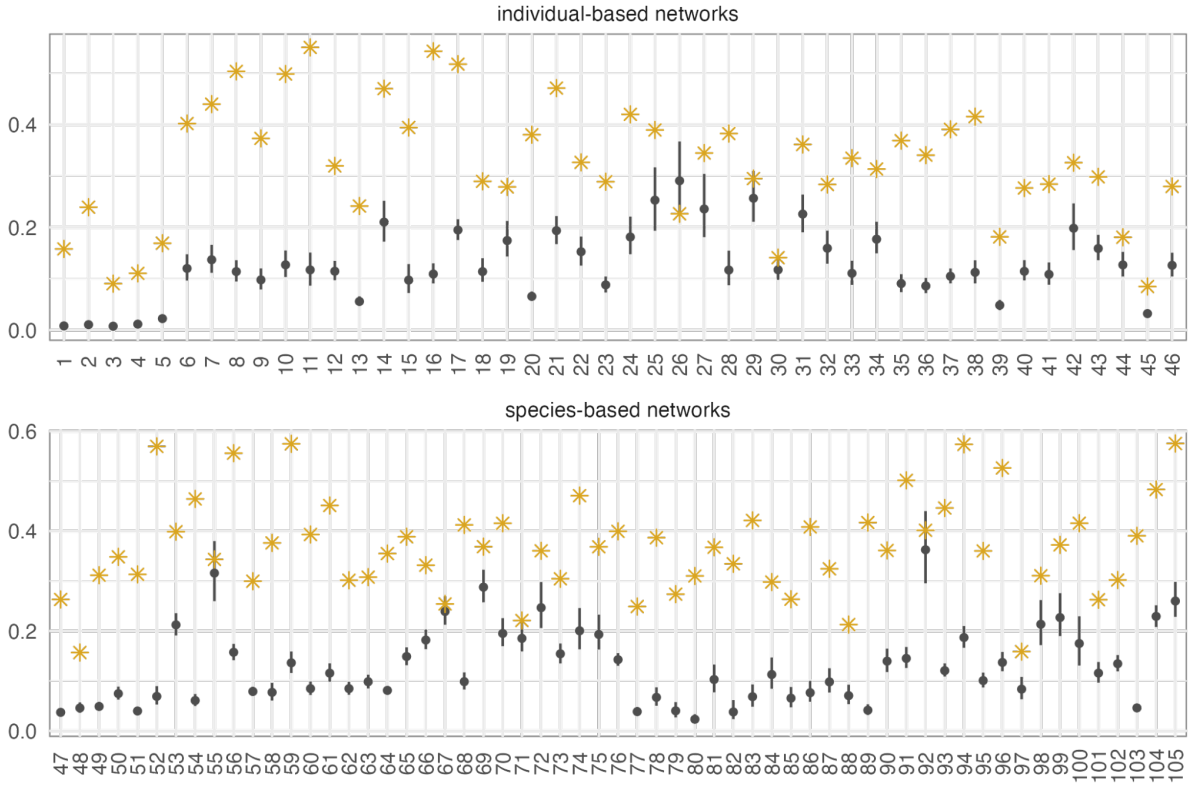
A. Connectance



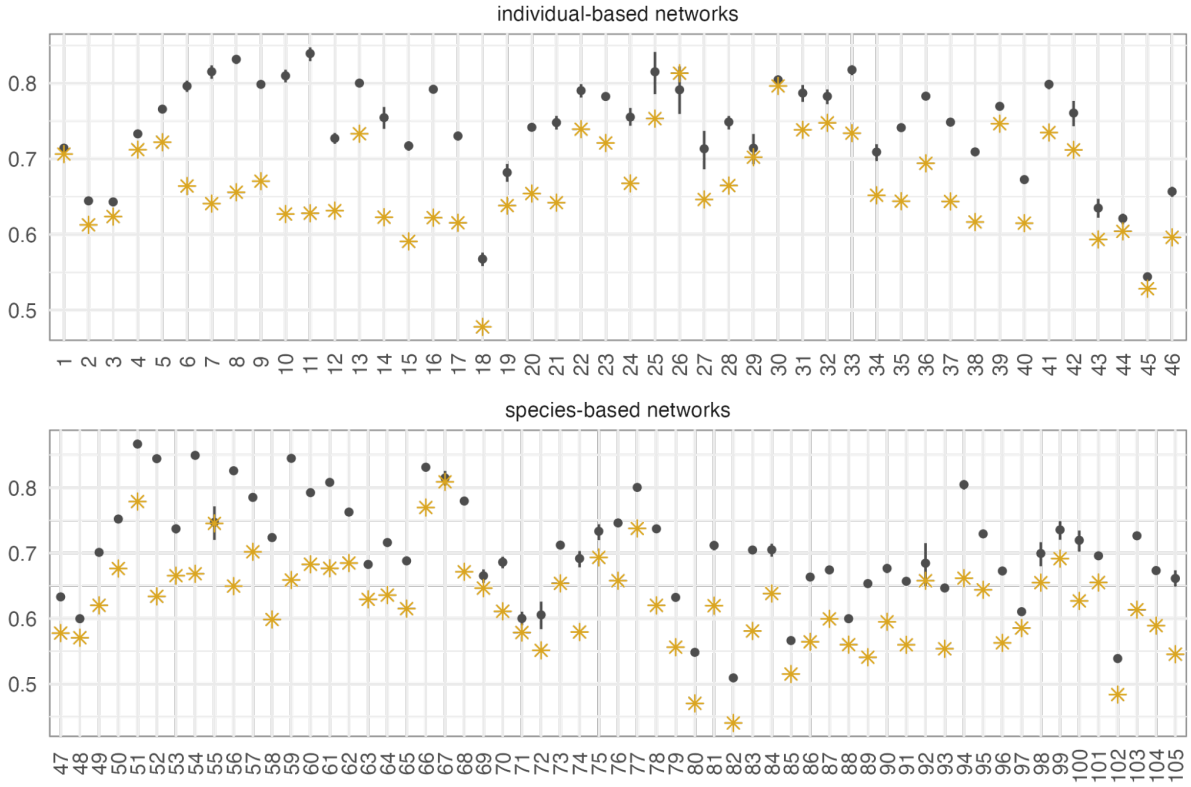
B. Weigthed NODF



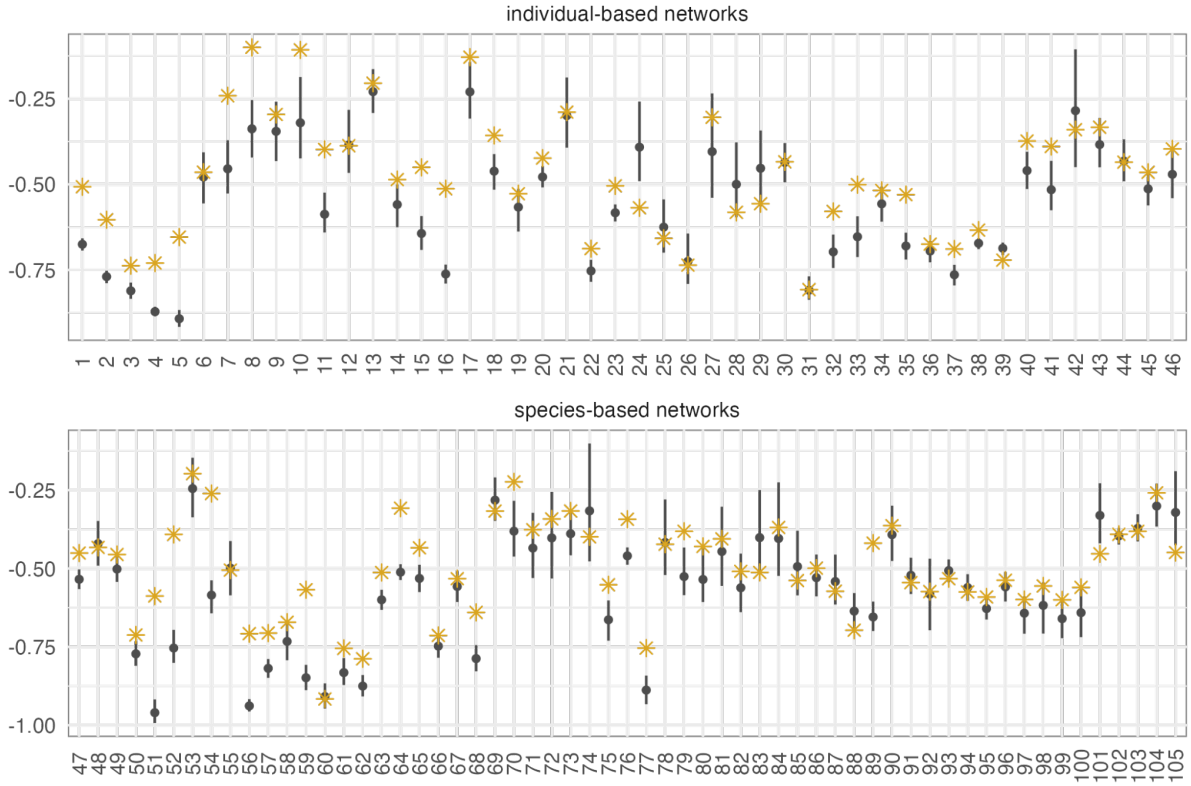
C. Modularity



D. Interaction evenness



E. Assortativity



F. Centralization

