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., a keystone predator)[1]. However, all species participate in multiple types of interactions within their biological comunities[2], and it remains unclear whether this functional importance extends across interaction types. Species interaction networks combining multiple types of interactions are quite well positioned to solve this puzzle, but so far results are contradictory[3–7]. We conducted a global meta-analysis of tripartite interaction networks to examine whether species functional importance in one niche dimension is mirrored in other niche dimensions. We show that the importance of keystone species is positively correlated across multiple dimensions of species' ecological niche, independently from species' abundance, interaction outcome (mutualistic/antagonistic) or intimacy (temporary/permanent interactions). These results show for the first time, that keystone species tend to be disproportionately relevant not only for one but for multiple ecosystem functions. Such multidimensionality of keystone species will likely have profound implications on the architecture, functioning, and resilience of entire ecosystems.

Main text: Keystone species play critical roles in ecosystems stability[1,8], and are thus a popular concept in ecological research and conservation practice. Understanding how these species might affect ecosystem responses to multiple threats is a central question in ecology[2,9]. However advances have been hindered by an excessive compartmentalization of studies focusing on a single function at a time and by the identification of keystone species based on slightly different criteria[10]. A frequently used definition characterizes keystone species as those species whose proportional importance for a given ecological process (e.g., herbivory, parasitism, pollination, etc.) greatly surpasses that of other more abundant species in the community[8]. Due to the intrinsic difficulty of quantifying species contributions to multiple ecological functions at the community level, most research on the role of keystone species has focused on a single ecological function[e.g.1]. However, all species establish many different types of interactions with other species in their surroundings[2,11], thus playing multiple ecological roles that together define their multidimensional niche[12,13]. For example, many birds include insects and seeds in their diets, thus acting simultaneously as predators (antagonists) and as seed dispersers (mutualists)[14], and if insects and seeds are not available, some of these birds might consume nectar, eventually acting as pollinators[15]. Furthermore, many of these birds will be preyed upon by carnivores or consumed by scavengers[16]. Such a myriad of ecological functions raises the question of whether keystone species are equally important for all their multiple niche dimensions or, alternatively, if they tend to be particularly important for a single function or dimension.

In order answer this question, we first need to quantify species roles across multiple niche dimensions under a unified theoretical framework (i.e., a common currency), a task that poses a significant challenge[17]. While food webs have been studied for a long time[1], recent advances in ecological network theory and in the availability of high-quality empirical datasets have increased our ability to make sense of the intrinsic complexity of biological communities[18]. 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' ecological niche[19]. Nevertheless, the study of ecological networks with species-level resolution is still dominated by bipartite networks, where species form two groups linked by a single type of interaction[3], such as pollination[20], seed dispersal[21], or parasitism[22].

Studies exploring species importance across two or more interaction types at a time under a network framework have recently started to emerge[4–6] but are still rare[3]. Earlier work[3] suggested that important plant species might have greater ratio of mutualistic to antagonistic interactions than expected by chance. More recent research presents contradictory results, reporting a positive association between the importance of birds as seed dispersers and pollinators[4], but no association in the importance of bats as frugivorous and nectarivorous[7], or between plants for their mycorrhizal fungi and their frugivores[5]. However, none of these pairwise comparisons accounted for the effect of species abundance as a key driver of interaction frequency and species importance.

We now know that both species abundance and richness have positive and independent effects on ecosystem multifunctionality[23,24], with more abundant species being more important contributors to community functioning[25]. The effect of abundance emerges from neutral processes, where all individuals have an equivalent functional contribution regardless of their species identity[26]. In turn, species importance is the combined result of species' local abundance, which drives the underlying encounter probability between species (the mass action hypothesis), and species' interaction preferences, as determined by morphological, physiological, and ecological traits[27]. 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 from the same community, coupled by a shared set of species at the interface of the

paired networks (Fig. 1A). These networks encompass six distinct interaction types: herbivory, parasitism, seed dispersal, pollination, commensalism, and mycorrhizas (Extended Data Table 1). Each tripartite network had on average 162 species (min.=25; max.=690) and 367 links (min.=56; max.=1414). These networks had on average 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 the two matrices (Extended Data Table 1).

