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Title: Tripartite networks show that keystone species can multitask

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Abstract: The importance of keystone species is often defined based on a single type of interaction (e.g., keystone predator). However, it remains unclear whether this functional importance extends across interaction types. We conducted a global meta-analysis of interaction networks to examine whether species functional importance in one niche dimension is mirrored in other niche dimensions, and whether this is associated with interaction outcome (mutualistic/antagonistic) or intimacy (temporary/permanent). We show that the importance of keystone species is positively correlated across multiple dimensions of species' ecological niche, independently from species' abundance, interaction outcome or intimacy. This suggests that keystonness multidimensionality is a widespread phenomenon and can be used to identify keystone species across several interaction types, playing a central role in determining ecosystem resilience and defining conservation strategies.

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One sentence summary: Importance of keystone species is positively associated across ecological niche dimensions regardless of species' abundance.

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Main text: Keystone species are essential for ecosystem functioning and stability (*1*, *2*), and are thus a popular concept in ecological research and conservation practitioners, even if often identified based on slightly different criteria (reviewed in *3*). A frequently used definition characterizes keystone species as those species whose proportional importance for a given ecological process (e.g., herbivory, parasitism, pollination, or seed dispersal) greatly surpasses that of other more abundant species in the community (*2*). Due to the intrinsic difficulty of quantifying species contributions to ecological functions at the community level, most research on the role of keystone species has focused on a single ecological function, such as predation in food web studies (e.g. *1*). However, all species establish different types of interactions with other species in their surroundings (*4*, *5*), thus playing multiple ecological roles that together define their multidimensional niche (*6*, *7*). For example, many birds include insects and seeds in their diets, thus acting simultaneously as antagonists, when preying upon insects or destroying the ingested seeds, and mutualists, if seeds escape digestion and are dispersed away from the parental plant (*8*). If insects and seeds are not available, some of these birds might opportunistically consume nectar, eventually acting as pollinators (*9*). Furthermore, most of these birds will be preyed upon by carnivores or consumed by scavengers (*10*). Such a myriad of ecological functions raises the question of whether keystone species are simultaneously important for their multiple niche dimensions or, alternatively, if they tend to be particularly so for a single function or dimension.

In order answer this question, we first need to quantify species roles across multiple niche dimensions under the same theoretical framework, a task that poses a significant challenge (*11*). While food webs have been studied for a long time (*1*), recent increases in availability of high quality empirical datasets and advances in ecological network theory have increased our ability to make sense of the intrinsic complexity of biological communities (*12*). By simultaneously considering species (nodes) and the interactions (links) that bind them together into functional communities, ecological network analysis has offered a valuable tool to explore the emergent patterns generated by the biotic interactions that define a species'

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ecological niche (*13*). Nevertheless, the study of ecological networks with species-level resolution is still dominated by bipartite networks, where species of two groups are linked by a single type of interaction, such as pollination (*14*), seed dispersal (*15*), or parasitism (*16*). Only more recently, some studies have started to explore the relationship between two types of species interactions within a network framework (*17–20*). For instance, recent research suggests a positive correlation between the importance of mammals as seed dispersers and seed predators (*17*) and also between birds acting as seed dispersers and pollinators (*18*), but no association in the importance of frugivorous and nectarivorous bats (*19*) or between plant mycorrhizal fungi and frugivores (*20*). However, none of these pairwise comparisons accounted for the effect of species abundance as a key driver of species importance.

We now know that both species richness and abundance have positive and independent effects on ecosystem multifunctionality (*21*, *22*), with more abundant species being more important contributors to community functioning (*23*). The effect of abundance may result from neutral processes, with all individuals having an equivalent functional contribution regardless of species identity (*24*). In turn, species importance is the combined result of two components: species' local abundance or densities, which drives the underlying encounter probability between species – the "mass action hypothesis", and species' interaction preferences, as determined by morphological, physiological and ecological traits (*25*). Disentangling these two components is thus essential to correctly identify the role of "keystone species" in their communities.

Here, we explored whether species' functional importance, in terms of their impact on other co-occurring species, i.e., keystone species status, is maintained across different interaction types. To this end, we assembled a global dataset of 18 quantitative tripartite networks, each composed by two bipartite subnetworks coupled by a shared set of species at the interface of the paired networks (Fig. 1A). Overall, these networks encompass six distinct interaction types: herbivory, parasitism, seed dispersal, pollination, commensalism, and mycorrhizas (Table

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S1). Each tripartite species interaction network had on average 162 species (min. = 25; max. = 690) and 367 links (min. = 56; max. = 1414). These networks had an average of 58 species at the intermediate level (min. = 9; max. = 359), of which, on average, 23 species (min. = 7; max. = 155) participated in both bipartite subnetworks, thus forming the interface between them (Table S1).

Based on this dataset, we performed a meta-analysis (*26*) testing what extent a species' functional importance in one niche dimension is correlated with its importance in a second niche dimension (represented by the interactions in the two bipartite subnetworks, Fig. 1B-D). We then explored whether the any relationships found were driven by (1) the relative abundance of the species, (2) the outcome of the interaction (mutualistic *vs* antagonistic), or (3) the intimacy of the interaction (temporary *vs* permanent). We independently quantified species importance for each niche dimension by estimating species strength, a species-level network descriptor expressing to what extent a trophic level depends on each species from another level, calculated as the cumulative sum of species dependencies (*26*, *27*). This allowed us to test, for example, if the functional importance of each plant species for the entire pool of pollinators is correlated with its importance for the entire pool of herbivores in an herbivore-plant-pollinator tripartite network (Fig. 1).