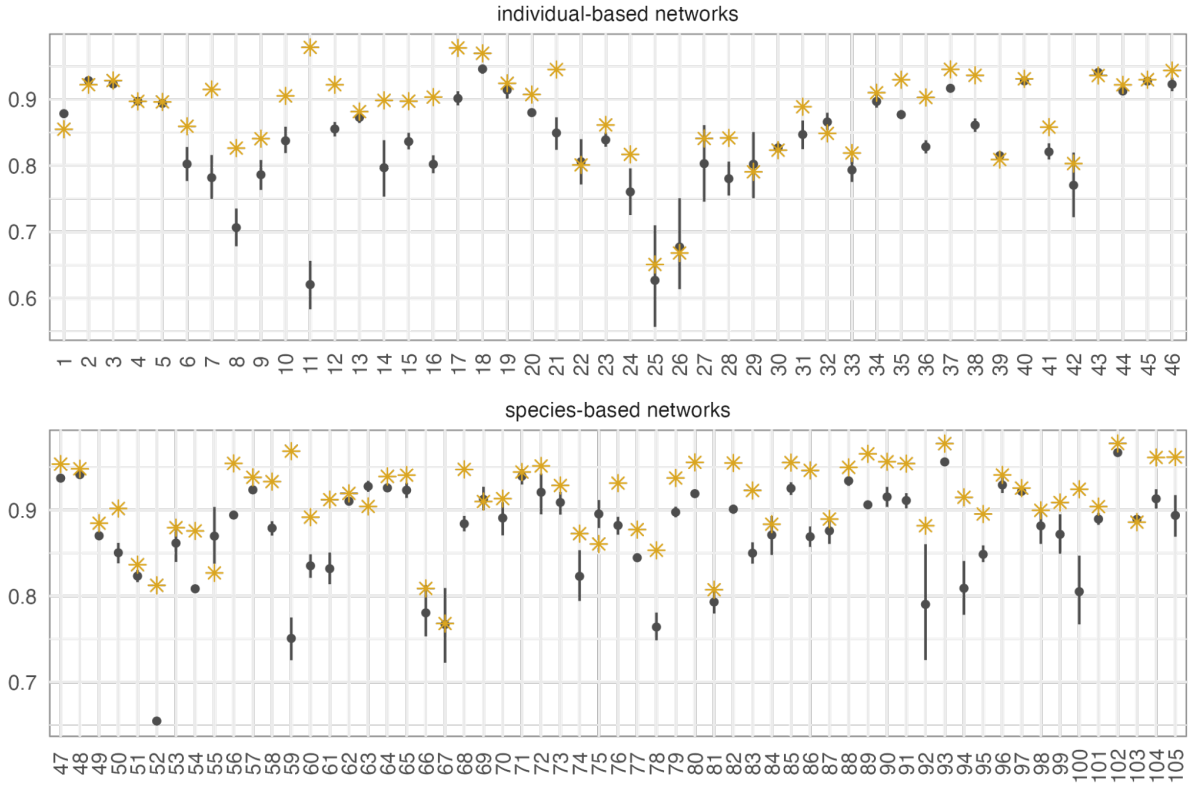


Figure S4. Network-level metrics for individual-based and species-based networks. Yellow asterisks represent empirical values and gray points intervals represent null model values (mean and 95% CI). Networks whose empirical value falls outside the confidence intervals are significantly different to their random expectation ($p > 0.05$). The null model algorithm used is Patefield algorithm which preserves marginal totals.

