

Uncovering structural features that underlie coexistence in an invaded woody plant community with interaction networks at multiple life stages

Nicole L. Kinlock^{1,*}

1. Department of Ecology & Evolution, Stony Brook University, Stony Brook, New York 11794, USA

* Corresponding author; e-mail: nlkinlock@gmail.com

This is the peer reviewed version of the following article: Kinlock, N. L. (2021). Uncovering structural features that underlie coexistence in an invaded woody plant community with interaction networks at multiple life stages. *Journal of Ecology*, 109(1), 384–398, which has been published in final form at <https://doi.org/10.1111/1365-2745.13489>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions. This article may not be enhanced, enriched or otherwise transformed into a derivative work, without express permission from Wiley or by statutory rights under applicable legislation. Copyright notices must not be removed, obscured or modified. The article must be linked to Wiley's version of record on Wiley Online Library and any embedding, framing or otherwise making available the article or pages thereof by third parties from platforms, services and websites other than Wiley Online Library must be prohibited.

Abstract

1. Understanding the patterns of competitive and facilitative interactions within and among species in plant communities is a central goal of plant ecology, because these patterns determine species coexistence and community dynamics. Network theory provides tools that allow these patterns to be quantified, and can provide greater understanding of important community properties, including community stability, than can documenting pairwise species interactions.

2. I characterized the interactions of multiple, co-occurring invasive and native species in an old field woody plant community to build plant interaction networks at two different life stages. With the goal of identifying structural features that may operate to maintain species coexistence, I characterized the architecture of these networks at multiple scales: the entire network, the substructures that compose the network, and species' roles within substructures.

3. I found that species-level pairwise interactions alone did not provide an accurate or sufficiently detailed picture of community structure. Rather, using a network approach, I identified substructures that have the potential to promote and hinder species coexistence in interactions among seedlings. Characterizing the nuances of network substructures was illuminating, as the size of the substructures and the pattern of interaction intensities within substructures influence the expected effects on species coexistence. Including interactions at multiple life stages was also important; the seedling species that benefited most from the nested structure of facilitative interactions with adults occupied subordinate roles in substructures with other seedlings. This role reversal at different life stages is a potential factor promoting coexistence in the community. Last, the network framework was useful for comparing species' roles between native and invasive members of the community, and the three invasive species in this system had different, life-stage dependent strategies in interactions with co-occurring plants.

4. *Synthesis.* The interplay of network architecture and substructures within plant communities and among plants at different life stages is important for understanding species coexistence. In the plant community characterized in this study, there were several features that may promote coexistence, and these features were not observable in interactions within a single life stage or when considering pairwise interactions independently.

Keywords

Competition, facilitation, intransitivity, invasive species, networks, network substructures, plant-plant interactions, woody plants

Introduction

Plant communities include both competitive and facilitative interactions, often occurring in concert (Callaway & Walker, 1997), and these interactions have an important role in community structure and dynamics (Connell & Slatyer, 1977; Keddy, 2001). The balance of competition and facilitation among and within species can promote or hinder coexistence by influencing the niche and fitness differences among species (Chesson, 2000; Godoy, Bartomeus, Rohr & Saavedra, 2018). An important goal of community ecology is to identify and characterize stabilizing and destabilizing structural features in communities. For instance, community structures in which intraspecific interactions are stronger than interspecific interactions have been shown to promote stability (Chesson, 2000; Barabás, Michalska-Smith & Allesina, 2017; Adler, Ellner & Levine, 2010), as have deviations from competitive hierarchies (Laird & Schamp, 2006; Allesina & Levine, 2011; Soliveres & Allan, 2018). One way to identify these features that has frequently been used is to compare rankings of species' interaction effects and responses in communities (e.g., Keddy, Twolan-Strutt & Wisheu, 1994; Howard & Goldberg, 2001). However, this can be an inadequate approach, because these metrics involve only pairwise effects and do not incorporate multispecies mechanisms that can influence coexistence (Levine, Bascompte, Adler & Allesina, 2017). Methods used in the past to study plant interactions at the community level have involved fitting parameters in a dynamic model with empirical data. These parameters are then used to identify structural features in the community (stabilizing niche differences, Godoy & Levine 2014; higher-order interactions, Mayfield & Stouffer 2017). Currently, these models have only been developed for annual plant systems, and have not been generalized to communities of perennial plants at different life stages. Interactions among plants depend on life stage, and interactions among plants of different life stages can have an important impact on community dynamics (Armas & Pugnaire, 2009) and thus coexistence (Chu & Adler, 2015).

Network theory provides a set of tools to analyse and quantify the structure and dynamics of complex systems with many interacting parts, and plant communities can be represented as networks in which species are linked by competitive and facilitative interactions. With plant interaction networks, it is possible to explore potential mechanisms driving community dynamics and local diversity by quantifying emergent properties that cannot be determined by metrics like species richness or comparisons of pairwise species interactions (Losapio & Schöb, 2017; Saiz, Gómez-Gardeñes, Borda & Maestre, 2018; Losapio, Montesinos-Navarro & Saiz, 2019; Kinlock, 2019). Networks are composed of smaller substructures, which are the interactions among species subsets in the network (Milo *et al.*, 2002). Past studies of substructures in food webs (e.g., Stouffer, Camacho, Jiang & Nunes Amaral, 2007), animal

social networks (e.g., [Waters & Fewell, 2012](#)), and plant-pollinator networks (e.g., [Cirtwill, Roslin, Rasmussen, Olesen & Stouffer, 2018](#)) provide system-specific quantitative measures of community structure. Observed patterns of substructures found in ecological networks give insight into community dynamics ([Mersch, 2016](#); [Stouffer & Bascompte, 2010](#)) and assembly ([Baiser, Elhesha & Kahveci, 2016](#)).

Three-species substructures in plant interaction networks have been previously analysed in order to compare the frequency of transitive and intransitive substructures ([Godoy, Stouffer, Kraft & Levine, 2017](#); [Saiz, Le Bagousse-Pinguet, Gross & Maestre, 2019](#)). In a transitive substructure, species form a competitive hierarchy and can be ranked by their competitive ability, e.g., hypothetical species A outcompetes species B and C, and species B outcompetes C. This pattern hinders coexistence in the absence of stabilizing niche differences, as species A competitively excludes species B and C ([Keddy & Shipley, 1989](#); [Gallien, Zimmermann, Levine & Adler, 2017](#)). In an intransitive substructure, species deviate from a hierarchy, forming a loop in which species A outcompetes species B, species B outcompetes C, but species C outcompetes A. This pattern stabilizes species coexistence, even in the absence of niche differences ([Durrett & Levin, 1998](#); [Laird & Schamp, 2006](#); [Gallien *et al.*, 2017](#)). Four-species substructures, which have not been previously measured in plant communities, are more varied. Even though intransitivity is often cited as a stabilizing mechanism in communities, four-species intransitive loops (and other even-numbered loops) have been found to be destabilizing in theoretical studies ([Allesina & Levine, 2011](#); [Vandermeer, 2011](#); [Gallien, 2017](#)). Additionally, the degree of intransitivity in network substructures can vary continuously, from strongly transitive to strongly intransitive, depending on the asymmetry of the reciprocal interactions in the substructure (asymmetric interactions strengthen transitive or intransitive patterns, [Gallien *et al.*, 2017](#); [Gallien, Landi, Hui & Richardson, 2018](#)). The position of a given species in a particular substructure (*sensu* [Stouffer, Sales-Pardo, Sirer & Bascompte, 2012](#)) is a quantitative species-level metric that incorporates network interactions. For example, a transitive three-species substructure has three unique positions: the top, middle, and bottom species in the hierarchy; and an intransitive three-species substructure has one unique position (all species are equally positioned in the loop). By including information about direct and indirect interactions from network substructures, species' positions are useful representations of species' roles in communities ([Cirtwill & Stouffer, 2015](#)).