Results

For those species at the interface of each tripartite network, we calculated the Pearson's correlation coefficient between the (log-transformed) species strength for the two subnetworks (*26*). We found a positive and statistically significant overall correlation of species strength between paired subnetworks (mean Pearson's $r = 0.42$, $z = 3.33$, $p < 0.001$; Fig. 2, Table 1, and Table S2 for correlations for each individual network). To understand if this correlation was affected by species relative abundance, we needed to remove its effect from the interaction strengths. To this end, we standardized all matrices according to the "mass action hypothesis", which assumes that the encounter probability between species is mainly driven by the product of their local abundances, and any deviation from this is the result of species preferences (*25*, *26*). We thus obtained

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"interaction preference matrices". As above, for each of the standardized matrices we obtained a (log-transformed) standardized species strength and calculated again Pearson's correlation coefficients. Accounting for species abundances reduced the correlation of species strength between paired subnetworks in 16 of the 18 studies (paired t-test: $t = 3.31$, df = 17, p = 0.004; mean difference = 0.11). However, even after accounting for species abundances the overall correlation of standardized species strength between paired subnetworks was weaker but remained positive, and statistically significant, across studies (mean Pearson's r = 0.24, z = 2.41, p = 0.016; Fig. 2, Table 1, and Table S2 for correlations for each individual network).

Heterogeneity in correlation coefficients among studies was larger than expected by chance (species strength: $QE = 72.403$, df = 17, $p < 0.001$; standardized species strength: $QE = 39.524$, df = 17, p = 0.002, Table 1), and accounted for a relatively high proportion of the total variability among studies (species strength: $I^2 = 80.2\%$; standardized species strength: $I^2 = 63.3\%$, Table 1).

To explore the potential sources of such heterogeneity, we classified each subnetwork according to their interaction outcome (antagonistic vs. mutualistic) and intimacy (permanent vs. temporary) (*26*). These subgroup analyses indicated that the mean correlations of unstandardized and standardized species strength were consistent among subgroups, even if uncertainty was larger for those combinations of interaction outcome and intimacy that were represented by fewer networks, and despite being more evident for networks with antagonist or permanent interactions (Fig. 2 and Table 1). Accordingly, including interaction outcome and intimacy as moderators (i.e., explanatory variables) in the model, accounted for virtually no heterogeneity in the correlations of unstandardized species strength (Table 1 and Table S3).

Discussion

Natural communities are bound together by multiple types of biotic interactions. Understanding how species and biotic interactions couple ecological processes

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across multiple functional levels is critical to advance our understanding of ecosystem structure and functioning (*28*), and for predicting the effects of global change on ecosystem resilience (*29*). Our meta-analysis of tripartite networks revealed that, overall, species' importance – in terms of their functional effects on other species – is positively associated across multiple ecological niche dimensions, irrespective of species abundance (Fig. 2, Table 1, and Table S3). This means that species that interact strongly with many other species in one dimension of their niche also tend to be the most connected in other niche dimensions. As a result, species that have a disproportionate importance for a particular ecosystem function (i.e., keystone species) also tend to be important for other functions in the communities they integrate. This seems to be a general pattern as we found no evidence that the strength of this positive association depends on whether the interaction is antagonistic or mutualistic and on whether it is temporary (e.g., pollination or seed dispersal) or permanent (e.g., plant-fungal interactions).

It is well established that abundance is an important driver of a species' overall effect on ecosystem functioning (*21*, *22*). Under the assumptions of the neutral theory of biodiversity (*24*), we would expect no significant correlation in species importance across multiple dimensions of their niche, beyond that explained by species relative abundances. By calculating species strength based on interaction preference matrices, we were able to isolate the effect that abundance has on interaction frequencies. We showed that species abundance indeed contributes to the correlation in species strength across different niche dimensions, as these correlations consistently became weaker after we removed the effect of species abundance. However, we still found a significant positive signal of species functional importance across multiple interaction networks (Fig. 2, Table 1, Table S2 and Table S3). This indicates that species preferences, related to trait-matching, physiological needs, or seasonal changes to partners species strongly contribute to the functional importance of species across the range of biotic interactions that characterize their ecological niche.

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A likely mechanism underlying species' keystonness across multiple ecological functions is the existence of important traits that modulate species' interactions patterns across different functional groups. For instance, previous work has shown that visual or olfactory flower traits can attract both pollinators and herbivores (*30*), and that herbivore-induced plant defence mechanisms can affect interactions with pollinators (*31*). In addition, selection from both pollinators and herbivores can result in the correlated evolution of plant traits related to these interactions (e.g., flower morphology and self-incompatibility; *34*). Body size is another such trait that might play a key role in interaction probabilities in certain networks. For example, small birds are disproportionately important for linking pollination and seed dispersal networks (*33*). Because similar mechanisms might shape other types of interactions, identifying traits or trait syndromes that regulate species interactions in multiple niche dimensions could be key to understand the structure of multidimensional interaction networks.