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

Metric	Type	Observed mean ± SD	Nulls mean ± SD	Average difference ± SD
Connectance	ind	0.3 ± 0.1	0.48 ± 0.01	-0.18 ± 0.12
	sp	0.29 ± 0.13	0.42 ± 0.01	-0.13 ± 0.1
Weighted NODF	ind	30.52 ± 12.26	50.48 ± 4.05	-19.96 ± 12.68
	sp	29.66 ± 11.53	46.96 ± 3.61	-17.29 ± 9.32
Modularity	ind	0.33 ± 0.12	0.13 ± 0.01	0.2 ± 0.11
	sp	0.37 ± 0.1	0.13 ± 0.01	0.24 ± 0.11
Interaction evenness	ind	0.67 ± 0.07	0.74 ± 0	-0.08 ± 0.05
	sp	0.62 ± 0.07	0.71 ± 0	-0.08 ± 0.04
Assortativity	ind	-0.48 ± 0.17	-0.55 ± 0.03	0.07 ± 0.09
	sp	-0.5 ± 0.15	-0.57 ± 0.04	0.06 ± 0.11
Centralization	ind	0.88 ± 0.07	0.84 ± 0.01	0.04 ± 0.06
	sp	0.91 ± 0.05	0.87 ± 0.01	0.04 ± 0.04

Population specialization (TNW ~ WIC)