There are additional metrics that can characterize the network structure of interactions in plant communities. Interactions which are effectively one-sided (e.g., interactions between adult shrubs/trees and seedlings) can be represented with a bipartite network. Different network metrics are used to estimate structure in bipartite networks, such as nestedness. In a nested network, for example, most interactions are between a few adult and seedling

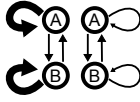
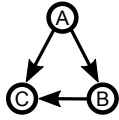
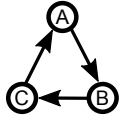
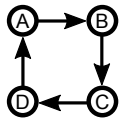
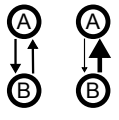
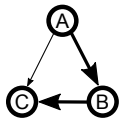
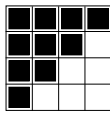
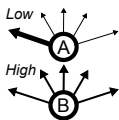
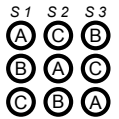
species, and other species share nested subsets of those interactions. Nestedness in facilitation networks of nurse plants and seedlings has been positively associated with the resistance of the community to extinction (Verdú & Valiente-Banuet, 2008; Losapio & Schöb, 2017). Species' interaction diversities can be also be measured in plant communities. Interaction diversity is a metric (based on Shannon entropy) that is a measure of how equally distributed interactions are in a community (Montoya & Yvon-Durocher, 2007). Thus, while species' interaction effects and responses are measures of the mean intensity of species interactions, interaction diversity is a measure of the distribution of species interactions, and it reflects whether a species has very different interactions with different species (species-specific interactions, low interaction diversity) or similar interactions with all species (high interaction diversity) (Blüthgen, Fründ, Vázquez & Menzel, 2008).

Invasive species have altered community composition, ecosystem functioning, and biotic interactions, exerting impacts worldwide (Ehrenfeld, 2010; Vilà *et al.*, 2011; Catford, Vesk, Richardson & Pyšek, 2012). Competition and facilitation are central forces in biological invasions (Simberloff & Von Holle, 1999; Levine, Vila, Antonio, Dukes, Grigulis & Lavorel, 2003). The way in which these interactions influence invasive establishment and dominance is not clear, as evidence does not support an overwhelming competitive strategy shared by invasive species (e.g., competitive superiority, Levine *et al.* 2003; Vilà & Weiner 2004; Maron & Marler 2008), but rather a suite of interaction types occurring among invasive and native species (including facilitation, Maron & Connors 1996; Cavieres, Quiroz & Molina-Montenegro 2008; Saccone, Pagès, Girel, Brun & Michalet 2010; Tecco *et al.* 2007). In addition, interactions among multiple invaders are understudied (Kuebbing, Nuñez & Simberloff, 2013), which is problematic because co-occurring invaders may benefit one another, leading to increasing invader impacts (Simberloff & Von Holle, 1999). Using a network approach to characterize a plant community with multiple native and invasive species allows for a holistic understanding of the composite interaction strategies as embedded within the larger community.

I investigated community structure of an old field plant community at multiple life history stages using an experimental study, and I used network analysis as a way to account for the direct and indirect effects of interactions in the community. I characterized community structure in terms of networks of competitive and facilitative interactions in order to identify and quantify features of community architecture that promote or hinder species coexistence. These features and their predicted effects on species coexistence and exclusion are detailed in Table 1. I conducted a manipulative field experiment and a garden experiment including seven woody native and invasive species, and used these to quantify pairwise interactions at two different life stages: among seedling pairs (the seedling-seedling network) and between adult shrubs and seedlings (the adult-seedling network). This dual network description of

the community allowed for the identification of species that undergo a role reversal between the seedling and adult life stages, which is a feature that can contribute to community stability (Gallien, 2017). I constructed networks using interaction weights from the experimental results, and calculated species-level and network-level metrics. Species-level metrics included measures of interaction effect and response (which involve only pairwise effects), species' positions in network substructures, and species' interaction diversities (both of which involve network effects). Network-level metrics included network substructure analysis and nestedness. The goals of this study were (1) to detect the prevalence and strength of competitive and facilitative interactions in the community, (2) to compare species' pairwise effects with species' network effects, (3) to compare species-level and network-level metrics at different life stages, and (4) to compare species-level effects of invasive and native species in this community. I found that while measuring only species' pairwise effects reveals destabilizing, hierarchical patterns in the community, the more detailed network analysis, which involves both pairwise and indirect network effects, reveals a richer system of substructures underlying the community's architecture and dynamics. Identifying, quantifying, and analysing the interplay of such community substructures is crucial for furthering our understanding of plant communities.

Table 1. Features of network architecture and their expected influence on species coexistence or exclusion

Network feature		Description and expected impacts on coexistence	References
Intraspecific and interspecific competition		Intraspecific competition that is stronger than interspecific competition reflects stabilizing niche differences among species and promotes coexistence.	Chesson (2000); Adler <i>et al.</i> (2010)
Transitive structures		Hierarchical patterns in which species can be ranked by their ability to outcompete others. Destabilizes species coexistence because species with lower competitive abilities are excluded (in the absence of stabilizing niche differences).	Keddy & Shipley (1989); Gallien <i>et al.</i> (2017)
Intransitive structures with odd numbers of species		Species outcompete one another in a loop and cannot be ranked by their competitive abilities. This pattern creates negative frequency-dependent growth rates that can stabilize species coexistence (even in the absence of sufficient niche differences), as species in the loop alternately increase and decrease growth rates.	Durrett & Levin (1998); Laird & Schamp (2006)
Intransitive structures with even numbers of species		In an intransitive loop with an even number of species, the same pattern in which species in the loop alternately increase and decrease growth rates can destabilize species coexistence, as species' growth rates are exacerbated rather than limited.	Allesina & Levine (2011); Vandermeer (2011); Gallien (2017)
Interaction asymmetry		Reciprocal interactions can be symmetric or asymmetric in intensity. Increasingly asymmetric interactions reflect increasing differences in competitive ability. Asymmetric interactions strengthen network-level patterns.	Gallien <i>et al.</i> (2017)
Weak intransitivity		Deviation from strongly transitive or intransitive structures; for example, a relatively weak interaction between the top and bottom species in an otherwise hierarchical transitive structure. These deviations can stabilize species coexistence by reducing differences in competitive abilities among species.	Gallien <i>et al.</i> (2018)
Nestedness		A pattern in which a few species have most of the interactions, and other species have nested subsets of those interactions. In nurse plant facilitation networks, nested patterns are associated with community resistance to extinction.	Verdú & Valiente-Banuet (2008); Losapio & Schöb (2017)
Interaction diversity		The number and evenness of interactions directed towards or away from a species. In mutualistic networks, higher interaction diversity means that interactions are more redundant, which may stabilize coexistence.	Blüthgen <i>et al.</i> (2008)
Life stage differences in competitive ability		Species competitive abilities vary at different life stages and species cannot competitively exclude one another in all contexts, a pattern that can stabilize species coexistence.	Zhang & Lamb (2012); Gallien (2017)