Notably, this signal appears to be consistently preserved across antagonistic and mutualistic as well as temporary and permanent interactions (Fig. 2 and Table S2). This suggests that irrespective of these interaction characteristics, keystone species have a strong impact on other species in more than one dimension of their functional niche. The fact that in the subgroup analyses, this signal was most obvious in networks containing antagonistic and permanent interactions, and less so in networks with mutualistic and temporary interactions, may be explained by the relatively low sample sizes in the latter groups (Fig. 2 and Table 1).

The identification of keystone species for ecosystem functioning has long been a central topic in ecology and conservation (*4*, *34*). Our study provides evidence that the importance of these species is not restricted to single niche dimensions but extends across multiple dimensions of their functional niche (*35*). Our findings also imply that this multidimensionality of keystone species is a general phenomenon that can couple distinct ecological functions. Accordingly, the loss of keystone species likely intensifies trophic cascades and rapid community collapse (*5*, *36*). In this regard our study also implies that the benefits of protecting keystone species

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are not restricted to single ecosystem functions but are likely to extend across multiple ecosystem functions (*37*). This shows that biotic interactions are not only critical to understand specific ecosystem functions, such as predation, disease transmission, or pollination, but also that the dimensionality of species interactions is vital for structuring entire ecosystems and probably determines their sensitivity to perturbations or species extinctions (*38*).

It is important to realize that bipartite networks (those focusing on a single interaction type) represent an abstraction imposed by sampling constraints. However, there are still relatively few studies simultaneously quantifying multiple interaction types at the same site (*17*, *20*). Therefore, it is now increasingly clear that only by jointly considering the multiple dimensions that characterize species interaction networks can we get closer to understanding the intrinsic complexity of real ecosystems (*6*, *7*, *28*). However, given the novelty and the number of interaction networks sampled, the present results can be taken as a starting point to delve into the interplay between abundance, interaction type, species traits and (co-) evolutionary history as promising avenues for future research. We show that keystone species tend to be disproportionately important across multiple niche dimensions, regardless of their abundance, interaction outcome or intimacy. It must also be considered that to relate structure and function in interaction networks we need much more information on the contribution of each species to the different functions. We advocate that more comprehensive datasets that integrate all these aspects are required for a deeper understanding of how species interactions shape ecosystem structure and function.

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RH, ST, JA, BR, and LGC conceived the research idea.

ST and JA developed and implemented the statistical analysis.

ST wrote the manuscript.

All authors contributed data, discussed, and reviewed the manuscript.

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Supplementary Materials

Materials and Methods

Tables S1-S3

References 39-66

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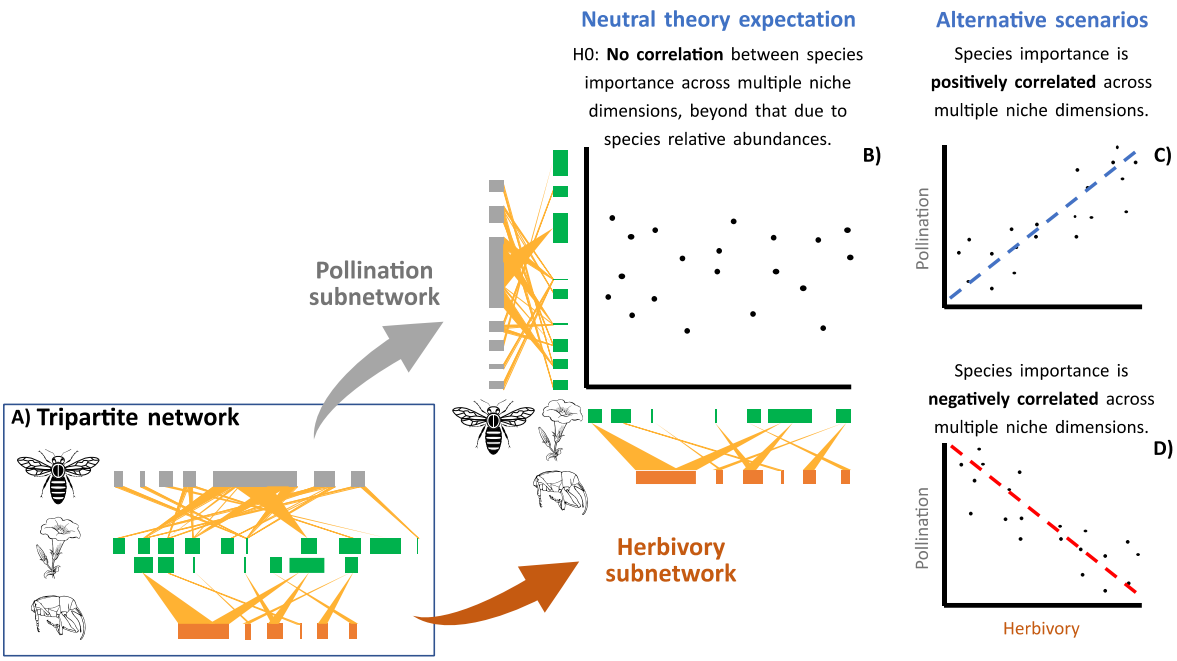

Fig. 1. Conceptual model for the importance of species participating in more than one ecological function, in a tripartite network.