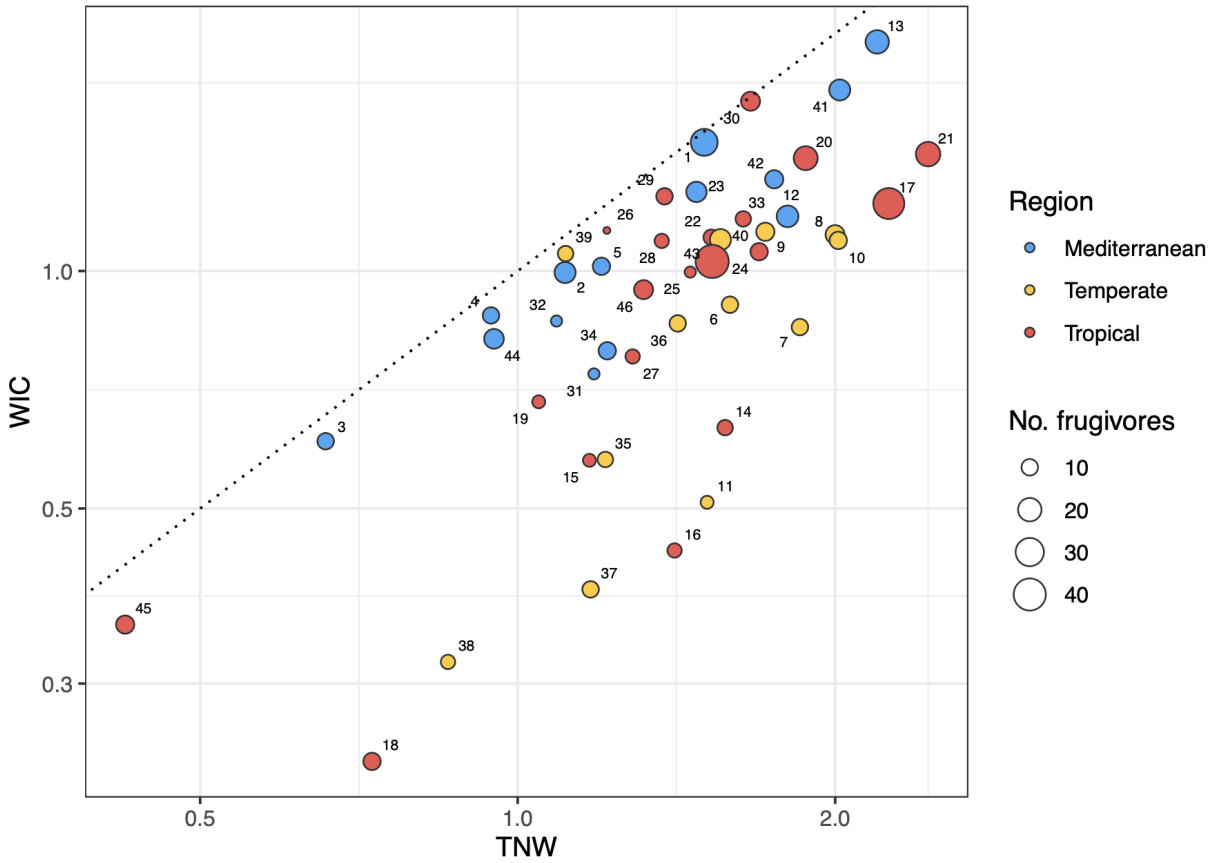


Figure S5. Within Individual Component (WIC) versus Total niche width (TNW) for individual-based frugivory networks. Point size is proportional to the number of observed frugivore species in the network, point color indicates the geographic region and number the network id (see Table S1). Note the log-scale in both axes. The dotted line represents a 1:1 ratio, in which the WIC would be equal to the TNW indicating individual niche widths that encompass the whole population niche width. The closer the networks are to the line, the higher WIC/TWN (i.e., lower individual specialization). Networks including many frugivore species tend to have a wider interaction niche (TNW), but not necessarily higher levels of individual specialization (WIC/TNW, i.e., far from the 1:1 line).