Based on this dataset, we took a meta-analysis approach testing to what extent 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 explored whether any relationship found was driven by (1) species relative abundances, (2) the outcome of the interactions (mutualistic vs antagonistic), or (3) the intimacy of the interactions (temporary vs permanent). We independently quantified species importance for each niche dimension by estimating species strength, a species-level descriptor calculated as the cumulative sum of each species "dependencies" and reflecting each species potential to affect the other trophic level[28]. In this way, species strength is a good indicator of species importance in the community[4,21] and is particularly relevant for being independent from species phylogenetic distances[29–31]. This allowed us to test, for example, if the functional importance of each plant species for pollinators is correlated with their importance for herbivores in an herbivore-plant-pollinator tripartite network (Fig. 1). Finally, performing a meta-analysis of 18 networks and 6 different interaction types allowed us to escape system-specific conclusions and explore general patterns on the multidimensionality of keystone species.

Results

We calculated the Pearson's correlation coefficient between the (log-transformed) species strength for the intermediate species linking the two subnetworks of each tripartite network. 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 Extended Data Table 2 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[27]. This standardization allowed us to recalculate the above correlations based on a new set of “interaction preference matrices” that exclude the effect of the estimated species abundances on interaction frequencies. 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). After accounting for species abundances, the overall correlation of standardized species strength between paired subnetworks was weaker, but still positive and statistically significant (mean Pearson’s r=0.24, z=2.41, p=0.016; Fig. 2, Table 1, and Extended Data Table 2 for individual networks correlations for each).

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

To explore potential sources of such heterogeneity, we classified subnetworks according to their interaction outcome (antagonistic vs. mutualistic) and level of intimacy (permanent vs. temporary). Mean correlations of unstandardized and standardized species strength were consistent across subgroups, even if uncertainty was larger for those combinations of interaction outcome and intimacy represented by fewer networks, being more evident for networks with antagonist or permanent interactions (Fig. 2 and Table 1). Including interaction outcome and intimacy as explanatory variables accounted for virtually no heterogeneity in the correlations of species strength (Table 1 and Extended Data Table 3).

Discussion

Natural communities are bound by multiple types of biotic interactions. Understanding how species and biotic interactions couple ecological processes across multiple functional levels is critical to advance our understanding of ecosystem structure and functioning[32], and for predicting the effects of global change on ecosystem resilience[33]. Our analysis of tripartite networks revealed that species' overall 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 Extended Data Table 3). This means that species that are disproportionately important for a particular ecosystem function, i.e., keystone species, also tend to be important for other functions in the community 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 or 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[23,24]. Under the neutral theory of biodiversity[26], we would expect no significant correlation in species importance across multiple dimensions, beyond that explained by species relative abundances. By calculating species strength based on interaction preference matrices, we were able to estimate and isolate the effect that abundance has on species interaction frequencies. We showed that species abundance indeed contributes to the correlation in species importance across different niche dimensions, as these correlations consistently became weaker after we removed its effect. However, we still found a significant positive signal of species functional importance across multiple interaction networks (Fig. 2, Table 1, Extended Data Table 2, and Extended Data Table 3). This indicates that intrinsic species preferences driven by other (i.e., non-neutral) factors, such as those related to morphological trait-matching[12], physiological constraints[7,34], temporal, and spatial overlap between

interacting species[35,36], and other drivers of foraging behaviour[37] strongly contribute to the functional importance of species across the range of biotic interactions that characterize their full ecological niche. Clarifying the relative contribution of the determinants of species interaction remains a central goal in community ecology[12,38]. Several of these drivers are naturaly associated with species evolutionary and phylogenetic history, such as species size and other morphological traits[12,39], while others are contingent on ecological (e.g., alternative resources, phenological mismatches[40]) and behavioural (e.g., fear landscapes[41]) contraints. Contrary to the effect of species abundances[27] there is still no satisfactory method to isolate the effect of phylogenetic relatedness from species preferences on pairwise interactions matrices[39]. Nonetheless, the correlations found on species strength are generaly assumed to be largely independent from species phylogentic relatedness[29–31].

A likely mechanism underlying species' keystonness across multiple ecological functions might be the existence of important traits that modulate species' interactions patterns across different functional groups. Body size in particular has been shown to affect interaction probabilities of different functional groups, such as seed dispersers, pollinators, or predators and preys[6,39]. Certain plant traits and plant-defence mechanisms can affect interactions with both pollinators and herbivores[42]. 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[43]). Identifying other traits or trait syndromes that regulate species interactions across 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. The fact that this signal was less obvious in networks of mutualistic and temporary interactions is probably related to the lower number of studies available in these groups and thus a lower statistical power (Fig. 2 and Table 1).