Panel A shows an example of a tripartite network composed of two bipartite subnetworks representing pollination (top) and herbivory (bottom). Grey, green and orange boxes represent species of pollinators, plants, and herbivores, respectively, while yellow lines represent the interactions between species. The importance of each species in the intermediate level (plants in the present example) can be assessed by calculating species strength (*27*), after normalizing matrices according to the mass action hypothesis, which accounts for species relative abundances (*25*). Panels B, C and D represent alternative hypotheses regarding the correlation of species importance across each paired subnetwork, namely: B) species importance in both sub networks is independent; C) species importance is positively correlated between the two considered functions, i.e. keystone species (top right) are equally relevant for both dimensions; and D) species importance is negatively correlated between the two considered functions, i.e. keystone species are only relevant either for pollination or for herbivory, but not for both dimensions simultaneously.

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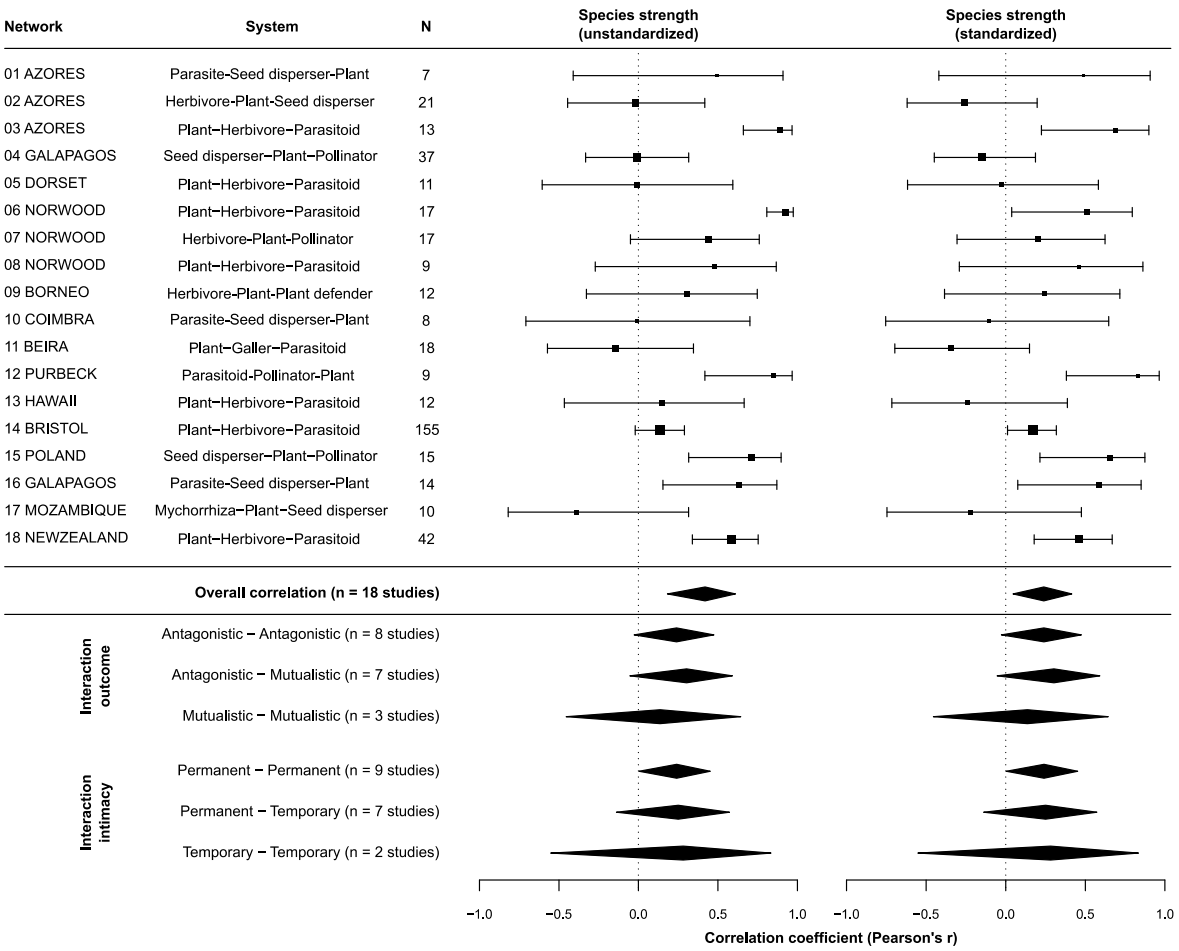

Fig. 2. Forest plot with the results of the meta-analysis.

Results of the meta-analysis on the Pearson's correlation coefficient (*r*) of species strength for species participating in paired ecological functions (subnetworks) in 18 tripartite networks (i.e., interface species) (Table 1). **N** is the number of species common to both subnetworks. The correlation coefficient of each tripartite network is represented by the square at the centre of the 95% confidence interval and its size is proportional to **N**. Diamonds represent the overall weighted correlation coefficient and its 95% confidence interval (individual values in Table S2).

Table 1. Results of the meta-analysis of the tripartite networks. The random model is the model without moderators and includes all studies. The subsequent rows present the models for each combination of interaction outcome and intimacy, each with three combinations of interactions. Pearson's *r* is the overall correlation coefficient [95% confidence interval] of each model; df are the degrees of freedom of the model; I^2 is the heterogeneity among correlation coefficients that is not due random sampling variance; n is the number of studies included in each model; *QM* is the amount of heterogeneity accounted by moderators; p is significance of the Q-test for heterogeneity; and *QE* is the amount of heterogeneity across studies included in the models. For full results of the meta-analytical models see Table S3 in Supporting Information. Correlations for which the 95% confidence interval did not overlap zero are given in bold.