Materials and Methods

Study site and focal species

I characterized the pairwise interactions between seedling pairs and between adult plants and seedlings among focal species in an old field plant community in New England. The field experiment was conducted in an old field in the Yale-Myers Research Forest in northeastern Connecticut, USA, which has a humid temperate climate. The field was used for agriculture until the 1960s, and has been periodically mowed since. The field exists in a matrix of mixed deciduous-coniferous forest stands that were abandoned in the mid 19th century after having been used for pasturing or agriculture (Meyer & Plusnin, 1945). Soil at the site is sandy loam (Web Soil Survey, 2017). The site is dominated by herbaceous species, including *Solidago rugosa* Mill., *Poa pratensis* L., *Daucus carota* L., *Erigeron* L. spp., and *Symphyotrichum* Nees spp., and by small trees and shrubs (personal observation). There were seven shrub and small tree species in the field site with substantial populations (i.e., more than one or two isolated individuals) that were the focal species in this study. Invasive species included: *Rosa multiflora* Thunb. (Rosaceae), an invasive shrub in northeast and Midwest North America that was purposely introduced from eastern Asia in the 19th century for horticulture; *Elaeagnus umbellata* Thunb. (Elaeagnaceae), an invasive nitrogen-fixing shrub/small tree in eastern North America that was introduced from Asia c. 1830 for horticulture (Black, Fordham & Perkins-Veazie, 2005); and *Berberis thunbergii* DC. (Berberidaceae), an invasive shrub in eastern North America that was purposely introduced in 1875 from east Asia for ornamental horticulture (Silander & Klepeis, 1999). Species native to eastern North America included: *Rubus occidentalis* L. (Rosaceae), *Cornus racemosa* Lam. (Cornaceae) (both shrubs), *Rhus typhina* L. (Anacardiaceae) (multi-stemmed tree or large shrub), and *Pinus strobus* L. (Pinaceae) (tree that is a pioneer species in old fields). I will use the genus names to refer to each species for convenience.

Experimental design

Seed sources and species-specific germination treatments (stratification and scarification) are described in Appendix B, Table S1. In April 2016, I germinated seeds in trays with 10 cm of Sunshine Mix #4 potting medium (Sun Gro Horticulture, 60% peat moss and 40% perlite) in a greenhouse. Once the seeds germinated, I transplanted each seedling in a cone-tainer (Stuewe & Sons, Inc., Corvallis, OR) with a diameter of 38 mm and a depth of 140 mm. Germination success was uneven among species and was very low for both *Pinus* and *Rosa*. Seedlings were transplanted in the field after the last killing frost in mid May 2016.

For the seedling-seedling experiment, I measured all possible intra- and interspecific pairwise combinations of seedlings to determine interaction intensity between each species pair using a target-neighbour design (Goldberg & Werner, 1983). In 7.6 litre pots (22 cm in both diameter and depth), a central target plant was surrounded by four evenly spaced neighbouring plants approximately 10 cm away to ensure interaction (see Appendix B, Fig. S2). Control pots with a central target plant and no neighbours were also planted, for a total of 56 treatments (7 species \times 8 neighbour treatments). The number of replicates was unequal due to low germination rates for *Pinus* and *Rosa*. There were two replicates for each treatment with *Rosa* as the neighbour species, three replicates for each treatment with *Pinus* as the neighbour species, and five replicates for all other treatments. A majority of *Rosa* seedlings were equal-aged transplants from the field site (81 *Rosa* transplants, six germinated from seeds). Soil was taken from the field site to maintain consistency in soil environments between the seedling-seedling and the adult-seedling experiments. I placed pots randomly in a grid to control for microclimate variation and re-randomized the position three times over the course of the experiment. The pots were placed outdoors at the field site and remained outside for the duration of the experiments. I watered the pots to field capacity as needed.

For the adult-seedling experiment, I only measured interactions directed towards the seedlings, as I can assume that the seedlings have no significant effect on the adult plant given the size disparity (e.g., Lortie & Turkington 2008, but see Schöb *et al.* 2014). At the old field site, I planted seedlings of all target species under the canopy of five adult individuals each of *Rosa*, *Elaeagnus*, *Berberis*, *Rubus*, and *Pinus*. Adults were approximately 1–2 meters tall and similarly wide. *Rhus* and *Cornus* adults were localized to one area of the field outside of the experimental area and were not included as adult study species. Underneath the canopy of each adult, I cleared aboveground vegetation from four perpendicular wedges 1 m from the centre of the plant and kept these wedges clear for the duration of the experiment (see Appendix B, Fig. S3). This kept the area around the seedlings free of regrowth and establishment while maintaining patches of natural vegetation around the adult individual to prevent an unnatural response of the adult to the absence of competition. In five control patches with no adult individual, I cleared four wedges and planted all seedlings in an identical pattern.

Aboveground biomass of target seedlings from the seedling-seedling and adult-seedling experiments was harvested in September 2016. The numbers of replicates for each treatment at the end of the experiment are in Appendix B, Table S2. Death by herbivory appeared to affect only three of the seedlings in the seedling-seedling experiment, and two seedlings in the adult-seedling experiment; all other deaths were attributable to other stressors, primarily water stress. Harvested biomass was dried to constant mass at 60°C and weighed.

Constructing plant interaction networks

I constructed plant interaction networks from the seedling-seedling experiment and the adult-seedling experiment. I estimated plant performance in all species combinations with an interaction index, relative interaction intensity (RII). In each network, interactions were directed edges from the neighbour/adult species node toward the target species node, where RII_{ij} represents the effect of neighbour/adult species j on target species i . RII is an index ranging between $(-1, 1)$ that can represent both competitive and facilitative interactions without assuming either competition or facilitation *a priori* (Armas, Ordiales & Pugnaire, 2004). To determine RII for interactions in the seedling-seedling experiment, I calculated the mean performance of the target species in the treatment with the target seedling growing with neighbouring seedlings in an interspecific or intraspecific mixture (P_{mix}) and compared that to the mean performance of the target species in the treatment without neighbouring seedlings (P_{control}). I calculated RII similarly for the adult-seedling experiment, except that P_{mix} was seedling performance under the canopy of the adult and P_{control} was seedling performance in open control plots. I estimated plant performance as the final aboveground biomass at harvest (in g). Variance for RII was estimated as in Armas et al. (2004), assuming unequal variances within treatment and control groups. For treatments with too few surviving replicates to estimate variance, variance was imputed using a Bayesian gamma generalized linear regression (methods in Appendix A). A negative RII indicates that the target species performed worse in interspecific/intraspecific mixture than alone, and a positive RII indicates that the target species performed better in interspecific/intraspecific mixture than alone.