The identification of keystone species has long been a central topic in ecology and conservation[2,9]. 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[44]. Our findings also imply that this multidimensionality of keystone species is a general phenomenon that couples distinct ecological functions. Accordingly, the loss of keystone species may intensify trophic cascades and rapid community collapse, as these species can trigger parallel responses across different functions eventually leading to systemic failure[4,11]. On the other hand the benefits of protecting keystone species will likely extend across multiple ecosystem functions, some of which might not be original conservation targets[45]. This suggests 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 and species extinctions[32,46].

It is important to realize that bipartite networks (those focusing on single interaction types) represent an abstraction imposed by sampling constraints. Still, relatively few studies simultaneously quantify multiple interaction types at the same site[3–5]. Therefore, it is 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[12,13,32]. We show that keystone species tend to be disproportionately important across multiple niche dimensions regardless of their abundance, interaction outcome or intimacy. This study represents an important step to explore the multidimensionality of keystone species and its results are still constrained by the number and type of empirical tripartite networks available. The rapid advances on the compilation of more, larger, and more detailed datasets, incorporating multiple ecosystem functions under a unified network framework will likely foster a deeper understanding of how keystone species shape ecosystem structure, function, and resilience.

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Table 1. Results of the meta-analysis of the tripartite networks.

The random model (i.e., model without moderators) includes all studies. The subsequent rows present the models for each combination of interaction outcome and intimacy, each with three combinations of interactions. For full results of the meta-analytical models see Extended Data Table 3. Correlations for which the 95% confidence interval did not overlap zero are given in bold.

	Species strength (original)		**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	

[1]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.

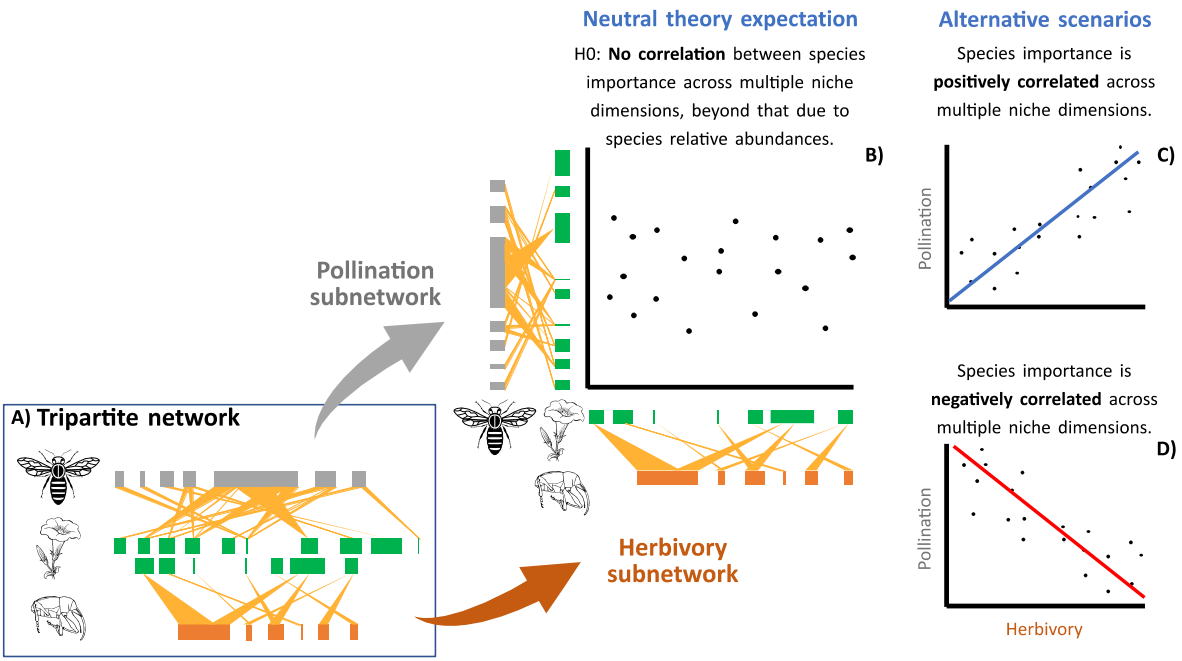

Fig. 1. Conceptual model for the importance of species participating in two ecological functions in a tripartite network.