	Species strength (unstandardized)		**Species strength (standardized by abundance)**	
	Pearson's *r*	I^2	Pearson's *r*	I^2
Random effects model (no moderators, n = 18)	**0.42 [0.18, 0.61]**	50.2%	**0.24 [0.05, 0.42]**	63.3%
Test for heterogeneity between studies	QE = 72.403, df = 17, p < 0.001		QE = 39.524, df = 17, p = 0.002	
Subgroups: Interaction outcome				
Antagonistic + Antagonistic (n = 8)	**0.50 [0.08, 0.76]**	88.8%	**0.24 [-0.03, 0.48]**	65.2%
Antagonistic + Mutualistic (n = 7)	**0.41 [0.12, 0.64]**	38.9%	0.30 [-0.05, 0.59]	53.7%
Mutualistic + Mutualistic (n = 3)	0.17 [-0.50, 0.71]	81.9%	0.14 [-0.45, 0.64]	76.0%
Test for difference between subgroups	*QM* = 0.892, df = 2, p = 0.640		*QM* = 0.327, df = 2, p = 0.849	
Subgroups: Interaction intimacy				
Permanent + Permanent (n = 9)	**0.48 [0.11, 0.73]**	86.7%	**0.24 [0.00, 0.45]**	58.1%
Permanent + Temporary (n = 7)	0.34 [-0.04, 0.63]	58.5%	0.25 [-0.14, 0.57]	58.6%
Temporary + Temporary (n = 2)	0.39 [-0.44, 0.86]	86.2%	0.28 [-0.55, 0.83]	87.0%
Test for difference between subgroups	*QM* = 0.287, df = 2, p = 0.867		*QM* = 0.001, df = 2, p = 0.999	

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Supplementary Materials for

Tripartite networks show that keystone species can multitask

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This PDF includes:

Material and Methods

Tables S1-S3

References 39-66

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Materials and Methods

Data set

We assembled a global dataset comprising 18 quantitative tripartite networks, each composed of two bipartite subnetworks, representing distinct types of interaction. Overall, these networks encompass six distinct interaction types: herbivory, parasitism, seed dispersal, pollination, commensalism, and arbuscular mycorrhizal association (Table S1). Sampling of both subnetworks coincided in time and space for each tripartite network. When studies included data from nearby plots/sites, these were pooled together, after checking if such pooling made biological/ecological sense (i.e., if those species and interactions can be considered as part of the same community). In order to explore the potential underlying patterns explaining eventual correlations between species importance across their niche dimensions, we characterized each tripartite network regarding the interaction outcome and intimacy of its subnetworks (Table 1), using these as moderators (i.e., variables driving the variation between studies) in a meta-analysis. Interaction outcomes were classified as either antagonistic or mutualistic, resulting in three combinations of outcomes: antagonistic-antagonistic, antagonistic-mutualistic, and mutualistic-mutualistic. Interaction intimacy describes “the degree of physical proximity or integration of partner taxa during their life cycles” (*39*). Because we had access to a limited number of tripartite networks, we followed a conservative approach and classified the degree of interaction intimacy as permanent (high intimacy) or temporary (low intimacy) (*28*, *40*). Permanent interactions are those in which one of the partners is physically or physiologically dependent of the other for a significant proportion of their life cycles (e.g., the interaction between mycorrhizal fungi and plants, or parasitoids and their hosts), and temporary interactions are those where such dependencies are restricted to short periods of phenological matching (e.g., the interaction between plants and their pollinators or seed dispersers). This classification resulted in three combinations of intimacy levels: permanent-permanent, permanent-temporary, and temporary-temporary.

Standardizing interaction matrices and species preferences

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In order to estimate interaction preferences that are independent of species relative abundances, we standardized all network matrices according to the "mass action hypothesis" (following *25*). The mass action hypothesis states that species local abundances drive the probability of encounter between two species, and that deviations from this assumption are due to species interaction preferences (*25*). The networks included in this study were assembled independently for various purposes and include a plethora of sampling techniques to quantify interaction frequencies, which is in turn affected by species relative abundances (*41*, *42*). In addition, this standardization procedure also has the advantage of converting all interaction frequencies to the same currency.

If we have a quantitative species interaction matrix B, each entry $B_{i,j}$ of this matrix encodes the weight of the interaction between species i and j that can be decomposed into species interaction preferences ($\gamma_{i,j}$) and mass action ($x_i x_j$, the product of the effective abundances of the interacting species), that is

$$B_{i,j} = \gamma_{i,j} x_i x_j.$$

We can then remove the effect of species effective abundances and rescale matrices to obtain estimates of species preferences:

$$\gamma_{i,j} = \frac{B_{i,j}}{x_i x_j}.$$

If an interaction is not recorded $B_{i,j} = 0$ then $\gamma_{i,j} = 0$; otherwise, when an interaction is present, $B_{i,j} > 0$ and $\gamma_{i,j} \neq 0$. In the latter case, we apply a logarithm transformation obtaining:

$$\log B_{i,j} = \log \gamma_{i,j} + \log x_i + \log x_j,$$

which under the mass action hypothesis is $\log \gamma_{i,j} = 0$, thus $\gamma_{i,j} = 1$.