Network metrics

On each network, I calculated multiple network metrics that characterized the structure of the community. To measure the interaction effect of each species, I calculated out-strength, and to measure the interaction response for each species, I calculated in-strength. Mean out-strength for species i is $\frac{1}{n} \sum_{j=1, j \neq i}^n \text{RII}_{ji}$, and mean in-strength of species i is $\frac{1}{n} \sum_{j=1, j \neq i}^n \text{RII}_{ij}$. These metrics are analogous to indices of mean competitive effect and response (e.g., Goldberg & Fleetwood, 1987). Strengths and their variances were estimated using the Markov-chain Monte Carlo (MCMC) sampler JAGS (Plummer, 2003) function ‘dsum’, where observed RIIs were assumed to be normally distributed with known variances (i.e., $\text{RII}_{\text{observed}} \sim \mathcal{N}(\text{RII}, \text{var}_{\text{observed}})$), and the prior distribution for estimated RII was constrained to be Uniform $[-1, 1]$. All Bayesian analyses were conducted using the package ‘R2jags’ in the R environment, version 3.5.2 (Su & Yajima, 2015; R Core Team, 2018),

with three chains of 500,000 MCMC iterations sampling every 10th iteration, and discarding the first 50,000 samples as burn in. Convergence was determined using thresholds for the Gelman-Rubin diagnostic <1.1 and effective sample size >1000 (Gelman & Rubin, 1992).

I measured the nestedness of the adult-seedling network including only competitive interactions and including only facilitative interactions. I used the weighted nestedness based on overlap and decreasing abundance metric (wNODA, Pinheiro, Felix, Dormann & Mello, 2019; Almeida-Neto & Ulrich, 2011), calculated using the R package ‘bipartite’ (Dormann, 2011; Dormann, Frund, Bluthgen & Gruber, 2009; Dormann, Gruber & Fründ, 2008). wNODA can range from 0 (non-nested) to 100 (perfectly nested).

I calculated species’ interaction diversities (measured as Shannon entropy) in both networks (Bersier, Banašek-Richter & Cattin, 2002) (equations are in Appendix A). Diversities of interactions directed towards species and directed away from species were calculated. Interaction diversity was measured including only competitive interactions and including only facilitative interactions.

Observed network metrics were compared to network metrics that were measured with null models of network configurations, as are commonly implemented in studies of ecological networks (Vázquez & Aizen, 2003). As there is no universally accepted null model appropriate for all types of ecological networks, it is convention to compare several null models that manipulate structural features of interest. For null model I, network weights were randomly shuffled using the ‘shuffle.web’ algorithm in the ‘bipartite’ package. This preserves the connectivity, the number of facilitative and competitive interactions, and the distribution of weights in the network. Thus with null model I, it is assumed that there are no characteristic differences in interactions among species. For null models IIA and IIB, the connectivity and the number of facilitative and competitive interactions were conserved, as were the marginal sums of the network. For these null models, binary interactions were assigned given the ‘vaznull’ algorithm in the ‘bipartite’ package, and weights were assigned as random uniform variates that summed to species’ in-strengths (null model IIA) and out-strengths (null model IIB) in the empirical networks. While it is possible to conserve all marginal sums for positive integer weighted networks, e.g., with the Patefield algorithm (Patefield, 1981), there is no such algorithm for signed noninteger weighted networks. Nestedness and interaction diversity calculated on the empirical network were compared to the distribution calculated on 1,000 randomized networks constructed using null models I, IIA, and IIB. Confidence intervals and P -values were calculated directly from the distributions under the null models (Veech, 2012).

I measured the frequencies of all three- and four-species substructures in the seedling-seedling network. The seedling-seedling network was converted to a binary competitive

outcomes matrix (Laird & Schamp, 2006). Binary competitive outcomes were determined by comparing reciprocal species interactions, i.e., species i outcompetes species j if $\text{RII}_{ji} < \text{RII}_{ij}$. Competitive outcomes were also measured using stricter criteria, which I will refer to as relevant competitive outcomes, in which one species outcompetes another only if its inter-specific effect was stronger than its intraspecific effect (i.e., species i outcompetes species j if $\text{RII}_{ji} < \text{RII}_{ii}$ and $\text{RII}_{ji} < \text{RII}_{ij}$). The frequencies of unique network substructures were measured with the binary competitive outcomes and relevant competitive outcomes matrices (substructures are shown in Fig. 3). The seedling-seedling network was also converted to a weighted competitive outcomes matrix, where nonzero elements were equal to the mean absolute difference in interaction intensity between the winning and losing species. This preserves information about the asymmetry of the interactions between species pairs. Species' roles were measured as the frequency at which a species occupied a particular position in a substructure (positions are shown in Fig. 3). Additionally, the mean competitive asymmetry for a given species in a given position was measured. The frequencies of substructures and species' positions in the seedling-seedling network were compared with the frequencies in 10,000 null networks in which interactions were randomly shuffled (null model I). This makes it possible to determine whether particular substructures or positions are over- or under-represented in the observed network relative to a network in which the species-level variation has been randomized (Stouffer *et al.*, 2007, 2012). Confidence intervals and P -values were calculated using the distributions of test statistics (frequency and competitive asymmetry) under the null model.

To measure the degree of intransitivity in three-species substructures, I used the intransitivity indicator index (IC) developed by Gallien and colleagues (2018). The index was calculated using normalized net interaction effects in each three-species substructure. The normalized net effect of species j on species i , e_{ij} , is $\frac{(\text{RII}_{ji} - \text{RII}_{ij})}{\max(\text{RII})}$, where $\max(\text{RII})$ is the maximum interaction intensity in the substructure (the signs of RIIs were inverted to calculate this metric). For substructures including facilitative interactions, the range of RII was used instead of the maximum. This way, normalized net effects were bounded between -1 and 1 . The IC for a given three-species substructure (with species i , j , and k) was calculated as, $\text{IC} = e_{ij} + e_{jk} - e_{ik}$. The index, which is bounded between -1 and 3 , measures the degree of intransitivity in a network substructure: $\text{IC} < 0$ is strongly transitive, $0 < \text{IC} < 2$ weakly intransitive, and $\text{IC} > 2$ strongly intransitive.