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, and yellow lines represent interactions between species. The importance of each species in the intermediate level (plants in the present example) can be assessed by calculating species strength[28] after normalizing matrices according to the mass action hypothesis, which accounts for species relative abundances[27]. 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 functions, i.e. keystone species (top right) are equally relevant for both dimensions; and D) species importance is negatively correlated between the two functions, i.e. keystone species are only relevant either for pollination or for herbivory, but not for both dimensions simultaneously. Silhouettes used in this figure sourced from Open Clipart and available under a CC0 1.0 licence.

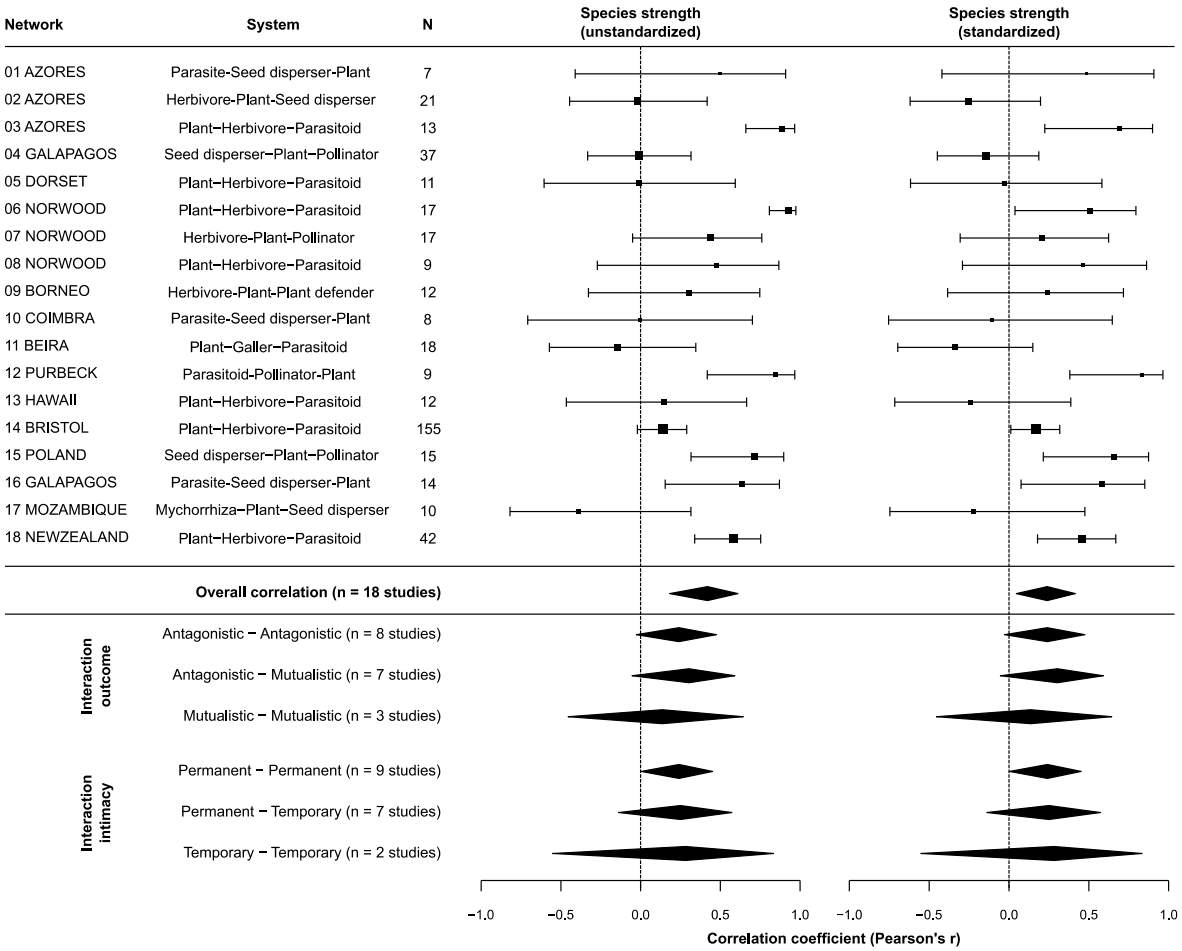

Fig. 2. Forest plot with the results of the meta-analysis.

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 a square at the centre of the 95% confidence interval and its size proportional to **N**. Diamonds represent the overall weighted correlation coefficient and its 95% confidence interval (individual values in Extended Data Table 2).

