

A Meta-analysis of Plant Interaction Networks Reveals Competitive Hierarchies as well as Facilitation and Intransitivity

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ABSTRACT: The extent to which competitive interactions and niche differentiation structure communities has been highly controversial. To quantify evidence for key features of plant community structure, I recharacterized published data from interaction experiments as networks of competitive and facilitative interactions. I measured the network structure of 31 woody and herbaceous communities, including the intensity, distribution, and diversity of interactions at the species-pair and community levels to determine the generality of competition, winner-loser relationships, and unequal interaction allocation. I developed novel methodology using meta-analysis to incorporate interaction uncertainty into estimates of structural metrics among independent networks. Plant communities were competitive, but intraspecific interactions were sometimes more intense than interspecific interactions. On the whole, interactions were imbalanced and communities were transitive. However, facilitation, balanced interactions, and intransitivity were common in individual communities. Synthesizing network metrics using meta-analysis is an original approach with which to generalize community structure in a systematic way.

Keywords: networks, competition, facilitation, plant communities, meta-analysis, interaction uncertainty.

Introduction

An ecological community, defined as a set of interacting species or individuals connected by the flow of resources or interactions, is well suited to representation as a network, which provides a quantitative estimate of the complexity and structure of the community. Network metrics approximate the general architecture of a certain type of system, meaning that aspects of the structure of complex networks can be summarized by a few key values. Plant communities have recently been evaluated as networks (Soliveres et al. 2015; Godoy et al. 2017; Stouffer et al. 2018), but the net-

work architecture of plant communities across a variety of species combinations and habitats has not been previously characterized. Competition and facilitation are both prominent forces, often operating simultaneously, that structure plant communities (Callaway and Walker 1997). Current understanding about the nature of plant interactions is composed of interpretations from isolated pairwise experiments. With a network approach, it is possible to quantitatively estimate structure at the community level, for example, competition/facilitation intensity, interaction imbalance, community transitivity, and the distribution of species' effects. I developed a meta-analytic approach incorporating interaction uncertainty to synthesize network structural metrics in order to quantitatively estimate plant community structure using experimental studies of woody and herbaceous plant interactions in greenhouses, gardens, and fields.

I determined the prevalence and intensity of competition and facilitation within and among plant communities, interactions linked to community structure and dynamics (Connell and Slatyer 1977; Allesina and Levine 2011; Soliveres et al. 2015). I also determined whether intraspecific interactions were stronger than interspecific interactions in these communities, a phenomenon associated with the maintenance of species richness in coexistence theory. I measured the effects of competitive and facilitative additive indirect interactions in plant communities. In a competitive interaction between two species, competition from a third species may benefit the first species. This phenomenon, indirect facilitation, may be important for the maintenance of species richness in plant communities (Levine 1999; Callaway and Pennings 2000).

I measured interaction imbalance in plant communities using a network approach. Imbalance occurs when one species has a strong effect on the other with little reciprocal effect. Imbalance is expected when plants with different resource-capturing abilities compete (Harper 1977) and can lead to competitive exclusion (Weiner 1990). Scaling up to

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the community level, I estimated whether and to what extent communities are hierarchical, or transitive. In transitive plant communities, species are strictly ranked by their ability to outcompete species of lower rank. Transitivity has been observed in many studies of plant communities (e.g., Miller and Werner 1987; Panetta and Randall 1993; Roxburgh and Wilson 2000), though transitivity ends in competitive exclusion of all but the dominant species in the absence of external forces. Determining whether winner-loser relationships exist at the interaction level (imbalance) or the community level (transitivity) is important for understanding and modeling community dynamics, and deviations from strict winner-loser patterns could promote species coexistence through internal structure rather than external forces (Kerr et al. 2002; Laird and Schamp 2006, 2008; Allesina and Levine 2011).

Adopting a network framework to describe plant communities allows for structural comparisons with other real-world (empirical rather than theoretical) networks. For example, trophic networks (Dunne et al. 2002) and mutualistic networks (Jordano et al. 2003), as well as nonbiological networks like the World Wide Web (Adamic and Huberman 2000), have distributions of node effects characterized by a few nodes with strong effects and many nodes with weak effects on the system (they are right skewed). In many networks, this pattern is even more exaggerated (they are heavy tailed). Also, the diversity of plant interactions, or the uniformity of species' effects, can be compared to other networks as weighted connectance. This metric is related to measures of the uniformity of biomass flux in trophic networks (Bersier et al. 2002) or the degree of specialization in mutualistic networks (Blüthgen et al. 2006, 2007), in which species' effects can be uniform (generalists) or nonuniform (specialists). Plant communities might be expected to have higher-weighted connectances relative to previously studied networks, as plants likely compete with all neighboring species to some degree, given that all plants share similar resource requirements.

I conducted a systematic review to identify greenhouse, garden, and field experiments that have measured pairwise interactions in woody and herbaceous plant communities. I used plant performance data from each study to create plant interaction networks and calculate network metrics among all studies as well as grouped by experimental design and community characteristics. Network metrics were combined using meta-analytic methods that incorporate interaction uncertainty. By synthesizing plant interaction networks, I predicted that (1) species' effects on the community were competitive on average; (2) species' indirect effects on the community were less competitive than their direct effects; (3) plant communities were structured by winner-loser relationships, in which reciprocal interactions were imbalanced and communities were transitive; (4) plant interaction

networks had higher-weighted connectance than currently described networks; and (5) the distributions of interactions were right skewed, or characterized by a few strongly interacting species and many weakly interacting species.

Methods

Systematic Review

I searched the literature for studies measuring pairwise interactions in plant communities using the Web of Science database on March 3, 2016, and refined the search to English manuscripts in relevant research areas, yielding 2,032 studies (for the search phrase and PRISMA flow diagram, see the appendix and fig. A1; the appendix, including figs. A1–A3, is available online). I first screened titles and abstracts and then full articles, excluding studies if they failed to meet any of the following inclusion criteria: (1) the study includes at least three species, (2) the study species are seed-bearing plants, (3) all pairwise interactions that occurred in the community were measured, (4) plant performance measurements in the presence of neighbors were reported, and (5) the study includes new data. I found 30 studies with sufficient data and data from my own fieldwork (methods in the appendix) to include in the meta-analysis. These 31 studies ranged in species number from three to 10 species, with a mean of 4.6 species.

Constructing Networks from Extracted Data

In plant interaction networks, nodes are species and connections (edges) are interactions. Edges are the intensity of the interaction of neighbor species j on target species i . For each study, I used extracted data on the performance of plants (usually biomass) in pairwise combinations to calculate interaction indexes that represented edge intensities (m_{ij}). In order to be able to compare networks with diverse species, locations, and experimental designs, I selected a single interaction index to calculate edges in all networks. Relative interaction intensity (RII) is an index with desirable properties: it is symmetric around zero, bounded between -1 and 1 , and can be used to quantify both competition and facilitation (Armas et al. 2004). Negative values of RII represent competition, while positive values of RII represent facilitation. In 27 of the 31 networks, RII was calculated using plant performance of target individuals in interspecific mixtures relative to performance in monocultures (table 1). For studies that included true control treatments with a single target individual and no neighbors ($n = 15$), RII was calculated using plant performance of target individuals in mixtures/monocultures relative to the true control treatment (table 1). For 11 studies, RII was calculated using both methods (additional details in the appendix). The interpretation of competition and facilitation is

Table 1: Formulae for the relative interaction index (RII)

	Formula	Variables
Calculated for studies with monoculture treatments ($n = 27$)	$m_{ij} = \frac{P_{mix_{ij}} - P_{mono_{ii}}}{P_{mix_{ij}} + P_{mono_{ii}}}$	P = plant performance; mono, mix = plants growing in monoculture or mixture, respectively
Calculated for studies with true control treatments only ($n = 15$)	$m_{ij} = \frac{P_{mix_{ij}} - P_{ctrl_i}}{P_{mix_{ij}} + P_{ctrl_i}}$	ctrl = plant growing alone

Note: RII is calculated as the interaction intensity (m_{ij}) for each plant interaction in the networks, where m_{ij} is a measure of the effect of species j on species i .

different between the two types of control treatment; that is, with a monoculture control, facilitation means that the target species had increased performance in an interspecific combination relative to an intraspecific combination, while with a true control, the target species had increased performance in an interspecific combination relative to growing alone. On each network, I calculated a variety of metrics, which characterize the structure of the community in ways comparable both within plant communities and across other types of communities.