I also calculated the relative intransitivity (RI) index using the binary competitive outcomes matrix. The RI index was calculated using the variance of the column sums in the network, and comparing this to the minimum and maximum possible variances of the column sums for an equal-sized matrix, $\text{RI} = 1 - (\text{var}_{\text{obs}} - \text{var}_{\text{min}}) / (\text{var}_{\text{max}} - \text{var}_{\text{min}})$ (Laird &

Schamp, 2006). Transitive networks have high variance and intransitive networks have low variance. An RI index of 0 describes a maximally transitive community and 1 describes a maximally intransitive community. The RI of the seedling-seedling network was compared with the RI of 10,000 null networks in which interactions were randomly shuffled (null model I).

Results

In the seedling-seedling experiment, all 49 pairwise interactions among the seven study species were quantified (Fig. 1a, b). A majority of the interactions (94%) in the seedling-seedling network were competitive. Three facilitative interactions were measured, and in all cases *Rosa* was the recipient species. Interspecific interaction intensities (RII_{ij}) ranged from -0.90 (competitive) to 0.45 (facilitative), with a mean of -0.40 . All intraspecific interactions (RII_{ii}) were competitive, but varied in intensity; they were relatively strong for *Rubus* (-0.67) and *Rhus* (-0.66), moderate for *Cornus* (-0.46), and weak for *Berberis* (-0.21), *Elaeagnus* (-0.16), *Pinus* (-0.13), and *Rosa* (-0.05).

In the adult-seedling field experiment, 34 pairwise interactions between adults and seedlings were measured, missing one interaction in which *Elaeagnus* was both the adult and the seedling species (seedlings died in all replicates) (Fig. 1c, d). There were 24 competitive interactions and 10 facilitative interactions in the network. Eight of the 10 facilitative interactions were directed towards invasive *Elaeagnus* and *Berberis* seedlings. Interaction intensities ranged from -0.67 to 0.77 with a mean of -0.14 .

Competitive effects and responses

All seedling species had negative mean out-strengths, meaning that they had competitive mean effects on other seedlings in the community (Fig. 2a). Native *Rhus* had the strongest competitive mean effect, followed by invasive *Rosa*, native *Pinus*, and *Rubus*, all relatively equal in competitive mean effect (i.e., their credible intervals overlapped considerably). Last, native *Cornus* and invasive *Elaeagnus* and *Berberis* had the weakest (relatively equal) competitive mean effects. Native seedlings had negative mean responses (i.e., negative mean in-strengths) that were similar to one another in intensity, while the three invasive seedling species had divergent responses (Fig. 2a). *Berberis* seedlings had strongly negative mean responses, *Elaeagnus* seedlings moderately negative mean responses, and *Rosa* seedlings had no significant response. In contrast, the four native species had moderately strong competitive mean responses to other seedlings.

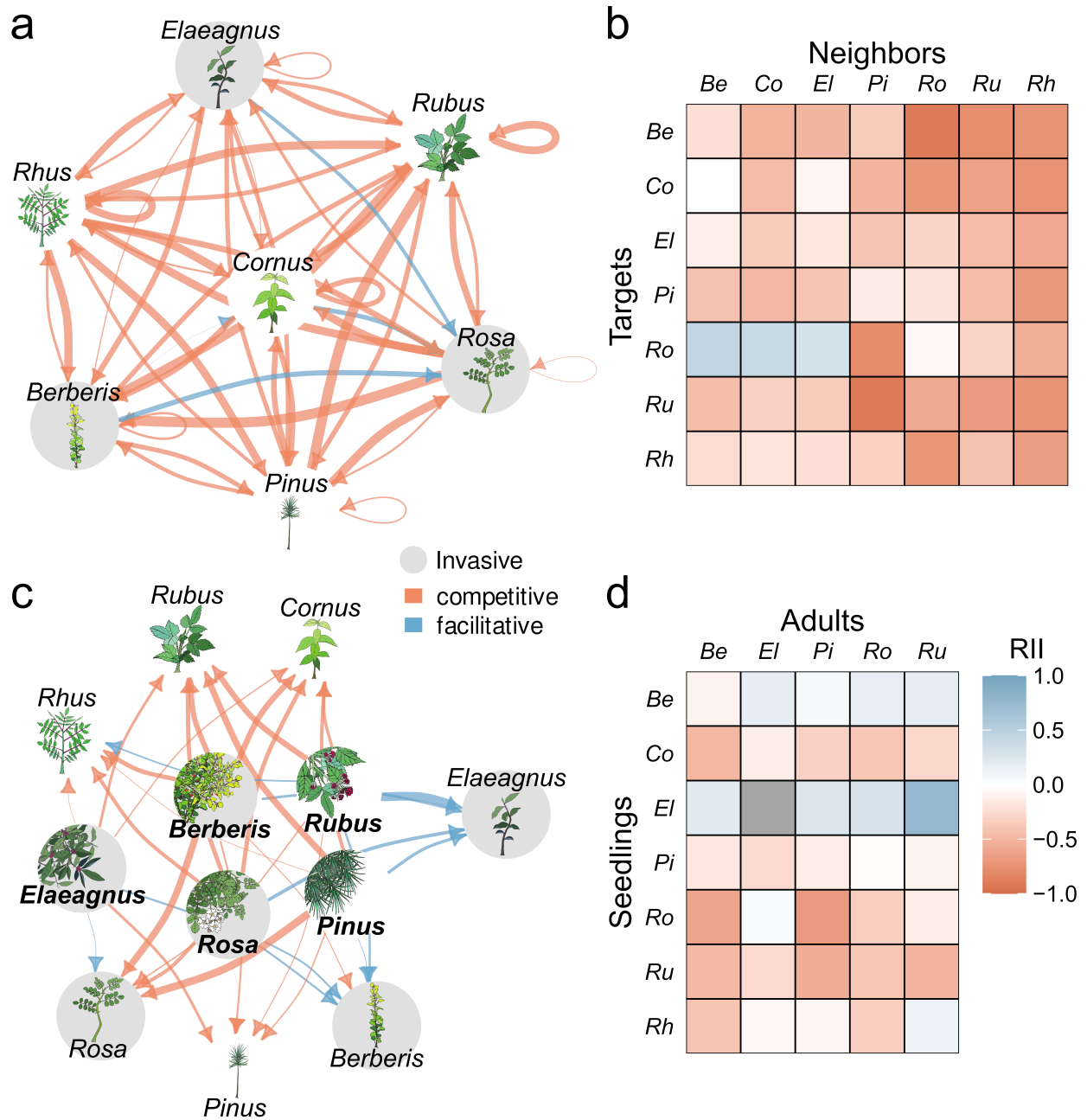


Figure 1. Seedling-seedling (a, b) and adult-seedling (c, d) interaction networks. Network visualizations (a, c): nodes are species (light grey nodes are invasive at the study site), edges are interaction intensities, RII_{ij} . Edge widths are proportional to interaction intensity. Arrows point from the neighbour/adult species towards the target species. Blue edges represent facilitative interactions ($RII > 0$) and red edges represent competitive interactions ($RII < 0$). Bold genus names are adults, and all other nodes are seedlings. Matrix visualizations (b, d): the colour of the matrix element is the interaction intensity, RII_{ij} of neighbour/adult species j on target species i . Species are abbreviated as the first two letters in the genus name. One interaction in which seedlings died in all replicates is shown in grey.