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 associations (Extended Data Table 1). 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 biological 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 level of intimacy of its subnetworks (Extended Data Table 1), using these as moderators (i.e., variables driving the variation between studies) in a meta-analysis. Interaction outcomes of each subnetwork were classified as either antagonistic or mutualistic, resulting in three combinations of outcomes in the tripartite networks: antagonistic-antagonistic, antagonistic-mutualistic, and mutualistic-mutualistic. Interaction intimacy describes "the degree of physical proximity or integration of partner taxa during their life cycles"[47]. 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)[32,48]. 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

In order to estimate interaction preferences that are independent from species relative abundances, we standardized all network matrices according to the "mass action hypothesis" (following Staniczenko et al.[27]). 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[27]. The networks included in this study were assembled independently for various purposes and by using different sampling methods to quantify interaction frequencies, which are in turn affected by species relative abundances[49,50]. 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 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[51] using the function *GetPreference*[27]. 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 quantified 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 original and standardized subnetworks, we quantified the importance of each species at the interface of the two subnetworks, by calculating a key species-level descriptor, namely species strength[28]. 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[4,21,49,52]. 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 referred to as standardized species strength. This descriptor requires the calculation of the dependence of each species *i*, from a given network level, on each species *j* from the other network level:

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

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*[53].

Meta-analysis

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

To estimate the overall correlation across all tripartite networks we took a meta-analysis approach and estimated the associated variance and 95% confidence intervals. Pearson's coefficients were standardized using Fisher's r-to-Z transformation, which stabilizes the variance of the coefficients[54], and 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[55,56]. In this model, the contribution of each study is weighted by its estimated variance, 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.

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

This results in individual z-values with small variances having greater weights than those with large variances[57]. 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). We then 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[58] 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[58]. 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 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*[59].

Data availability:

Datasets used in this work are available from figshare: https://doi.org/10.6084/m9.figshare.14333198.

Code availability:

R code used to perform the meta-analysis and generate forest plot is available from figshare: https://doi.org/10.6084/m9.figshare.14334038.

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Acknowledgments:

Funding:

ANC was supported by the Portuguese Science Foundation – FCT/MCTES (transitory norm contract DL57/2016/CP1370/CT89).

AT was supported by CGL-2017- 88122-P from the Spanish Ministry of Science.

BR was supported by the ‘Juan de la Cierva Incorporación’ fellowship (Spanish MICIU, IJCI-2017-33475) and the University of Cádiz (UCA/REC17VPCT/2021).
EM, FALN, RH, SRE and ST were supported by the Portuguese Science Foundation – FCT/MCTES (grants PTDC/AAG-REC/4896/2014, SFRH/BD/130942/2017, CEECIND/00092/2017, IF/00462/2013, CEECIND/00135/2017, respectively, and all by grant UID/BIA/04004/2020).
LPS was supported by the Portuguese Science Foundation – FCT/MTCES (CEECIND/02064/2017).
LGC was supported by the Portuguese Science Foundation – FCT/MTCES via the EU Lisbon 2020 program (project EUCLIPO-028360), and by the Brazilian National Council for Scientific and Technological Development (CNPq. Universal 421668/2018-0; PQ 305157/2018-3).

Author contributions:

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.

Competing interests:

Authors declare no competing interests.