Network Metrics

Out-strength is a measure of a species' effect on other species in the community, and in-strength is a measure of the community's effect on a species. In-strength is calculated as the sum of all direct interactions from all other species in a network toward species i ($\sum_{j \neq i} m_{ij}$) and out-strength as the sum of all interactions from species i toward all other species ($\sum_{j \neq i} m_{ji}$). Competitive strengths are less than zero and facilitative strengths greater than zero. I calculated the mean strength for all species in each network, standardizing by species richness, to quantify the net magnitude of the interactions in each community.

I also calculated mean indirect interaction effects—or the average of the direct effects of neighbor species on target species weighted by the interactions one step removed from the direct interaction—assuming no higher-order interactions (see appendix). Interactions between species do not occur in isolation, and indirect effects give an estimate of how other interactions in the network could influence direct interactions. I calculated indirect effects on all species in a network and the mean indirect effect for each network.

I quantified the imbalance of interactions in plant communities as the difference in interaction strength between reciprocal interactions, or the absolute difference between

m_{ij} and m_{ji} . Larger differences represent more imbalanced interactions (the maximum possible imbalance is equal to the range of RII, 2.0). I then calculated the mean of all interaction imbalances in a network. I also measured the mean percentage of asymmetric interactions in each network (sensu Keddy and Shipley 1989), where an asymmetric interaction occurs if $m_{ij} > 0$ and $m_{ji} < 0$, implying that species i —which experiences stronger intraspecific competition relative to interspecific competition with species j —benefits from the interaction, while species j —which experiences stronger interspecific competition with species i relative to intraspecific competition—is harmed by the interaction. Asymmetry was calculated only for networks with interactions measured relative to monoculture.

I quantified transitivity in each network using the relative intransitivity (RI) index (Laird and Schamp 2006). In a transitive network, species can be ranked by their ability to outcompete all lower-ranking species, or form a hierarchy. In an intransitive network, species deviate from a hierarchy. To calculate this index, the network is converted to a binary competitive outcomes matrix, where a 1 means the column species outcompetes the row species. The variance of column sums from the matrix is then calculated. Transitive networks have high variance (one column species outcompetes all row species, one outcompetes all but one, etc.), and intransitive networks have low variance. From the competitive outcomes matrix, the RI index is calculated as $1 - (\text{var}_{\text{obs}} - \text{var}_{\text{min}}) / (\text{var}_{\text{max}} - \text{var}_{\text{min}})$, where var_{obs} is the variance of column sums, and var_{min} and var_{max} are the minimum and maximum possible variances of column sums of a competitive outcomes matrix with the same number of species (Laird and Schamp 2008). An RI index of 0 describes a completely transitive community, and 1 describes a maximally intransitive community.

I calculated weighted connectance in each network, the density of edges each weighted by the Shannon diversity of interactions per species. In networks with the same density of interactions, weighted connectance is higher if each species' interactions are more uniform in intensity. Weighted connectance was calculated as in Bersier et al. (2002; see appendix). Weighted connectance was calculated on networks consisting of the absolute value of interaction intensities, as well as on networks considering only competitive interactions (i.e., removing facilitative interactions from each network) and networks considering only facilitative interactions.

Additional analyses are detailed in the supplemental PDF, including determining the difference in species' effects on the community between invasive and native species, species with C_4 and C_3 photosynthetic pathways, and nitrogen-fixing and non-nitrogen-fixing species; the conservation of species' roles across multiple communities; network structure under different abiotic conditions; and whether interactions in networks are additive.

Meta-analysis

To generalize the structure of plant communities, I combined the network metrics from each network using a novel meta-analytic approach. In this approach, I incorporated multiple levels of variation from within studies and among studies. From each study, I extracted an estimate of variance for the metric of plant performance in each pairwise plant species interaction. For two studies that were missing estimates of variation in plant performance, I imputed the standard deviation from studies with complete data using a Bayesian gamma generalized linear model (methods in appendix).

As I used mostly published data in this study, I did not have the raw data necessary to construct a likelihood function of plant performance. Instead, I used the estimates of the mean and variance of plant performance from the study to generate simulated data (Bolker et al. 2013; Gimenez et al. 2014). Plant performance of species i interacting with species j , P_{ij} , was modeled as a gamma variate. Shape (α) and rate (τ) were estimated using moment matching with the sample mean and variance of plant performance extracted from the study. Simulations were conducted in the Markov-chain Monte Carlo (MCMC) sampling software JAGS (Plummer 2003), simulating 1,000 plant performance values for each pairwise interaction. Increasing the simulation size did not appreciably change the results.

To estimate the variance of network metrics, the simulated data were used in a Bayesian bootstrap (Rubin 1981) implemented with the R package *bayesboot* (Bååth 2016) to generate the posterior probability distribution of the network metric. The posterior weights of the simulated data were uniform Dirichlet distributed with the same number of dimensions as the sample size from the study. Bayesian bootstrap samples weighted by probabilities from the uniform Dirichlet distribution are nonparametric approximations of the distribution of the network metric. The bootstrapped plant performance data were used to calculate RIIs for pairwise interactions, forming a bootstrapped network of the interactions in the community. I then calculated all network metrics (mean in-strength and out-strength, transitivity, etc.) on the bootstrapped network. This was iterated 10,000 times to create a bootstrapped distribution of each network metric. The variance for each metric was estimated using the variance of the bootstrapped distribution.

I fit Bayesian random effects normally distributed meta-analytic models for each network metric, where estimates from each network were pooled toward a common mean. I used noninformative priors; the prior for the grand mean effect size was normally distributed, centered at zero with a precision of 0.001, and the prior for among-network precision was gamma distributed with shape and rate of 0.001. Groupwise meta-analyses were also fit, with separate means

for each experimental setting (greenhouse, garden, or field), habitat (communities from grassland habitats vs. all other habitats), growth habit (all species herbaceous or at least some species woody), and plant age (all juveniles or at least some adults). For groupwise models, the noninformative priors for each mean were normal distributions centered at zero with a precision of 0.001. Models for metrics RI and weighted connectance had truncated normal priors for mean effect size, bounded between 0 and 1.

All models were run with MCMC sampling in the program JAGS using the *R2jags* package (Su and Yajima 2015) for R version 3.3.1 (R Core Team 2015), with three parallel chains of 500,000 draws from the posterior, discarding the first 50,000 as burn-in and sampling every 10 iterations. (Code for running all analyses is available in a supplementary zip file.)¹ Convergence was determined using a Gelman-Rubin diagnostic <1.1 and effective sample size $>1,000$ (Gelman and Rubin 1992). Effect sizes were considered significant if 95% credible intervals (CRIs) did not include zero, and groupwise differences in effect size were considered significant when 95% CRIs did not overlap. A Bayesian principal components analysis was performed on standardized mean estimates of network metrics from all networks using the package *bPCA* (<https://github.com/petrkeil/bPCA>) with noninformative priors, normal distributions for means, and an inverse Wishart distribution for the covariance matrix. In this method, the standardized data are fit to a multivariate normal distribution, and the eigenvalues, scores, and loadings are estimated given the covariance matrix from the multivariate normal distribution.

Distributions of Interactions

I fit symmetric/skewed and light-tailed/heavy-tailed models to the distributions of in-strengths and out-strengths. As the networks in this study generally had few species, I fit the distributions of in-strengths and out-strengths only for networks with five or more species. In-strengths and out-strengths for each network were fit to normal, exponential, lognormal, and Pareto distributions (the Pareto is a power law distribution). The normal distribution is symmetric with light tails, the exponential distribution is right skewed with light tails, and the lognormal and Pareto distributions are right skewed with heavy tails. The Pareto distribution has heavier tails relative to the lognormal distribution. For location parameters, noninformative normal priors centered at 0 with a standard deviation of 10^6 were used, and for shape and scale parameters, noninformative uniform priors with bounds between -10^6 and 10^6 or 0 and 10^6 were used. Models were run using the same MCMC

1. Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

methods. I validated models using posterior predictive checks, simulating data with the estimated parameter values from the posterior distributions for each fit, and comparing test statistics (mean, median, 90th percentile) from the simulated data with those estimated from the observed data. Model selection was performed using the widely applicable information criterion (WAIC) in the R package *loo*, which measures model fit according to information theory, penalizing for the number of parameters, and is consistent with a Bayesian framework (Watanabe 2010; Vehtari et al. 2015).