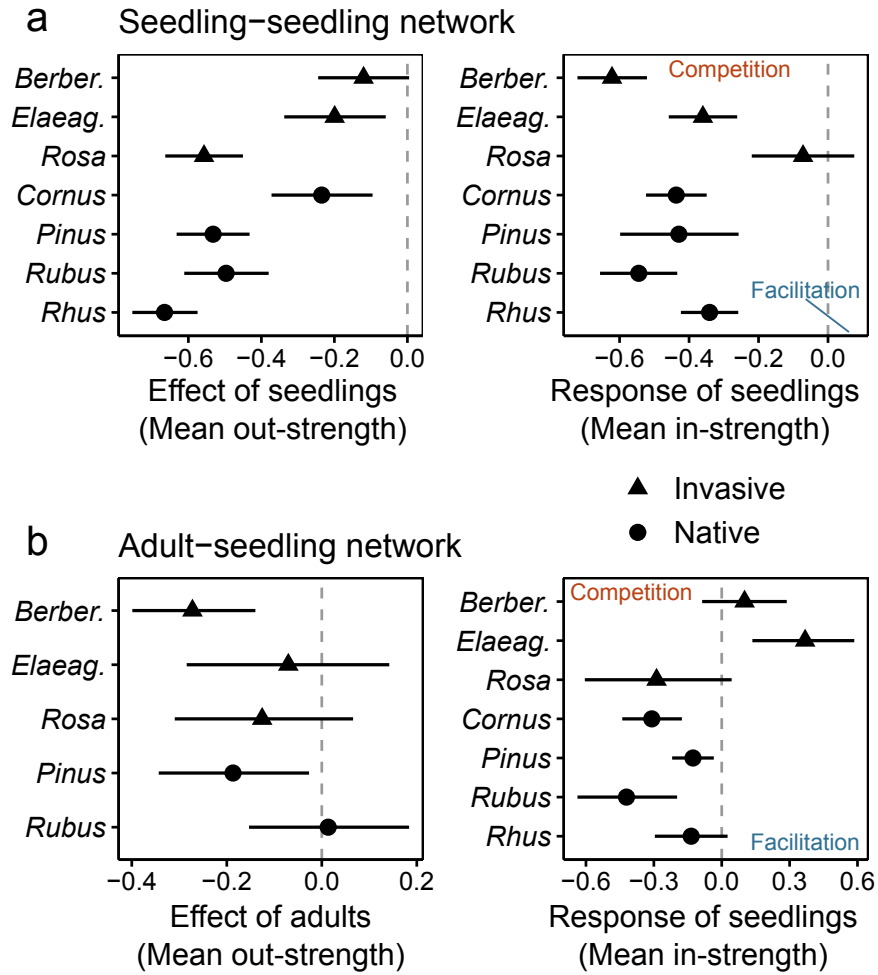


Figure 2. Comparison of mean out-strengths and mean in-strengths in the (a) seedling-seedling and (b) adult-seedling networks. Error bars are 95% credible intervals (CRIs).

Adults had similar competitive effects on species, i.e., the 95% CRIs of their mean out-strengths overlapped one another. Adult *Elaeagnus*, *Rosa*, and *Rubus* had no significant mean effect on the seedling community, meaning that their 95% CRIs overlapped zero (Fig. 2b). *Berberis* and *Pinus* adults had significantly competitive mean effects on seedlings. Seedling species differed in their responses to adults. On average, invasive *Elaeagnus* and *Berberis* were facilitated by adults (i.e., had positive mean in-strengths), while all native species and invasive *Rosa* had negative mean responses to adults (Fig. 2b).

Network architecture

Table 2. Frequencies of three- and four-species network substructures observed in the seedling-seedling network, compared with frequencies estimated using a null model of network structure.

ID	Substructure description	Obs.	Null Freq.*	P
<i>Competitive outcomes, interspecific interactions only</i>				
T3	Transitive	30	26.2 [22, 32]	0.134
I3	Intransitive	5	8.8 [3, 13]	0.217
T4	Transitive	22	13.1 [5, 25]	0.111
LL4	Lower intransitive 3-spp loop outcompeted by fourth sp	3	4.4 [0, 9]	0.605
UL4	Upper intransitive 3-spp loop outcompetes fourth sp	3	4.4 [0, 9]	0.606
I4	Intransitive	7	13.1 [2, 22]	0.342
<i>Relevant competitive outcomes, account for intraspecific interactions</i>				
T3	Transitive	14	9.3 [1, 22]	0.348
C3	Three-species chain	1	6.2 [1, 11]	0.062
PT3A	Partial transitive, top/middle spp do not outcompete	4	2.3 [0, 6]	0.236
PT3B	Partial transitive, two bottom spp do not outcompete	8	4.7 [1, 10]	0.127
I3	Intransitive	5	2.6 [0, 8]	0.227
PT4A	Partial transitive, two bottom spp do not outcompete	5	1.1 [0, 5]	0.040
PT4B	Partial transitive, two middle spp do not outcompete	5	0.5 [0, 3]	0.001
PI4	Partial intransitive, two intransitive sub-loops	3	1.2 [0, 5]	0.199
I4	Intransitive	4	1.7 [0, 9]	0.225

* Null frequency shown as mean [95% CI]

On the whole, the seedling-seedling network was neither fully transitive nor intransitive (RI = 0.36; null RI mean [95% CI] = 0.62 [0.21, 0.93]). Looking in depth at the frequencies of the three- and four-species substructures that composed the network, most substructures were transitive (86% of three-species substructures and 63% of four-species substructures). There were more transitive substructures than expected and fewer intransitive substructures.

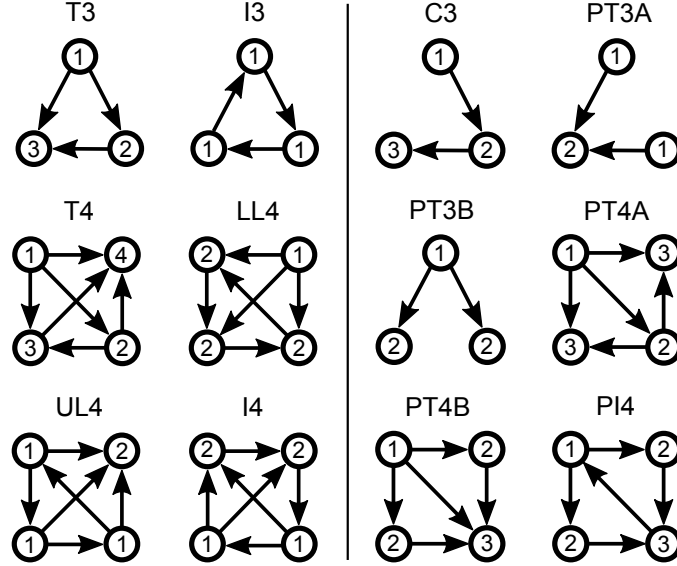


Figure 3. Three- and four-species substructures observed in the seedling-seedling competitive outcomes network. Arrows point from the “winning” species to the “losing” species in the pairwise interaction. Unique positions in each substructure are numbered. Substructure IDs are described in Table 2. Substructures to the right of the vertical line were only observed when competitive outcomes accounted for intraspecific interactions (relevant competitive outcomes).