We can re-arrange the log-equation as follows:

$$Y_{i,j} = \alpha_{i,j} X_i + \beta_{i,j} X_j + \epsilon_{i,j},$$

where $\alpha_{i,j}$ and $\beta_{i,j}$ are regression coefficients, X_i and Y_j are estimates of the abundances of the interacting species and are unknown, and $\varepsilon_{i,j}$ is an error term

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that correspond to the interaction preferences. We seek to find the best-fit for X_i and Y_j by minimizing the errors ε. When no errors exist, the standardized matrix is binary, with recorded interactions having $\gamma_{i,j} = 1$, and interactions are neutral and result exclusively from the probabilistic encounter between species, i.e., mass action effect. If errors are present, the solution for the best-fit for X_i and Y_j will result in at least some interactions having $\gamma_{i,j} \neq 0$, with interaction preferences being indicated by $\gamma_{i,j} > 1$ and averted interactions indicated by $\gamma_{i,j} < 1$. Interaction preference matrices were calculated in R (*43*) using the function *GetPreference* (*25*). This approach has the advantage of removing the effect of abundance on interaction frequency, which is essential for the accurate characterization of keystone species.

Estimating species importance

Once subnetworks were standardized, we proceeded to quantify the importance of each species at the interface of the two subnetworks for both dimensions of their niche (i.e., for the two subnetworks). Thus, for both the unstandardized and standardized subnetworks, we quantified the importance of all species at the interface of the two subnetworks, by calculating a key species-level descriptor, namely species strength (*27*). Species strength is a particularly useful index quantify the importance of species to the entire assemblage of interacting partners from other trophic level in a given network (*15*, *18*, *41*, *44*). For example, in an herbivore-plant-pollinator network, species strength was computed twice for each plant: firstly, reflecting its importance as a resource for the pollinator community, and secondly, reflecting its importance as a resource for the herbivore community. Species strength based on matrices that have been standardized by mass effects (i.e., abundance) is explicitly referred to as standardized species strength. The calculation of this descriptor requires to calculate the dependence of each species *i*, from a given network level, on each species *j* from the other network level:

$$b_{ij} = \frac{a_{i,j}}{A_i},$$

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with A_i being the sum of all interactions by species i, a_{ij} the interaction frequency between i and species j. Species strength is then the sum of the dependencies of species i on all species j from the other trophic level:

$$\text{Species strength}_i = \sum_{i=1}^{I} b_{i,j}.$$

Species strength was calculated with the R package *bipartite v2.08* (*45*).

Meta-analysis

For those species at the interface of each tripartite network, we calculated Pearson's correlation coefficient between their values of species strength for the two subnetworks, using both the unstandardized and standardized matrices. Species strength often presents a skewed distribution, and therefore was log-transformed to comply with the assumptions of Pearson's correlation. We used a paired *t*-test to assess if the correlations from unstandardized and standardized matrices differed.

To estimate the overall correlation across all tripartite networks we performed a meta-analysis and estimated the associated variance and 95% confidence intervals. Pearson's coefficients were standardized using a Fisher's r-to-Z transformation, which stabilizes the variance of the coefficients (*46*), that is obtained by:

$$Z_{r_i} = {}^{1}/_{2} \log e \left({}^{1 + r_i}/_{1 - r_i} \right),$$

where r_i is the Pearson correlation coefficient of the individual studies, with an approximate normal distribution with variance:

$$w_i = {}^{1}/_{n_i - 3},$$

where n_i is the sample size of the individual studies (in the present study the number of species participating in both functions and from which the correlations were calculated).

First, we implemented a random-effect model without moderators, which assumes that effect sizes come from different populations (*47*, *48*). In this model, the contribution of each study is weighted by its estimated variance,

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reducing the influence of studies with low sample sizes. The transformed effect sizes (i.e., Z-transformed Pearson's coefficients) are then used to calculate an average effect size, with each correlation coefficient weighted by the inverse of the within-study variance of the study from which it came from.

$$\bar{Z}_r = \sum_{i=1}^{k} w_i z_{r_i} \Big/ \sum_{i=1}^{k} w_i$$

This results in individual z-values with small variances having greater weights than those with large variances (*49*). Coefficients were considered statistically different from zero if confidence intervals did not overlap zero. In reporting results and their visual representation, Pearson's coefficients and corresponding 95% confidence intervals were back-transformed according to:

$$r_i = e^{(2z_i)} - 1 \Big/ e^{(2z_i)} + 1.$$

Second, we conducted a subgroup analysis to separately estimate the pooled correlation coefficient for each combination of interaction outcome (i.e., antagonistic-antagonistic, antagonistic-mutualistic, mutualistic-mutualistic) and for each combination of interaction intimacy (i.e., permanent-permanent, permanent-temporary, temporary-temporary). Finally, we used a mixed effects model to test whether the sign and magnitude of the correlation differed between the subgroups, i.e., between the different combinations of interaction outcome or intimacy. In this way, we allowed the within-group variances to vary between subgroups. To avoid overfitting, we included either interaction outcome or intimacy, but not both variables simultaneously, as moderators into the model.

We used the Cochran's Q-test (*50*), to test whether correlations were heterogeneous across the tripartite networks, with a significant result indicating the presence of heterogeneity (*QE*), i.e., the existence of differences in correlation coefficients between studies. We estimated the I^2 statistic to quantify the proportion of the total variance resulting from true heterogeneity among studies, i.e. differences between tripartite networks not resulting simply from random sampling variance (*50*). In models with moderators, the Q-test tests for the presence of significant heterogeneity accounted for by the different levels of the moderator variables (*QM*), i.e., differences in correlation coefficients

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between the different combinations of interaction outcome and intimacy. Finally, we estimated R^2 to quantify the proportion of heterogeneity accounted for by these moderators. All meta-analysis procedures were conducted using the R package *metafor v2.1-0* (*51*).