Interaction curves by frugivores

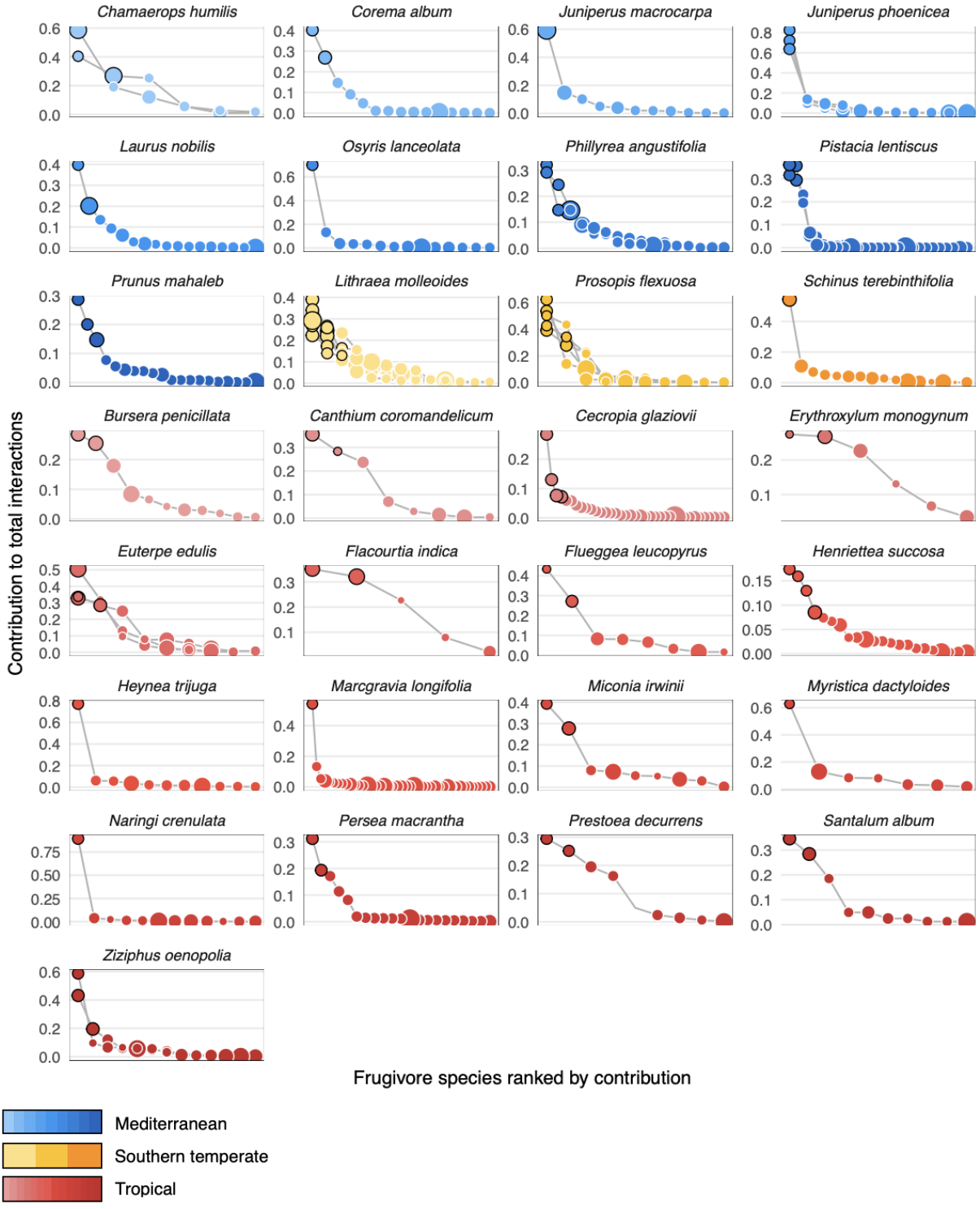


Figure S6. Relative contribution of each frugivore species (dots) to the total interactions of each plant species. Frugivores are ranked by decreasing contribution. Plant species with more than one population/network present several curves. Colors for each species correspond with different bioregions and different color shades differentiate plant species. Dots size represents frugivore body

mass relative to the mean body mass of the assemblage (z-score) and black outlines in dots indicate those frugivore species whose aggregate contributions account for at least 50% of the interactions.

Plant individuals' interaction profiles

Node-level metrics

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

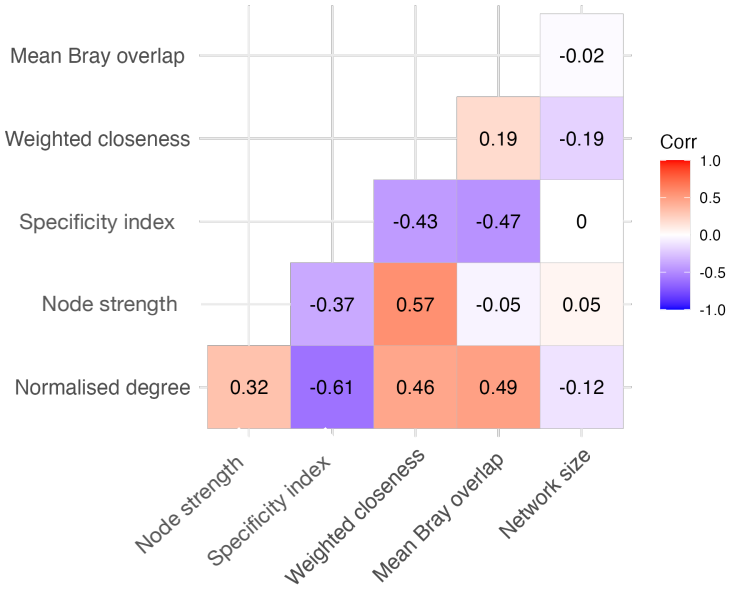


Figure S7. Correlation plot between selected node-level metrics. Numbers denote Pearson correlation coefficients (r) and the color its magnitude and direction.

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	1.11	0.71	0.59	0.58
Proportion of Variance	0.51	0.25	0.10	0.07	0.07
Cumulative Proportion	0.51	0.76	0.86	0.93	1.00
PC loadings:					
Normalised degree	-0.52	-0.20	-0.23	-0.72	-0.34
Node strength	-0.37	0.63	-0.20	0.40	-0.51
Specificity index	0.51	0.15	0.5	-0.28	-0.61
Weighted closeness	-0.45	0.38	0.7	-0.17	0.36
Mean Bray-Curtis overlap	-0.35	-0.63	0.40	0.46	-0.33