tures than expected under the null model (Table 2). The frequencies of three-species and four-species intransitive substructures were similar. A considerable number of four-species substructures were partially transitive/intransitive (31%, substructure IDs LL4 and UL4), meaning that they were composed of a mixture of transitive and intransitive three-species substructures. In comparison, looking at substructure frequencies using relevant competitive outcomes (in which a species outcompetes another only if its interspecific effect was stronger than its intraspecific effect), intransitive substructures were actually more common than expected under the null model (Table 2). While transitive three-species substructures were more common than expected using relevant competitive outcomes, completely transitive four-species substructures were relatively rare (6%) and most four-species substructures were partially transitive (i.e., otherwise transitive substructures that were missing interactions, substructure IDs PT4A and PT4B).

Invasive *Rosa* and native *Rhus* were significantly overrepresented in the top positions

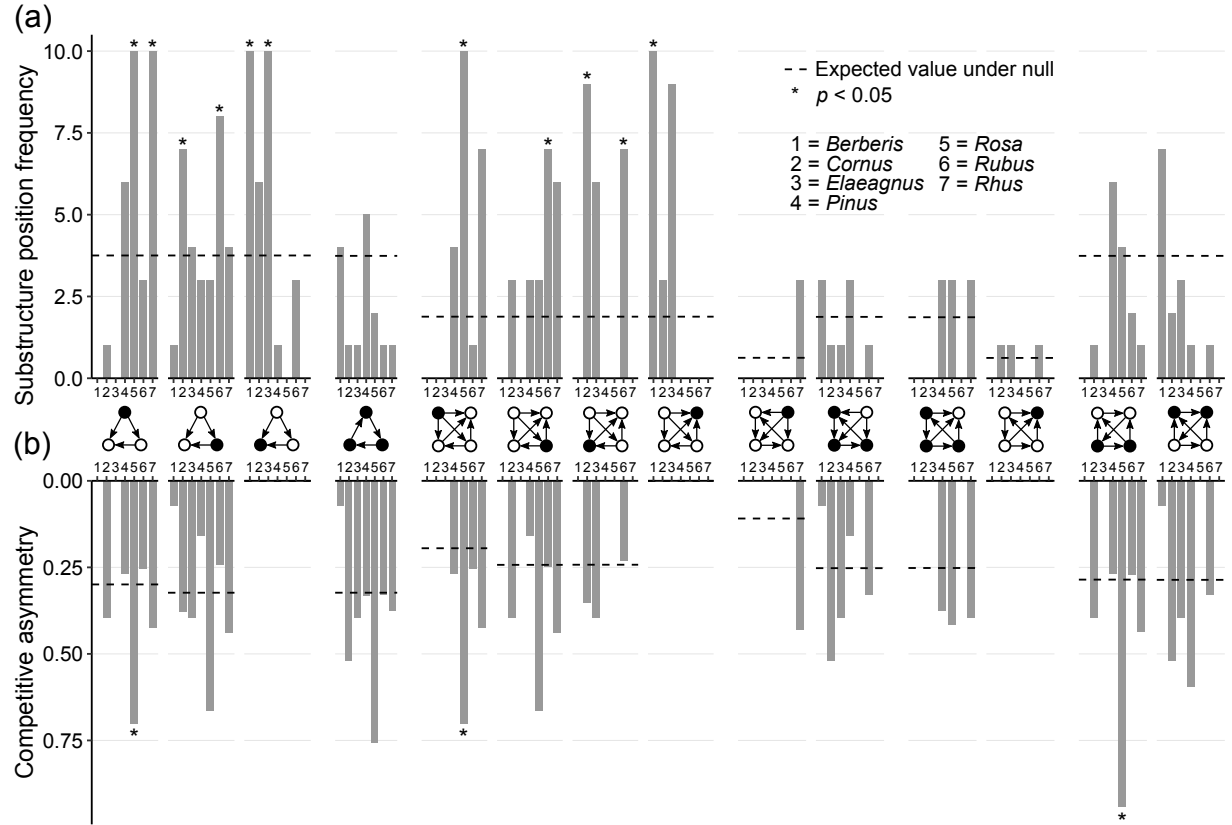


Figure 4. Species positions for all three- and four-species network substructures in the seedling-seedling competitive outcomes network. (a) The frequency at which species occupied a given position, indicated by the filled black circles, in a network substructure. (b) The competitive asymmetry of species in each position, measured as the mean amount by which the species outcompeted “losing” species. The expected values and P -values under null model I are shown.

of transitive hierarchical substructures (Fig. 4a). While *Rosa* was overrepresented in the top positions of both three- and four-species transitive hierarchies, *Rhus* was only overrepresented in three-species transitive hierarchies. Native *Rubus* and *Cornus* were overrepresented in the middle positions of transitive substructures, and invasive *Berberis* and *Elaeagnus* in the bottom positions of transitive substructures. Looking at species' positions using relevant competitive outcomes, *Berberis* and *Pinus* were overrepresented in the loop positions in intransitive three- and four-species substructures (Appendix B, Fig. S4). Interaction asymmetry varied considerably among species, and interactions with *Rosa* were significantly more asymmetric relative to interactions with other species (Fig. 4b).

The facilitative relationships in the adult-seedling network were significantly nested (wN-ODA = 53.9) relative to null model I, but not null models IIA or IIB (null model I wNODA = 28.8 [12.6, 44.1], $P = 0.007$; null model IIA = 46.6 [23.8, 69.5], $P = 0.247$; null model IIB = 36.4 [15.0, 57.9], $P = 0.068$; Appendix B, Fig. S5a). Thus, the nestedness of facilitative interactions was attributable to species-level interaction effects rather than to the distribution of interactions for a species. The species at the core of the facilitative interaction network were adults *Rubus* and *Rosa* and seedlings *Elaeagnus* and *Berberis*. The competitive relationships in the adult-seedling network were significantly nested relative to all null models (wNODA = 76.0, null model I = 53.2 [42.5, 63.9], $P < 0.001$; null model IIA = 61.6 [42.5, 64.0], $P = 0.009$; null model IIB = 56.1 [41.4, 70.8], $P = 0.004$; Appendix B, Fig. S5b). Competitive interactions were therefore nested as a result of both species-level effects and the distribution of interaction weights within a species. The interactions most deeply nested in the network of competitive interactions were adult *Berberis*, *Pinus*, and *Rosa* acting on seedlings *Rubus*, *Rosa*, and *Cornus*.