Table S1 – **Data sets description.** Location and geographic coordinates, network levels of interacting species, total number of species, number of species at the intermediate level (intermediate species), number of common species at the interface of the bipartite subnetworks (interface species), number of links, and size of each bipartite subnetwork of the tripartite networks used in the meta-analysis.

Data set	Location	Latitude/Longitude	Network levels	Total species	Intermediate species	Interface species	Links	Subnetwork size	References
01 AZORES	Azores, Portugal	37.794/-25.191	Parasite-Seed disperser-Plant	63	9	7	87	9x13-7x41	(*53*, Heleno unpubl)
02 AZORES	Azores, Portugal	37.794/-25.191	Herbivore-Plant-Seed disperser	94	53	21	165	31x36-41x7	(*53*)
03 AZORES	Azores, Portugal	37.794/-25.191	Plant-Herbivore-Parasitoid	79	37	13	110	31x36-13x12	(*54*)
04 GALAPAGOS	Galapagos, Ecuador	-0.738/-89.882	Seed disperser-Plant-Pollinator	390	163	37	1414	84x21-110x212	(*55*, *56*)
05 DORSET	Dorset, UK	50.823/-1.830	Plant-Herbivore-Parasitoid	51	25	11	87	25x11-11x15	(*57*)
06 NORWOOD	Bristol, UK	51.313/-2.321	Plant-Herbivore-Parasitoid	42	19	17	91	19x6-16x16	(*35*, *58*)
07 NORWOOD	Bristol, UK	51.313/-2.321	Herbivore-Plant-Pollinator	329	77	17	540	30x28-47x241	(*35*)
08 NORWOOD	Bristol, UK	51.313/-2.321	Plant-Herbivore-Parasitoid	69	28	9	60	28x30-9x11	(*35*)
09 BORNEO	Danum Valley, Borneo	4.967/117.800	Plant defender-Herbivore-Plant	89	13	12	180	13x43-13x32	(*59*)
10 COIMBRA	Coimbra, Portugal	40.217/-8.450	Parasite-Seed disperser-Plant	60	39	8	158	18x6-15x29	(*62,* da Silva unpub)
11 BEIRA	Beira Litoral, Portugal	40.221/-8.890	Plant-Galler-Parasitoid	93	31	18	56	31x22-18x40	(*61*)
12 PURBECK	Isle of Purbeck, UK	50.616/-2.043	Parasitoid-Pollinator-Plant	25	9	9	80	9x12-9x4	(*16*)
13 HAWAII	Hawaii, USA	23.417/-159.617	Plant-Herbivore-Parasitoid	68	29	12	94	28x32-13x7	(*62*)
14 BRISTOL	Bristol, UK	51.479/-1.984	Plant-Herbivore-Parasitoid	690	359	155	1312	357x139-157x192	(*63*)
15 POLAND	Białowieza, Poland	52.824/24.007	Seed disperser-Plant-Pollinator	357	15	15	1220	15x34-15x308	(*64*)
16 GALAPAGOS	Galapagos, Ecuador	-0.738/-89.882	Parasite-Seed disperser-Plant	114	36	14	241	15x13-16x84	(*56,* Heleno unpub)
17 MOZAMBIQUE	Gorongosa, Mozambique	-18.943/34.373	Mycorrhiza-Plant-Seed disperser	107	19	10	202	16x69-16x16	(*20*)
18 NEW ZEALAND	Nelson-Marlborough, New Zealand	-41.484/173.006	Plant-Herbivore-Parasitoid	204	90	42	502	68x76-42x61	(*65*, *66*)

Table S2 – **Pearson's *r* correlation coefficients for each tripartite network.** Pearson's *r* correlation coefficients, with the 95% confidence interval in brackets for each tripartite network included in the meta-analysis of unstandardized and standardized species strength for species participating in both ecological functions. The type of interaction of each subnetwork were characterized in terms of their interaction outcome (antagonistic vs. mutualistic) and level of intimacy (permanent vs. temporary).