Results

The 31 networks included in the meta-analysis measured 558 interactions among 114 unique species from 30 families. Species in networks were overwhelmingly herbaceous (23 networks) and perennial (22 networks). Study sites were generally in the United States and Western Europe, though there were several studies outside of this region (fig. A3). On average, experiments lasted 13 months. Data for all networks are deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.1sm06sp>; Kinlock 2019). There were no significant groupwise differences in any comparison (habitat, experiment setting, growth habit, or plant age) for any metric, as 95% CRIs overlapped, though there were nonsignificant patterns in many cases. All estimates from the meta-analysis are in table S1 (tables S1, S2 are available in the supplemental PDF).

Direct Interactions

Mean strength among networks where interactions were measured relative to true control treatments ($n = 15$) was significantly negative, meaning that species had competitive effects on other species on average (grand mean [95% CRI] = -0.16 [$-0.23, -0.09$]; fig. 1A, open square). With a true control, competition is defined as reduced performance in the presence of another species relative to growing alone. Facilitative interactions ($m_{ij} > 0$) were observed in nine of the true control networks, and among these, four networks had mean strengths with 95% CRIs that overlapped zero (fig. 1B). Among networks where interactions were measured relative to monoculture ($n = 27$), interspecific interactions were not significantly greater or less than intraspecific interactions, though on average, mean strength among networks where interactions were measured relative to monoculture was negative (interspecific $>$ intraspecific, -0.04 [$-0.10, 0.02$]; fig. 1A, closed square). Individually, many networks did have significantly negative (seven networks) or positive (intraspecific $>$ interspecific; four networks) mean strengths (fig. 1B). Among studies where networks were calculated using both a true control and a monoculture control ($n = 11$), there were four cases in which communities were

competitive on average, but intraspecific competition was stronger than interspecific competition. Networks measured in greenhouses were more competitive on average compared to those in fields, and networks of grassland species were more competitive on average relative to networks with species from other habitats. Networks with herbaceous species had more competitive species on average than those including woody species.

Indirect Interactions

Mean indirect effect among networks where interactions were measured relative to true control treatments was significantly facilitative (0.18 [$0.07, 0.29$]; fig. 2A). However, mean indirect effect among all networks with interactions measured relative to monoculture was not significantly different from zero (-0.06 [$-0.17, 0.05$]). Many individual networks had significantly positive or negative mean indirect effects (fig. 2B). Networks with grassland species had more facilitative mean indirect effects than those with species from other habitats. Among networks with interactions measured relative to true control treatments, networks with herbaceous species had more facilitative mean indirect effects compared to those with woody species, while the reverse was true for networks with interactions measured relative to monocultures.

Interaction Imbalance

Overall, interactions were imbalanced, meaning that the mean difference in reciprocal RII was high relative to the maximum interaction intensity (0.39 [$0.29, 0.49$]; maximum imbalance is 2.0; fig. 3A). Interactions in networks including adults were more imbalanced than in networks of juveniles, and interactions in networks with grassland species were less imbalanced than with nongrassland species. Imbalance was weaker among networks with interactions measured relative to a true control (0.26 [$0.18, 0.35$]). Looking at the percentage of interaction asymmetry in networks (where asymmetric interactions are defined as $m_{ij} > 0$ and $m_{ji} < 0$), most networks had a moderately high percentage of asymmetric interactions, though some had a very high or very low percentage (three networks $> 90\%$, four networks $< 20\%$ asymmetric interactions; fig. S1 [figs. S1–S12 are available in the supplemental PDF]). The posterior distribution for the grand mean percentage of asymmetric interactions among networks was flat and could not be reliably estimated.

Community Transitivity

Communities were transitive on average, with RI near 0 (0.01 [$0, 0.02$]; fig. 4A). However, many networks were not completely transitive, and nearly all networks showed some

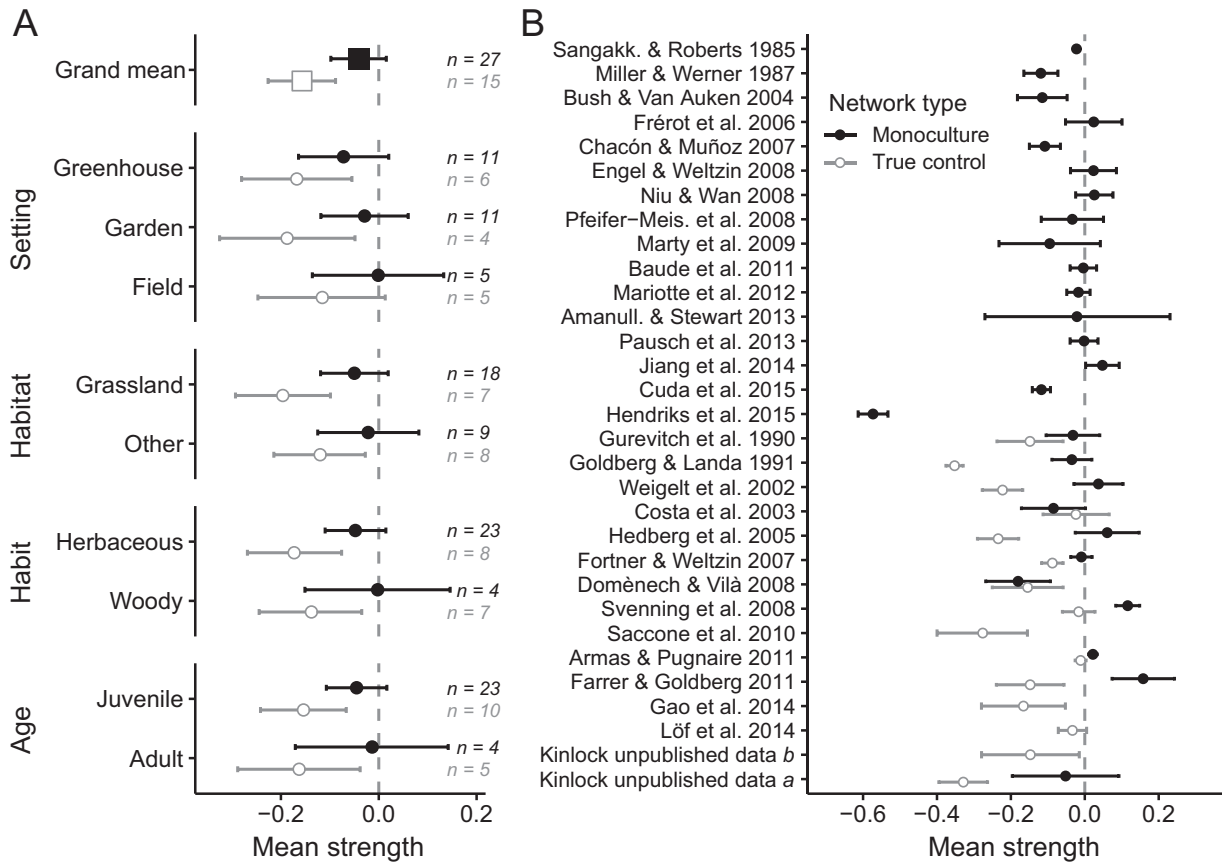


Figure 1: Mean strength of interactions among and within all networks. *A*, Among-network mean strength estimated from meta-analysis. Separate analyses were run using networks with interactions measured relative to monoculture controls (closed shapes, black lines) or true controls (open shapes, gray lines). Models of mean strength were fit using the entire data sets (squares), as well as groupwise, by experiment setting, habitat, growth habit, and plant age. Mean strength of interactions and 95% credible intervals (CRIs) are shown. *B*, Forest plot of mean strength for each network. Study-level effect sizes for network metrics in Bayesian random effects hierarchical meta-analyses are shown, with means and 95% CRIs. Estimates using networks with interactions measured relative to true control treatments are shown with gray, open circles.

variation in RI (fig. 4B). Networks with true controls were less transitive (0.05 [0, 0.16]). Networks including woody species were less transitive relative to networks with only herbaceous species, and networks including adults were less transitive than those with only juveniles. Networks with non-grassland species were less transitive than networks with grassland species.

Weighted Connectance

Weighted connectance among all networks was high (0.62 [0.58, 0.66]; maximum weighted connectance is 1.0; fig. 5A). Weighted connectance was lower among networks with interaction intensities measured relative to true controls (0.59 [0.48, 0.74]). Weighted connectance was higher in networks with herbaceous species than in networks including woody species, and weighted connectance was higher in networks

with grassland species compared to those with nongrassland species.