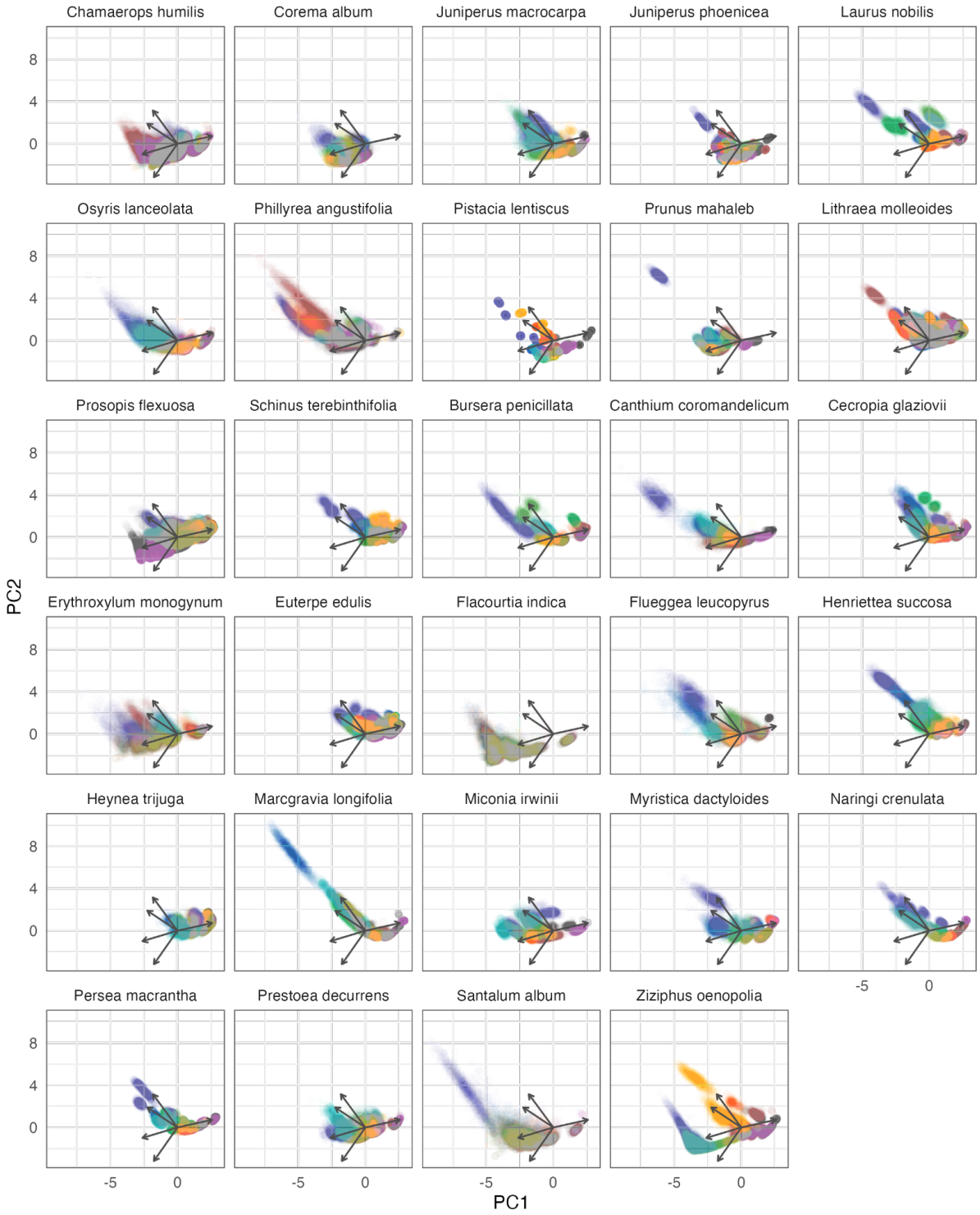


Figure S8. Principal Component Analysis for node-level metrics of individual plants in their respective networks. PCA multivariate space is faceted by plant species to facilitate display of plant individuals distribution in the multivariate space and the identification of outlying individuals. Note that some species present more than one population (i.e., more than one network, see Table S1). Each individual plant is represented by a point cloud with a different color and its node-level metrics were estimated using the full network posterior distribution (n = 1000 points per individual). It is visible how some individuals have well delimited point clouds, while some other individuals have

much more uncertainty due to lower sampling coverage. See Fig. 5 for information on what node-level metric represents each of the five arrows.