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Extended Data for

Tripartite networks show that keystone species can multitask

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Extended Data Table 1 | 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	[60] and Heleno unpublished
02 AZORES	Azores, Portugal	37.794/-25.191	Herbivore-Plant-Seed disperser	94	53	21	165	31x36-41x7	[61]
03 AZORES	Azores, Portugal	37.794/-25.191	Plant-Herbivore-Parasitoid	79	37	13	110	31x36-13x12	[62]
04 GALAPAGOS	Galapagos, Ecuador	-0.738/-89.882	Seed disperser-Plant-Pollinator	390	163	37	1414	84x21-110x212	[63,64]
05 DORSET	Dorset, UK	50.823/-1.830	Plant-Herbivore-Parasitoid	51	25	11	87	25x11-11x15	[65]
06 NORWOOD	Bristol, UK	51.313/-2.321	Plant-Herbivore-Parasitoid	42	19	17	91	19x6-16x16	[44,66]
07 NORWOOD	Bristol, UK	51.313/-2.321	Herbivore-Plant-Pollinator	329	77	17	540	30x28-47x241	[44]
08 NORWOOD	Bristol, UK	51.313/-2.321	Plant-Herbivore-Parasitoid	69	28	9	60	28x30-9x11	[44]
09 BORNEO	Danum Valley, Borneo	4.967/117.800	Plant defender-Herbivore-Plant	89	13	12	180	13x43-13x32	[67]
10 COIMBRA	Coimbra, Portugal	40.217/-8.450	Parasite-Seed disperser-Plant	60	39	8	158	18x6-15x29	[68] and da Silva unpublished
11 BEIRA	Beira Litoral, Portugal	40.221/-8.890	Plant-Galler-Parasitoid	93	31	18	56	31x22-18x40	[69]
12 PURBECK	Isle of Purbeck, UK	50.616/-2.043	Parasitoid-Pollinator-Plant	25	9	9	80	9x12-9x4	[22]
13 HAWAII	Hawaii, USA	23.417/-159.617	Plant-Herbivore-Parasitoid	68	29	12	94	28x32-13x7	[70]
14 BRISTOL	Bristol, UK	51.479/-1.984	Plant-Herbivore-Parasitoid	690	359	155	1312	357x139-157x192	[71]
15 POLAND	Białowieza, Poland	52.824/24.007	Seed disperser-Plant-Pollinator	357	15	15	1220	15x34-15x308	[46]
16 GALAPAGOS	Galapagos, Ecuador	-0.738/-89.882	Parasite-Seed disperser-Plant	114	36	14	241	15x13-16x84	[63] and Heleno unpublished
17 MOZAMBIQUE	Gorongosa, Mozambique	-18.943/34.373	Mycorrhiza-Plant-Seed disperser	107	19	10	202	16x69-16x16	[5]
18 NEW ZEALAND	Nelson-Marlborough, New Zealand	-41.484/173.006	Plant-Herbivore-Parasitoid	204	90	42	502	68x76-42x61	[72,73]

Extended Data Table 2 | 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)

Extended Data Table 3 | 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]**	***r* = 0.24 [0.05, 0.42]**
		QE = 72.403, df = 17	QE = 39.524, df = 17
		p < 0.001	p = 0.002
		I^2 = 80.2%	I^2 = 63.3%
Moderator: Interaction Outcome	Mixed-Effect Model	QE= 70.149, df = 15	QE = 38.092, df = 15
		p < 0.001	p = < 0.001
		I^2 = 80.0%	I^2 = 65.6%
		QM = 0.892, df = 2	QM = 0.327, df = 2
		p = 0.640	p = 0.849
		R^2 = 0.0%	R^2 = 0.0%
	Antagonistic + Antagonistic	***r* = 0.50 [0.08, 0.76]**	*r* = 0.24 [-0.03, 0.48]
		QE = 50.648, df = 7	QE = 16.750, df = 7
		p < 0.001	p = 0.019
		I^2 = 88.8%	I^2 = 65.2%
	Antagonistic + Mutualistic	***r* = 0.41 [0.12, 0.64]**	*r* = 0.30 [-0.05, 0.59]
		QE = 9.788, df = 6	QE = 13.034, df = 6
		p = 0.134	p = 0.043
		I^2 = 38.9%	I^2 = 53.7%
	Mutualistic + Mutualistic	*r* = 0.17 [-0.50, 0.71]	*r* = 0.14 [-0.46, 0.64]
		QE = 9.713, df = 2	QE = 8.309, df = 2
		p = 0.008	p = 0.016
		I^2 = 81.9%	I^2 = 76.0%
Moderator: Interaction Intimacy	Mixed-Effect Model	QE= 71.890, df = 15	QE = 38.862, df = 15
		p < 0.001	p = < 0.001
		I^2 = 80.8%	I^2 = 66.5%
		QM = 0.287, df = 2	QM = 0.001, df = 2
		p = 0.867	p = 0.999
		R^2 = 0.0%	R^2 = 0.0%
	Permanent + Permanent	***r* = 0.45 [0.11, 0.73]**	***r* = 0.24 [0.00, 0.45]**
		QE = 50.655, df = 8	QE = 16.755, df = 8
		p < 0.001	p = 0.033
		I^2 = 86.7%	I^2 = 58.1%
	Permanent + Temporary	*r* = 0.34 [-0.04, 0.63]	*r* = 0.25 [-0.14, 0.57]
		QE = 14.015, df = 6	QE = 14.4219, df = 6
		p = 0.030	p = 0.025
		I^2 = 58.5%	I^2 = 58.6%
	Temporary + Temporary	*r* = 0.39 [-0.44, 0.86]	*r* = 0.28 [-0.55, 0.83]
		QE = 7.221, df = 1	QE = 7.689, df = 1
		p = 0.007	p = 0.006
		I^2 = 86.2%	I^2 = 87.0%