For most networks with interactions measured relative to monoculture, weighted connectance of networks of competitive and facilitative interactions was similarly high (competitive weighted connectance = 0.50 [0.44, 0.56], facilitative = 0.47 [0.38, 0.54]; fig. S2A). However, for networks with interactions measured relative to a true control, competitive weighted connectance was usually much higher than facilitative weighted connectance (competitive weighted connectance = 0.54 [0.08, 0.94], facilitative = 0.14 [0.01, 0.26]; fig. S2B). Networks with species from nongrassland habitats, networks including woody species, and networks from field experiments had lower competitive weighted connectance and higher facilitative weighted connectance compared to networks with grassland species or herbaceous species or networks from greenhouse/garden experiments.

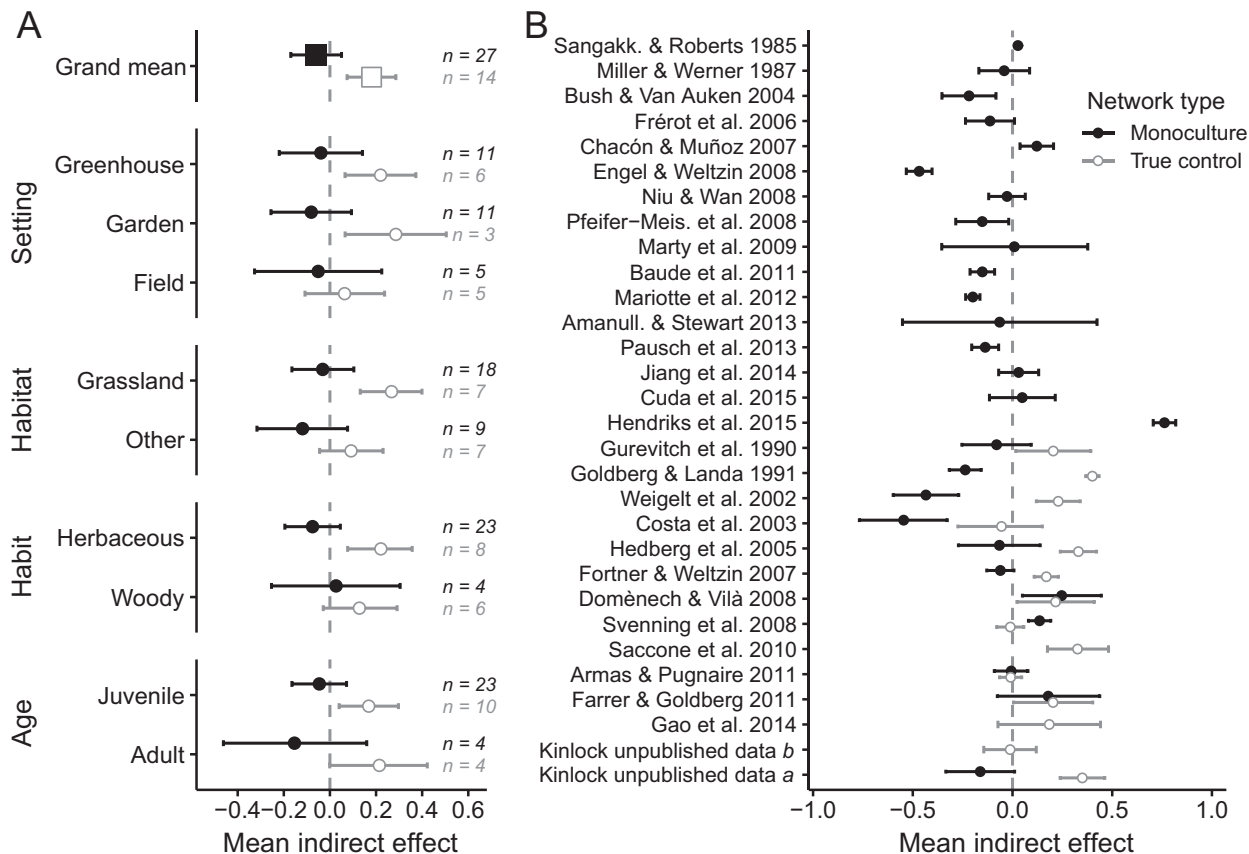


Figure 2: Mean indirect effects among and within all networks. *A*, Among-network mean indirect effect estimated from meta-analysis. *B*, Forest plot of mean indirect effect for each network.

Distributions of Interactions

In general, the distributions of in-strengths in networks were skewed but not heavy tailed (figs. S7, S8). While the Pareto distribution, a heavy-tailed distribution, was a good fit for distributions of in-strengths and out-strengths in five networks according to comparisons of mean WAIC, these were not good fits based on visual assessment, the uncertainty in WAIC, and posterior predictive checks (table S2). In particular, the Pareto distribution underestimated the medians of the empirical strength distributions, and both heavy-tailed distributions overestimated the tails. The exponential distribution also underestimated the medians of the strength distributions. The exponential distribution was a good fit to distributions of in-strengths in nine networks, the lognormal in three networks, and the normal in two networks. There was less of a clear pattern for distributions of out-strengths; the exponential distribution was a good fit in five networks, the lognormal in four networks, and the normal in three networks. Similar patterns emerged when looking at distributions based on strengths of interactions relative to true con-

trol treatments, although distributions were more symmetric (fit well by a normal distribution; figs. S9, S10).

Discussion

Competition, measured as decreased performance in the presence of another individual, was the predominant force in plant communities, similar to what has been found in other syntheses (Connell 1983; Gurevitch et al. 1992). However, the intensity of interspecific competition was not significantly greater than or less than intraspecific competition. In several networks where competition was dominant, intraspecific competition was stronger than interspecific competition. This is a potential stabilizing force in communities that can promote coexistence by allowing species to increase in abundance when rare. Also, facilitation, or increased performance in the presence of another species, was observed in many individual networks. While facilitation has been found to predominate in stressful environments, for example, alpine or arid habitats (Bertness and Shumway 1993; He et al. 2013), I found evidence of facilitation even among species

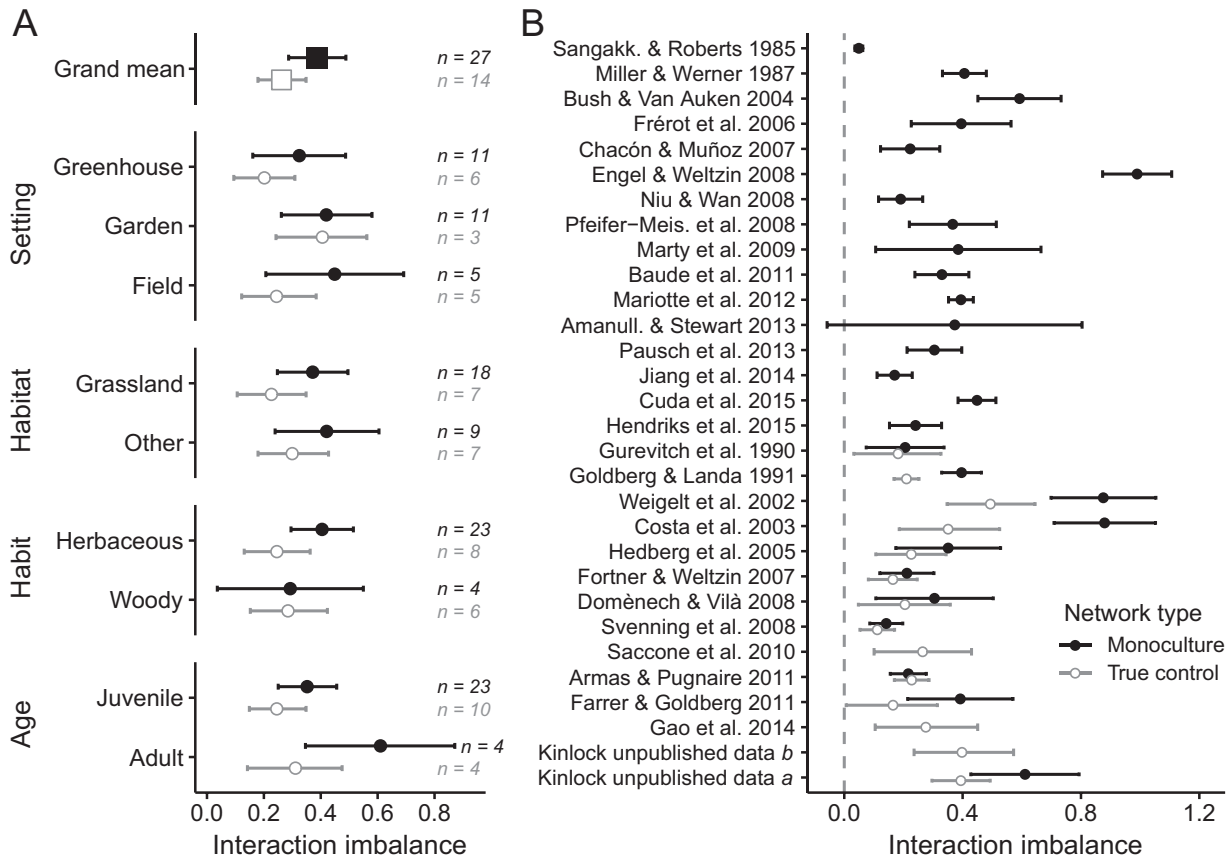


Figure 3: Interaction imbalance, measured as the absolute difference in interaction intensity for reciprocal interactions, among and within all networks. *A*, Imbalance estimated from meta-analysis. *B*, Forest plot of imbalance for each network.

from nonextreme habitats such as grasslands. By using a network approach, I was able to quantify interactions at the community level (species' effect on the community and vice versa), rather than considering pairwise interactions independently. A network approach also allows for comparisons of species' competitive effects given certain characteristics, and I found that, on average, species have less competitive effects on invasive species than on native species and that nitrogen-fixing species have more facilitative effects on other species relative to non-nitrogen-fixing species (fig. S9).