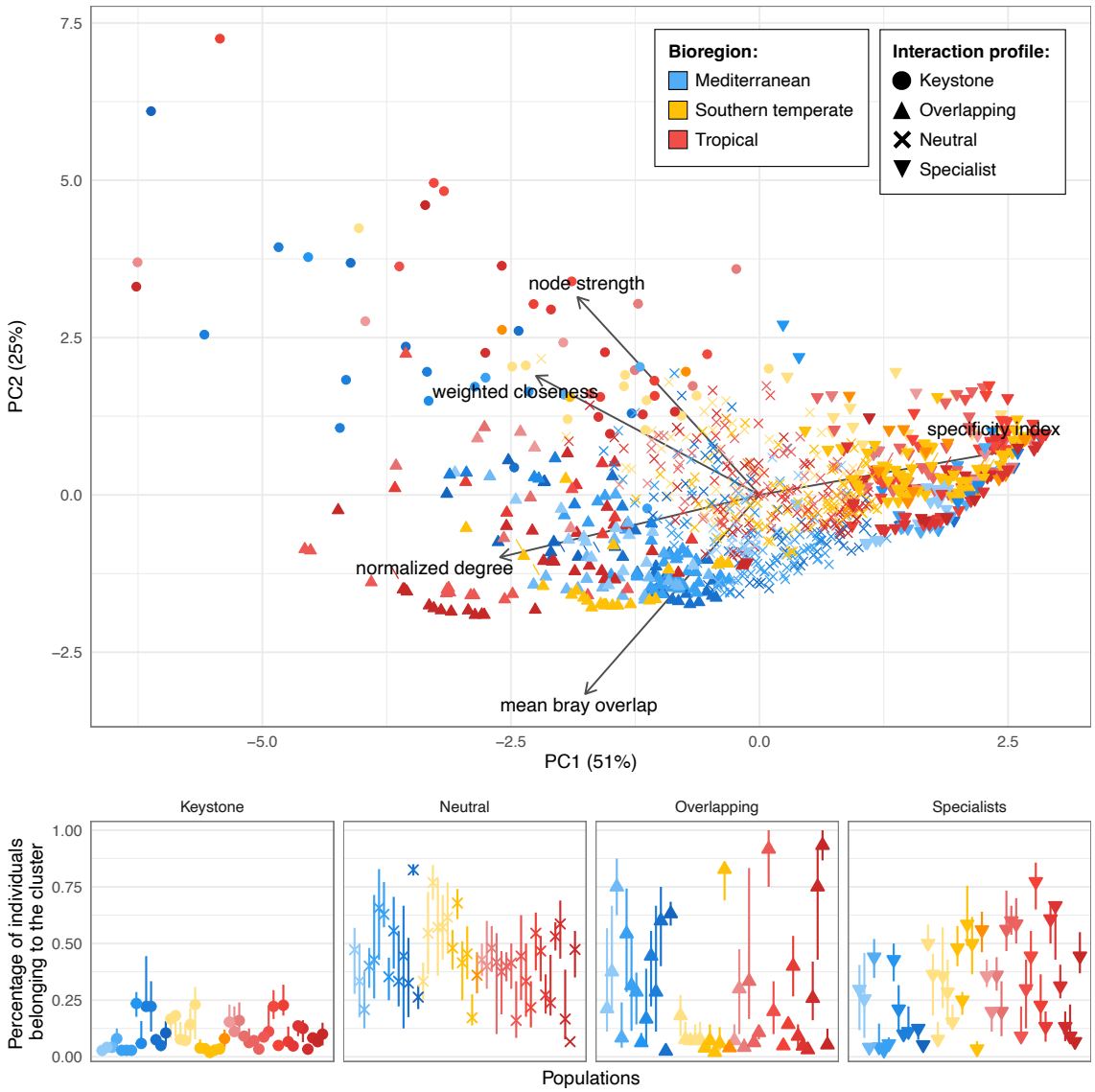


Figure S9. PCA for node-level metrics in all plant populations. Each point represents an individual plant. For each plant individual we have represented the centroid of its posterior distribution node-metric values, see Fig. S8. The shape of the points represents the most common categorization into one of the four different interaction profiles of each plant individual. The panel below shows the proportion of individuals within each population that fall into one of these clusters or interaction profiles. The interval of each point represents the 90% confidence interval for the 1000 cluster analysis repetitions. Colors indicate the bioregion and different shades refer to different plant species within each bioregion.

Software citations

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

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