			Pearson's *r* correlation coefficient (95% CI)	
Data set	**Interaction Outcomes**	**Level of Intimacy**	**Species strength (unstandardized)**	**Species strength (standardized by abundance)**
01 AZORES	Antagonistic-Mutualistic	Permanent-Temporary	0.50 (-0.41, 0.91)	0.49 (-0.42, 0.91)
02 AZORES	Antagonistic-Mutualistic	Permanent-Temporary	-0.02 (-0.45, 0.42)	-0.26 (-0.62, 0.20)
03 AZORES	Antagonistic-Antagonistic	Permanent-Permanent	0.89 (0.66, 0.97)	0.69 (0.22, 0.90)
04 GALAPAGOS	Mutualistic-Mutualistic	Temporary-Temporary	-0.01 (-0.33, 0.32)	-0.15 (-0.45, 0.19)
05 DORSET	Antagonistic-Antagonistic	Permanent-Permanent	-0.01 (-0.61, 0.59)	-0.03 (-0.62, 0.58)
06 NORWOOD	Antagonistic-Antagonistic	Permanent-Permanent	0.93 (-0.81, 0.97)	0.51 (-0.04, 0.80)
07 NORWOOD	Antagonistic-Mutualistic	Permanent-Temporary	0.44 (-0.05, 0.76)	0.20 (-0.10, 0.62)
08 NORWOOD	Antagonistic-Antagonistic	Permanent-Permanent	0.48 (-0.27, 0.87)	0.46 (-0.29, 0.86)
09 BORNEO	Antagonistic-Mutualistic	Permanent-Permanent	0.30 (-0.33, 0.75)	0.24 (-0.38, 0.72)
10 COIMBRA	Antagonistic-Mutualistic	Permanent-Temporary	-0.01 (-0.71, 0.70)	-0.11 (-0.75, 0.65)
11 BEIRA	Antagonistic-Antagonistic	Permanent-Permanent	-0.14 (-0.57, 0.35)	-0.34 (-0.70, 0.15)
12 PURBECK	Antagonistic-Mutualistic	Permanent-Temporary	0.85 (0.42, 0.97)	0.83 (0.38, 0.96)
13 HAWAII	Antagonistic-Antagonistic	Permanent-Permanent	0.15 (-0.47, 0.66)	-0.24 (-0.72, 0.39)
14 BRISTOL	Antagonistic-Antagonistic	Permanent-Permanent	0.14 (-0.02, 0.29)	0.17 (0.01, 0.32)
15 POLAND	Mutualistic-Mutualistic	Temporary-Temporary	0.71 (0.32, 0.90)	0.66 (-0.21, 0.87)
16 GALAPAGOS	Antagonistic-Mutualistic	Permanent-Temporary	0.63 (-0.15, 0.87)	0.58 (0.08, 0.85)
17 MOZAMBIQUE	Mutualistic-Mutualistic	Permanent-Temporary	-0.39 (-0.82, 0.32)	-0.22 (-0.75, 0.48)
18 NEW ZEALAND	Antagonistic-Antagonistic	Permanent-Permanent	0.58 (0.34, 0.75)	0.46 (0.18, 0.67)

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Table S3 - Meta-analysis full results. *r* - Pearson's correlation coefficient [95% confidence interval] of each model; *QE* - heterogeneity across studies; I^2 - % heterogeneity among correlation coefficients not due to random sampling variance; *QM* - heterogeneity accounted by moderators; df - degrees of freedom of the model; p - significance of the Q-test for heterogeneity; R^2 - % heterogeneity accounted for by moderators (each with three levels). Correlations in which the 95% CI did not overlap zero are given in bold.

		Species strength (unstandardized)	Species strength (standardized by abundance)
	Random model (no moderators)	***r* = 0.42 [0.18, 0.61]** QE = 72.403, df = 17 p < 0.001 I^2 = 80.2%	***r* = 0.24 [0.05, 0.42]** QE = 39.524, df = 17 p = 0.002 I^2 = 63.3%
Moderator: Interaction Outcome	Mixed-Effect Model	QE= 70.149, df = 15 p < 0.001 I^2 = 80.0%	QE = 38.092, df = 15 p = < 0.001 I^2 = 65.6%
		QM = 0.892, df = 2 p = 0.640 R^2 = 0.0%	QM = 0.327, df = 2 p = 0.849 R^2 = 0.0%
	Antagonistic + Antagonistic	***r* = 0.50 [0.08, 0.76]** QE = 50.648, df = 7 p < 0.001 I^2 = 88.8%	*r* = 0.24 [-0.03, 0.48] QE = 16.750, df = 7 p = 0.019 I^2 = 65.2%
	Antagonistic + Mutualistic	***r* = 0.41 [0.12, 0.64]** QE = 9.788, df = 6 p = 0.134 I^2 = 38.9%	*r* = 0.30 [-0.05, 0.59] QE = 13.034, df = 6 p = 0.043 I^2 = 53.7%
	Mutualistic + Mutualistic	*r* = 0.17 [-0.50, 0.71] QE = 9.713, df = 2 p = 0.008 I^2 = 81.9%	*r* = 0.14 [-0.46, 0.64] QE = 8.309, df = 2 p = 0.016 I^2 = 76.0%
Moderator: Interaction Intimacy	Mixed-Effect Model	QE= 71.890, df = 15 p < 0.001 I^2 = 80.8%	QE = 38.862, df = 15 p = < 0.001 I^2 = 66.5%
		QM = 0.287, df = 2 p = 0.867 R^2 = 0.0%	QM = 0.001, df = 2 p = 0.999 R^2 = 0.0%
	Permanent + Permanent	***r* = 0.45 [0.11, 0.73]** QE = 50.655, df = 8 p < 0.001 I^2 = 86.7%	***r* = 0.24 [0.00, 0.45]** QE = 16.755, df = 8 p = 0.033 I^2 = 58.1%
	Permanent + Temporary	*r* = 0.34 [-0.04, 0.63] QE = 14.015, df = 6 p = 0.030 I^2 = 58.5%	*r* = 0.25 [-0.14, 0.57] QE = 14.4219, df = 6 p = 0.025 I^2 = 58.6%
	Temporary + Temporary	*r* = 0.39 [-0.44, 0.86] QE = 7.221, df = 1 p = 0.007 I^2 = 86.2%	*r* = 0.28 [-0.55, 0.83] QE = 7.689, df = 1 p = 0.006 I^2 = 87.0%