I found interactions in these plant communities to be somewhat imbalanced relative to the intensity of interactions in the networks overall. This is similar to what has been found in a review and a synthesis assessing the imbalance of interactions in communities (Connell 1983; Keddy and Shipley 1989). However, interaction imbalance varied greatly among individual networks, some of which had more balanced interactions. Also, the percentage of asymmetric interactions, or interactions where species *i* benefits and species *j* does not ($m_{ij} > 0$ and $m_{ji} < 0$), was below 50% in eight of 27 networks. While imbalance describes pairwise

winner-loser relationships, transitivity describes winner-loser relationships at the scale of communities. This relationship between imbalance and transitivity was supported by the first principal component (PC) in a principal component analysis of network metrics, explaining 45.6% of the variance, which separated networks that were more imbalanced and transitive from those that were more balanced and intransitive (fig. S8; mean loadings for RI = -0.36, imbalance = 0.64). In general, these results suggest that plant communities are transitive, similar to Keddy and Shipley's (1989) synthesis of eight plant communities and Godoy and colleagues' (2017) analysis of 816 interaction triplets in a plant community. However, as with imbalance, several individual networks were intransitive, which has, in one study, been reported to be frequent in plant communities (Soliveres et al. 2015). Intransitivity and facilitation, both community-stabilizing forces, were associated in the second PC, which separated networks that were more facilitative and intransitive from competitive and transitive networks (fig. S8; 26.8% variance explained, mean loadings for RI = 0.42, strength = 0.64).

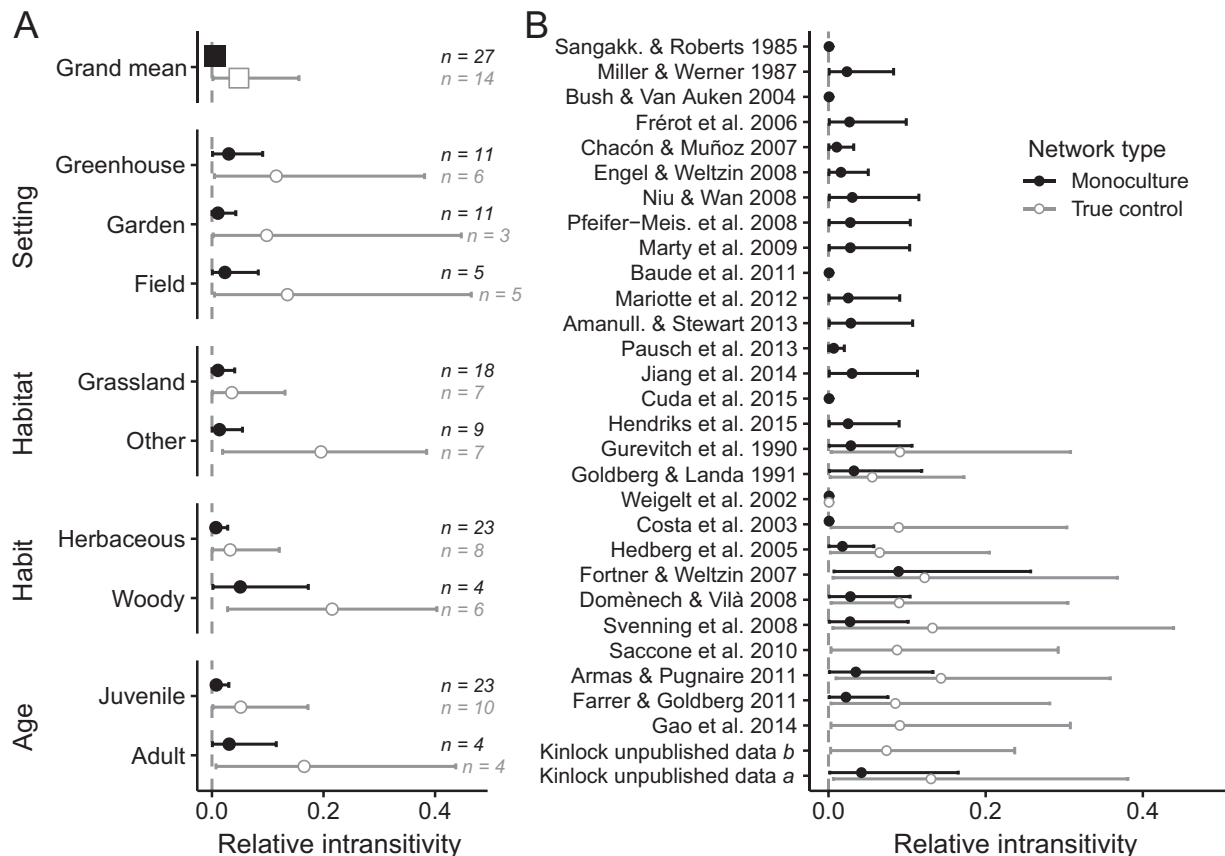


Figure 4: Relative intransitivity (RI), measured as the RI index, among and within all networks. More transitive networks (closer to zero) are more hierarchical. *A*, RI estimated from meta-analysis. *B*, Forest plot of RI for each network.

Plant interaction networks have higher weighted connectance compared to previously characterized ecological networks, which have approximately ranged from 0.02 in a plant-herbivore network (Macfadyen et al. 2009) to 0.2 in a plant-pollinator network (Power and Stout 2011). This is partly because of the small size and the density of interactions in these networks, which results from measuring all combinations of pairwise interactions that occur in the community. However, strong weighted connectance also implies more uniform distribution of interactions in plant communities. Competitive interactions were less uniform in networks with species from nongrassland habitats, networks including woody species, and networks from field experiments, compared to networks with grassland species or herbaceous species or networks from greenhouse/garden experiments.

Ecological studies of species interactions have classically been conducted in grassland communities with herbaceous plants, because these communities are well mixed, with little vertical structure and relatively short-lived species. However, one might expect species in a grassland community to be more competitive, with interactions more imbalanced

and more transitive compared to those in other habitats, because when sharing limited resources in a relatively undifferentiated habitat, small differences in resource uptake lead to imbalanced interactions and, at the community level, transitivity (Harper 1977; Weiner and Thomas 1986; Keddy and Shipley 1989). Indeed, grassland communities were more competitive on average and were more transitive relative to other communities, though interaction imbalance was not different. Additionally, facilitation and intransitivity were more common in plant communities including woody species, adult individuals, and species from nongrassland habitats such as forests, estuaries, or deserts. This suggests that characterizing interactions in nongrassland communities could reveal a higher frequency of structural features that promote coexistence.

I found that strengths in plant interaction networks were best fit by right-skewed, light-tailed distributions (i.e., exponential). Real-world networks tend to be best fit by right-skewed distributions, indicative of a few nodes with many, strong interactions and most nodes with few, weak interactions. However, some of the networks did have good fits to

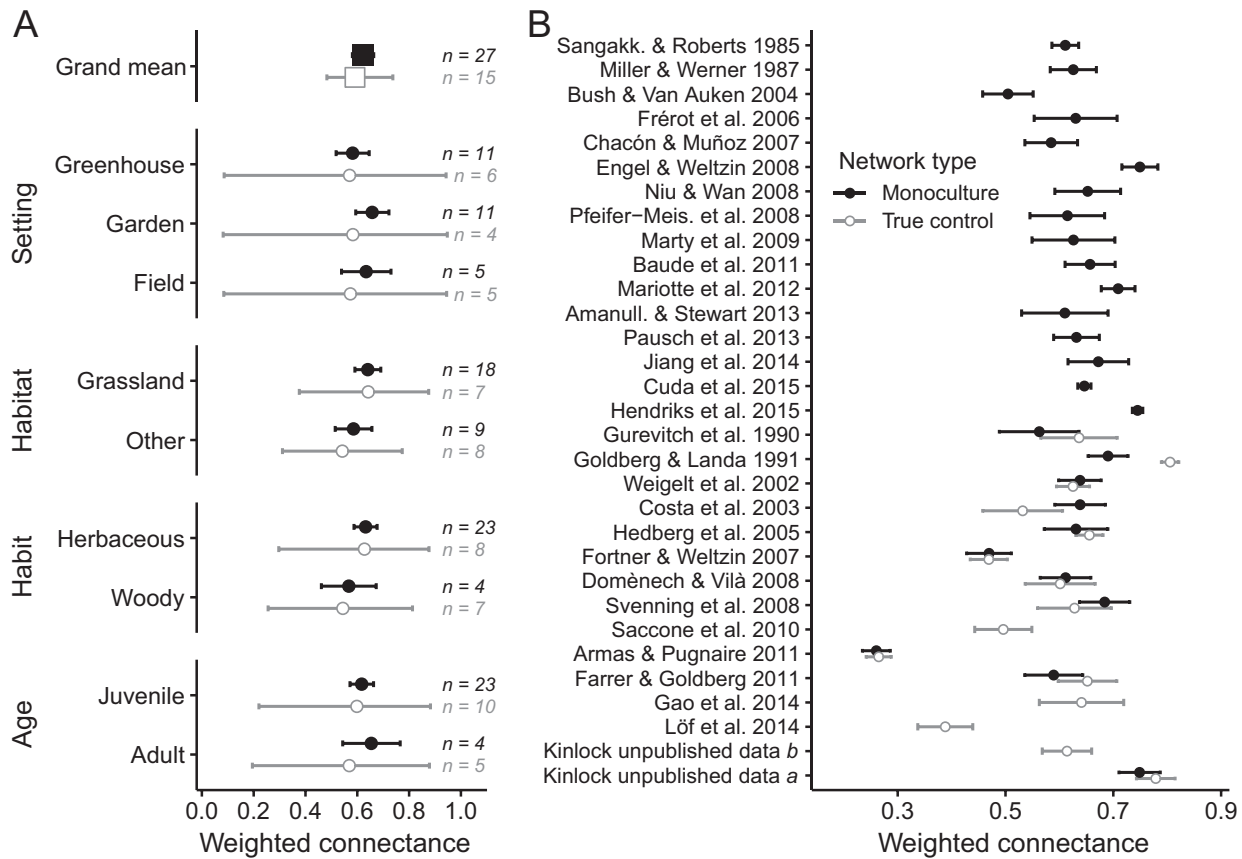


Figure 5: Weighted connectance among and within all networks. *A*, Weighted connectance estimated from meta-analysis. *B*, Forest plot of weighted connectance for each network.

a symmetric distribution, a characteristic of randomly generated networks, possibly because experiments tend to focus on the most abundant species in the community. Heavy-tailed interaction distributions (e.g., lognormal, Pareto) are apparent in many types of networks; power law distributions provide a good fit to distributions in networks of airline flights, scientific authorship (Barrat et al. 2004), and mutualistic ecological networks (Gilarranz et al. 2012). However, in a primate social network (Kasper and Voelkl 2009) and in a synthesis of trophic networks (Dunne et al. 2002), species' effects were right skewed but not heavy tailed, similar to what I found in plant communities. In a plant community, it is probably unlikely for very few species to be able to take a huge portion of resources from a limited pool, even if the networks included more species. Therefore, quantitative ecological networks like plant interaction networks may be fundamentally different from other types of networks that are not limited by resources (Stumpf and Porter 2012).

I have developed a meta-analytic method to incorporate within-study and among-study variation into network struc-

ture, and there was clearly a great deal of variation in all of the network metrics I analyzed. There have been syntheses of ecological networks in which the researchers assess structure across multiple networks in order to make generalizations about a certain type of community (Dunne et al. 2004; Vázquez et al. 2005; Olesen et al. 2007; Gilarranz et al. 2012; Schleuning et al. 2014); however, these syntheses do not incorporate interaction uncertainty/variability. Because variation is intrinsic to ecological communities, ignoring variability in syntheses of network metrics may give misleadingly precise estimates.

This study, as with all ecological meta-analyses, is limited by differences in experimental design, species composition, and abiotic conditions. It is nevertheless useful and informative to combine studies to be able to generalize across communities as well as to understand the sources of variation in effect size. Studies conducted in greenhouses, for example, had more competitive interactions than studies in gardens or in the field, although their networks were not more transitive or more imbalanced. Network structure

proved to be relatively resilient to different abiotic conditions, including nutrient availability and temperature; and in cases where the same species was included in different networks, species' effects on the community were sometimes, though not always, consistent across different studies (figs. S10, S11).

How well the networks in this study approximate plant communities in nature is unclear; in particular, the plant interaction networks represented here are small, with 10 or fewer species. It is challenging to measure plant interactions in larger communities, because the number of experimental treatments required increases factorially with species richness. To increase network size, interactions could be estimated from observational rather than experimental data, though there are trade-offs with that approach, for example, assuming that interactions alone drive the patterning of species as well as assuming that the type of interaction (competition or facilitation) is known a priori. In this study, there were no strong correlations between network size and mean strength, indirect effect, or imbalance (all Pearson's $r < \pm 0.3$). However, intransitivity was weakly positively correlated, and weighted connectance was weakly negatively correlated with network size; therefore, including more species could influence network structure. Future studies characterizing larger networks in plant communities could provide additional evidence of potential stabilizing forces that promote coexistence (e.g., intransitivity), though some evidence of these forces was also apparent in the small networks analyzed here.

Conclusion

I reinterpreted plant communities from the literature and my own fieldwork as networks of competitive and facilitative interactions and synthesized metrics of network structure while accounting for interaction variability. Plant interaction networks were competitive on average, and interactions and communities were characterized by patterns of clear winners and losers, as interactions were imbalanced and communities were transitive. However, facilitative interactions, balanced interactions, and intransitivity were present in some communities, particularly communities that included woody species and adult individuals. Networks with more intransitivity, facilitation, and balanced interactions separated from transitive networks with more competition and interaction imbalance. The distribution of strengths in plant communities was skewed but not heavy tailed, a pattern similar to other ecological networks with limited resources but differing from many other real-world networks. By synthesizing structural metrics of multiple plant interaction communities using meta-analysis, it was possible to make broad, quantitative generalizations about the nature of interactions in plant communities.

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Literature Cited

- Adamic, L. A., and B. A. Huberman. 2000. Power-law distribution of the World Wide Web. *Science* 287:2115.
- Allesina, S., and J. M. Levine. 2011. A competitive network theory of species diversity. *Proceedings of the National Academy of Sciences of the USA* 108:5638–5642.
- Amanullah and B. A. Stewart. 2013. Shoot:root differs in warm season C_4 -cereals when grown alone in pure and mixed stands under low and high water levels. *Pakistan Journal of Botany* 45:83–90.
- Armas, C., R. Ordiales, and F. I. Pugnaire. 2004. Measuring plant interactions: a new comparative index. *Ecology* 85:2682–2686.
- Armas, C., and F. I. Pugnaire. 2011. Plant neighbour identity matters to belowground interactions under controlled conditions. *PLoS ONE* 6:e27791.
- Bååth, R. 2016. bayesboot: an implementation of Rubin's (1981) Bayesian bootstrap. R package version 0.2.1. <https://CRAN.R-project.org/package=bayesboot>.
- Barrat, A., M. Barthelemy, R. Pastor-Satorras, and A. Vespignani. 2004. The architecture of complex weighted networks. *Proceedings of the National Academy of Sciences of the USA* 101:3747–3752.
- Baude, M., J. Leloup, S. Suchail, B. Allard, D. Benest, J. Méridet, N. Nunan, I. Dajoz, and X. Raynaud. 2011. Litter inputs and plant interactions affect nectar sugar content: plant interactions and nectar content. *Journal of Ecology* 99:828–837.
- Bersier, L.-F., C. Banašek-Richter, and M.-F. Cattin. 2002. Quantitative descriptors of food-web matrices. *Ecology* 83:2394–2407.
- Bertness, M. D., and S. W. Shumway. 1993. Competition and facilitation in marsh plants. *American Naturalist* 142:718–724.
- Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. Measuring specialization in species interaction networks. *BMC Ecology* 6:9.
- Blüthgen, N., F. Menzel, T. Hovestadt, B. Fiala, and N. Blüthgen. 2007. Specialization, constraints, and conflicting interests in mutualistic networks. *Current Biology* 17:341–346.
- Bolker, B. M., B. Gardner, M. Maunder, C. W. Berg, M. Brooks, L. Comita, E. Crone, et al. 2013. Strategies for fitting nonlinear ecological models in R, AD Model Builder, and BUGS. *Methods in Ecology and Evolution* 4:501–512.
- Bush, J. K., and O. W. Van Auken. 2004. Relative competitive ability of *Helianthus paradoxus* and its progenitors, *H. annuus* and *H. petiolaris* (Asteraceae), in varying soil salinities. *International Journal of Plant Sciences* 165:303–310.
- Callaway, R. M., and S. C. Pennings. 2000. Facilitation may buffer competitive effects: indirect and diffuse interactions among salt marsh plants. *American Naturalist* 156:416–424.

- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965.
- Chacón, P., and A. A. Muñoz. 2007. Competitive abilities among seedlings of three tree species differing in seed size: a garden experiment using species of Chilean temperate forest. *New Zealand Journal of Botany* 45:593–603.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122:661–696.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119–1144.
- Costa, C. S. B., J. C. Marangoni, and A. M. G. Azevedo. 2003. Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. *Journal of Ecology* 91:951–965.
- Čuda, J., H. Skálková, Z. Janovsky, and P. Pyšek. 2015. Competition among native and invasive *Impatiens* species: the roles of environmental factors, population density and life stage. *AoB Plants* 7: plv033–plv033.
- Domènech, R., and M. Vilà. 2008. Response of the invader *Cortaderia selloana* and two coexisting natives to competition and water stress. *Biological Invasions* 10:903–912.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences of the USA* 99:12917–12922.
- . 2004. Network structure and robustness of marine food webs. *Marine Ecology Progress Series* 273:291–302.
- Engel, E. C., and J. F. Weltzin. 2008. Can community composition be predicted from pairwise species interactions? *Plant Ecology* 195:77–85.
- Fortner, A. M., and J. F. Weltzin. 2007. Competitive hierarchy for four common old-field plant species depends on resource identity and availability. *Journal of the Torrey Botanical Society* 134:166–176.
- Frérot, H., C. Lefèbvre, W. Gruber, C. Collin, A. D. Santos, and J. Escarré. 2006. Specific interactions between local metallicolous plants improve the phytostabilization of mine soils. *Plant and Soil* 282:53–65.
- Gao, S., X. Pan, Q. Cui, Y. Hu, X. Ye, and M. Dong. 2014. Plant interactions with changes in coverage of biological soil crusts and water regime in Mu Us Sandland, China. *PLoS ONE* 9:e87713.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–511.
- Gilarranz, L. J., J. M. Pastor, and J. Galeano. 2012. The architecture of weighted mutualistic networks. *Oikos* 121:1154–1162.
- Gimenez, O., S. T. Buckland, B. J. T. Morgan, N. Bez, S. Bertrand, R. Choquet, S. Dray, et al. 2014. Statistical ecology comes of age. *Biology Letters* 10:20140698.
- Godoy, O., D. B. Stouffer, N. J. Kraft, and J. M. Levine. 2017. Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences. *Ecology* 98:1193–1200.
- Goldberg, D. E., and K. Landa. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology* 79:1013.
- Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *American Naturalist* 140:539–572.
- Gurevitch, J., P. Wilson, J. L. Stone, P. Teese, and R. J. Stoutenburgh. 1990. Competition among old-field perennials at different levels of soil fertility and available space. *Journal of Ecology* 78:727.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London.
- He, Q., M. D. Bertness, and A. H. Altieri. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters* 16:695–706.
- Hedberg, A. M., V. A. Borowicz, and J. E. Armstrong. 2005. Interactions between a hemiparasitic plant, *Pedicularis canadensis* L. (Orobanchaceae), and members of a tallgrass prairie community. *Journal of the Torrey Botanical Society* 132:401–410.
- Hendriks, M., J. M. Ravenek, A. E. Smit-Tiekstra, J. W. van der Paauw, H. de Caluwe, W. H. van der Putten, H. de Kroon, and L. Mommer. 2015. Spatial heterogeneity of plant-soil feedback affects root interactions and interspecific competition. *New Phytologist* 207:830–840.
- Jiang, L., Z. Lan, G. Liu, and P. Kardol. 2014. Interactive effects of nitrogen and water addition on competitive hierarchies between early- and late-successional plant species. *Polish Journal of Ecology* 62:665–678.
- Jordano, P., J. Bascompte, and J. M. Olesen. 2003. Invariant properties in coevolutionary networks of plant-animal interactions. *Ecology Letters* 6:69–81.
- Kasper, C., and B. Voelkl. 2009. A social network analysis of primate groups. *Primates* 50:343–356.
- Keddy, P. A., and B. Shipley. 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54:234.
- Kerr, B., M. A. Riley, M. W. Feldman, and B. J. Bohannan. 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* 418:171–174.
- Kinlock, N. L. 2019. Data from: A meta-analysis of plant interaction networks reveals competitive hierarchies as well as facilitation and intransitivity. *American Naturalist*, Dryad Digital Repository, <https://doi.org/10.5061/dryad.1sm06sp>.
- Laird, R. A., and B. S. Schamp. 2006. Competitive intransitivity promotes species coexistence. *American Naturalist* 168:182–193.
- . 2008. Does local competition increase the coexistence of species in intransitive networks. *Ecology* 89:237–247.
- Levine, J. M. 1999. Indirect facilitation: evidence and predictions from a riparian community. *Ecology* 80:1762.
- Löf, M., A. Bolte, D. F. Jacobs, and A. M. Jensen. 2014. Nurse trees as a forest restoration tool for mixed plantations: effects on competing vegetation and performance in target tree species. *Restoration Ecology* 22:758–765.
- Macfadyen, S., R. Gibson, A. Polaszek, R. J. Morris, P. G. Craze, R. Planqué, W. O. Symondson, and J. Memmott. 2009. Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? *Ecology Letters* 12:229–238.
- Mariotte, P., A. Buttler, D. Johnson, A. Thébault, and C. Vandenberghe. 2012. Exclusion of root competition increases competitive abilities of subordinate plant species through root-shoot interactions. *Journal of Vegetation Science* 23:1148–1158.
- Marty, C., A. Pornon, N. Escaravage, P. Winterton, and T. Lamaze. 2009. Complex interactions between a legume and two grasses in a subalpine meadow. *American Journal of Botany* 96:1814–1820.
- Miller, T. E., and P. A. Werner. 1987. Competitive effects and responses between plant species in a first-year old-field community. *Ecology* 68:1201.
- Niu, S., and S. Wan. 2008. Warming changes plant competitive hierarchy in a temperate steppe in northern China. *Journal of Plant Ecology* 1:103–110.

- Olesen, J. M., J. Bascompte, Y. L. Dupont, and P. Jordano. 2007. The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the USA* 104:19891–19896.
- Panetta, F. D., and R. P. Randall. 1993. *Emex australis* and the competitive hierarchy of a grazed annual pasture. *Journal of Applied Ecology* 30:373–379.
- Pausch, J., B. Zhu, Y. Kuzyakov, and W. Cheng. 2013. Plant interspecies effects on rhizosphere priming of soil organic matter decomposition. *Soil Biology and Biochemistry* 57:91–99.
- Pfeifer-Meister, L., E. M. Cole, B. A. Roy, and S. D. Bridgham. 2008. Abiotic constraints on the competitive ability of exotic and native grasses in a Pacific Northwest prairie. *Oecologia* 155:357–366.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Pages 20–22 in *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, Vienna.
- Power, E. F., and J. C. Stout. 2011. Organic dairy farming: impacts on insect-flower interaction networks and pollination. *Journal of Applied Ecology* 48:561–569.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Roxburgh, S. H., and J. B. Wilson. 2000. Stability and coexistence in a lawn community: experimental assessment of the stability of the actual community. *Oikos* 88:409–423.
- Rubin, D. B. 1981. The Bayesian bootstrap. *Annals of Statistics* 9:130–134.
- Saccone, P., J.-P. Pagès, J. Girel, J.-J. Brun, and R. Michalet. 2010. *Acer negundo* invasion along a successional gradient: early direct facilitation by native pioneers and late indirect facilitation by conspecifics. *New Phytologist* 187:831–842.
- Sangakkara, U. R., and E. Roberts. 1986. Competition between grasses during establishment and early growth. II. Effects of early germination in determining competition relationships. *Journal of Agronomy and Crop Science* 156:279–284.
- Schleuning, M., L. Ingmann, R. Strauß, S. A. Fritz, B. Dalsgaard, D. Matthias Dehling, M. Plein, et al. 2014. Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecology Letters* 17:454–463.
- Soliveres, S., F. T. Maestre, W. Ulrich, P. Manning, S. Boch, M. A. Bowker, D. Prati, et al. 2015. Intransitive competition is widespread in plant communities and maintains their species richness. *Ecology Letters* 18:790–798.
- Stouffer, D. B., C. E. Wainwright, T. Flanagan, and M. M. Mayfield. 2018. Cyclic population dynamics and density-dependent intransitivity as pathways to coexistence between co-occurring annual plants. *Journal of Ecology* 106:838–851.
- Stumpf, M. P. H., and M. A. Porter. 2012. Critical truths about power laws. *Science* 335:665–666.
- Su, Y.-S., and M. Yajima. 2015. R2jags: using R to run “JAGS.” R package version 0.5-7. <https://cran.r-project.org/web/packages/R2jags/index.html>.
- Svenning, J. C., T. Fabbro, and S. J. Wright. 2008. Seedling interactions in a tropical forest in Panama. *Oecologia* 155:143–150.
- Vázquez, D. P., R. Poulin, B. R. Krasnov, and G. I. Shenbrot. 2005. Species abundance and the distribution of specialization in host-parasite interaction networks. *Journal of Animal Ecology* 74:946–955.
- Vehtari, A., A. Gelman, and J. Gabry. 2015. Efficient implementation of leave-one-out cross-validation and WAIC for evaluating fitted Bayesian models. [arXiv:1507.04544](https://arxiv.org/abs/1507.04544).
- Watanabe, S. 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *Journal of Machine Learning Research* 11:3571–3594.
- Weigelt, A., T. Steinlein, and W. Beyschlag. 2002. Does plant competition intensity rather depend on biomass or on species identity? *Basic and Applied Ecology* 3:85–94.
- Weiner, J. 1990. Asymmetric competition in plant populations. *Trends in Ecology & Evolution* 5:360–364.
- Weiner, J., and S. C. Thomas. 1986. Size variability and competition in plant monocultures. *Oikos* 47:211.

References Cited Only in the Online Enhancements

- Clark, P. M., and R. D. Williams. 1978. Black walnut growth increased when interplanted with nitrogen-fixing shrubs and trees. Pages 88–91 in *Proceedings of the Indiana Academy of Science*. Vol. 88.
- Dormann, C. F. 2007. Competition hierarchy, transitivity and additivity: investigating the effect of fertilisation on plant-plant interactions using three common bryophytes. *Plant Ecology* 191:171–184.
- Foster, K. R., and T. Bell. 2012. Competition, not cooperation, dominates interactions among culturable microbial species. *Current Biology* 22:1845–1850.
- Fraser, L. H., and T. E. Milette. 2008. Effect of minor water depth treatments on competitive effect and response of eight wetland plants. *Plant Ecology* 195:33–43.
- Golivets, M., and K. F. Wallin. 2018. Neighbour tolerance, not suppression, provides competitive advantage to non-native plants. *Ecology Letters* 21:745–759.
- Hessman, F. V. 2009. Figure_Calibration. http://www.astro.physik.uni-goettingen.de/~hessman/ImageJ/Figure_Calibration/.
- Keddy, P., C. Gaudet, and L. H. Fraser. 2000. Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. *Journal of Ecology* 88:413–423.
- Kuebbing, S. E., and M. A. Nuñez. 2015. Negative, neutral, and positive interactions among nonnative plants: patterns, processes, and management implications. *Global Change Biology* 21:926–934.
- Macek, P., I. Prieto, J. Macková, N. Pistón, and F. I. Pugnaire. 2016. Functional plant types drive plant interactions in a Mediterranean mountain range. *Frontiers in Plant Science* 7:662.
- Moher, D., A. Liberati, J. Tetzlaff, and D. G. Altman. 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS Medicine* 6:6.
- Niu, S., Y. Zhang, Z. Yuan, W. Liu, J. Huang, and S. Wan. 2006. Effects of interspecific competition and nitrogen seasonality on the photosynthetic characteristics of C₃ and C₄ grasses. *Environmental and Experimental Botany* 57:270–277.
- Poulos, J. M., A. P. Rayburn, and E. W. Schupp. 2014. Simultaneous, independent, and additive effects of shrub facilitation and understory competition on the survival of a native forb (*Penstemon palmeri*). *Plant Ecology* 215:417–426.
- Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9:671–675.
- Segarra, J., J. Raventós, and M. F. Acevedo. 2005. Growth of tropical savanna grass plants in competition: a shoot population model. *Ecological Modelling* 189:270–288.
- Stinca, A., G. B. Chirico, G. Incerti, and G. Bonanomi. 2015. Regime shift by an exotic nitrogen-fixing shrub mediates plant facilitation in primary succession. *PLoS ONE* 10:e0123128.

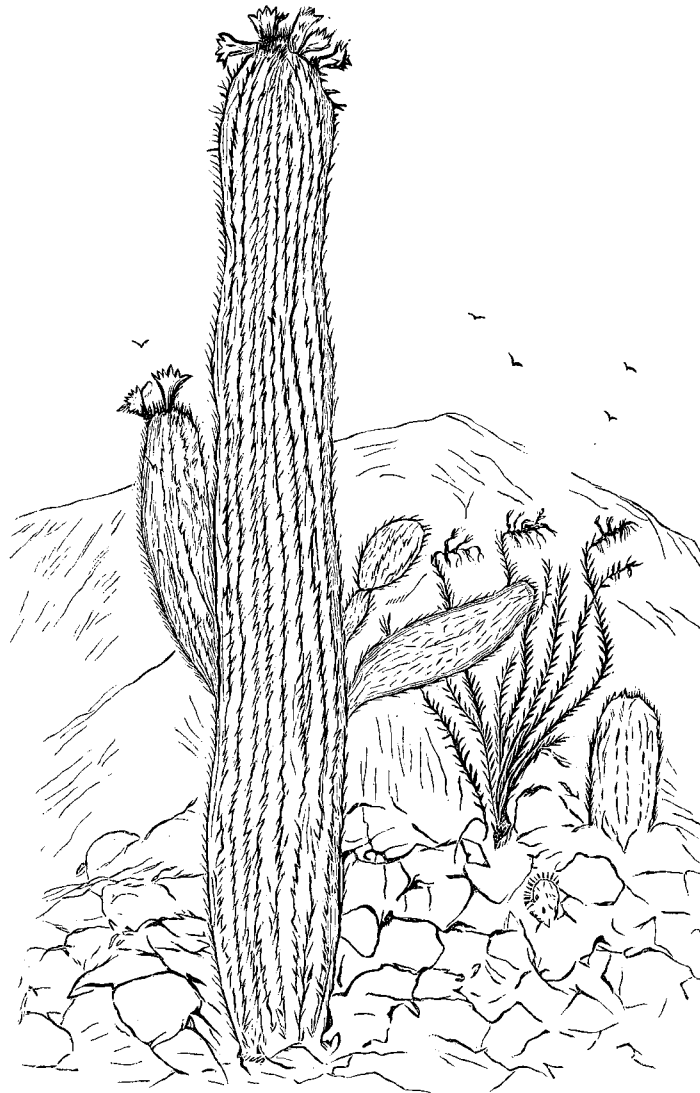
Temperton, V. M., P. N. Mwangi, M. Scherer-Lorenzen, B. Schmid, and N. Buchmann. 2007. Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. *Oecologia* 151:190–205.

Ulanowicz, R. E., and W. F. Wolff. 1991. Ecosystem flow networks: loaded dice? *Mathematical Biosciences* 103:45–68.

Vilà, M., and J. Weiner. 2004. Are invasive plant species better competitors than native plant species? evidence from pair-wise experiments. *Oikos* 105:229–238.

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“The cacti form a most conspicuous feature of mountain and desert. By far the most conspicuous and remarkable form is the *Cereus giganteus*, locally known as the ‘saguara’ cactus. . . . It is an upright fluted or ribbed pillar, each rib covered from bottom to top with a mass of sharp, straight thorns.” From “Botanical Notes from Tucson” by Jos. F. James (*The American Naturalist*, 1881, 15:978–987).