For several species, interaction diversities were reversed between the seedling-seedling and adult-seedling networks (Appendix B, Fig. S6). The competitive interactions directed towards invasive *Berberis* and *Elaeagnus* in the seedling-seedling network were significantly more evenly distributed than expected, while the diversities of their competitive interactions

with adults were zero. Thus, *Berberis* and *Elaeagnus* experienced homogeneous competitive effects from other seedlings, but not adults. In contrast, the competitive interactions directed towards invasive *Rosa* in the seedling-seedling network were significantly less evenly distributed than expected (i.e., other seedlings had variable, species-specific effects on *Rosa* seedlings), while the diversity of competitive effects of adults on *Rosa* seedlings was very close to the expected value (i.e., adults had similarly competitive effects on *Rosa* seedlings). Competitive interactions directed towards and away from native *Rubus* seedlings (and native *Rhus* and *Pinus*, to a lesser extent) were significantly more evenly distributed than expected in all contexts.

Discussion

In this study, I sought to identify and characterize the structural features that promote or hinder species coexistence in an invaded woody plant community at different life stages, and to compare structural features apparent at the species level and at the network level. Considering only species-level pairwise interactions among seedlings, species could be roughly ranked into three categories by their mean competitive effects. Only *Rhus* and *Rubus* had strong, limiting intraspecific competition. Adults had effectively indistinguishable, neutral mean effects on seedlings, which varied from competitive to facilitative depending on the seedling species. Among seedlings, invasive *Elaeagnus* and *Berberis* were the only species consistently facilitated by adults. By considering the interactions among seedlings and between adults and seedlings in a network framework, novel insight into the structure of these interactions was gained, and species that seemed to take on similar roles at the pairwise level were clearly differentiable.

Considering the matrix of interactions among seedlings as a whole, it was clear that the species could not be ranked strictly by their competitive abilities, as the RI of the seedling-seedling network was not zero. Without further analysis, this would suggest that

the community had intransitive loops that may stabilize the dynamics among seedlings in the community, promoting coexistence. However, by breaking down the network into substructures, characteristic patterns and species' roles were apparent, and these structures were neither exclusively stabilizing nor destabilizing. Both three-species and four-species transitive substructures were overrepresented in the seedling-seedling network even when intraspecific interactions were taken into account, as most species tended to have stronger effects on other species than they had on conspecifics. In the absence of stabilizing niche differences like strong intraspecific competition, transitive patterns lead to exclusion of species in the hierarchy and are thus destabilizing (Soliveres & Allan, 2018). Three-species and four-species intransitive substructures were present, and were relatively more common when accounting for intraspecific interactions. Three-species (and other odd numbers of species) intransitive patterns are stabilizing in communities, as they have the potential to generate negative frequency dependent population growth rates that promote species coexistence (Durrett & Levin, 1998; Allesina & Levine, 2011). In contrast, four-species (and other even numbers of species) intransitive substructures are destabilizing, as competition compounds through the system to alternatively increase and decrease species' abundances (Allesina & Levine, 2011; Vandermeer, 2011; Gallien, 2017). In this and other real plant communities, odd- and even-numbered intransitive patterns occur together, and the expected influence of intransitivity on species coexistence should be considered in this context.

However, there is additional layer of detail important in characterizing the substructures that make up plant communities. There are varying degrees of transitivity and intransitivity contingent on (1) the asymmetry of pairwise interactions (Gallien *et al.*, 2017), and (2) whether the transitive hierarchy is strong or weak (Gallien *et al.*, 2018). Three-species (odd) intransitive loops only have the potential to be stabilizing if pairwise interactions are asymmetric, meaning the effect of the winner species on the loser is much stronger than the effect of the loser species on the winner (Gallien, 2017). Interaction asymmetry varied considerably, especially across species (e.g., interactions with *Rosa* were very asymmetric,

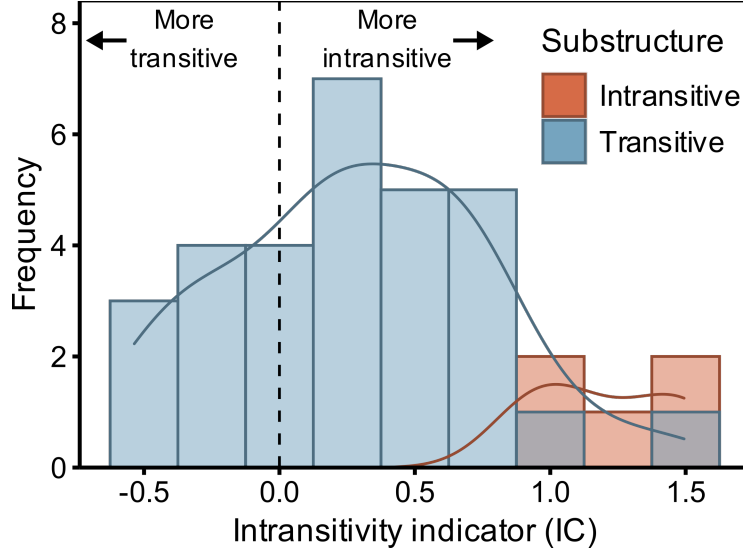


Figure 5. Histograms of IC for transitive and intransitive three-species substructures in the seedling-seedling network. IC is bounded between -1 and 3 . $IC < 0$ indicates transitive substructures, $0 < IC < 2$ weak intransitive, and $IC > 2$ strongly intransitive. Empirical densities are shown as lines.

Fig. 4b). Second, a transitive substructure is considered strong if the top species in the hierarchy has a very intense effect on the bottom species and a moderate effect on the middle species, and the middle species has a moderate effect on the bottom species (Gallien *et al.*, 2018). If this pattern differs, for example, if the top species has a weak effect on the bottom species, the transitive substructure is weakened (this pattern is known as weak intransitivity, Gallien *et al.*, 2018). Weak intransitive patterns delay or prevent competitive exclusion, making stable coexistence more likely (Gallien *et al.*, 2018). In this study, many transitive substructures were in fact weakly intransitive, i.e., IC was between 0 and 1 for the majority of transitive substructures (Fig. 5). Also, intransitive substructures in the seedling-seedling network were not strongly intransitive (IC of all intransitive substructures < 2 , Fig. 5).

Network structure in the adult-seedling network was strikingly different from the seedling-seedling network. Interactions with adults favoured seedling species that were disproportionately found in the bottom position in hierarchical network substructures in the seedling-seedling network, and for several species, the diversity of competitive and facilitative inter-

actions showed opposite patterns in the two networks. Though there was little difference among adults when comparing their pairwise, species-level effects on seedlings, a nested architecture was apparent for both facilitative and competitive interactions at the network level, thus differentiating the adult species. In contexts where facilitation by adult plants is a dominant interaction, e.g., desert or alpine ecosystems, nested patterns describe communities in which a generalist core of adult nurse species facilitate both generalist and specialist (including rare) seedlings, and in these contexts, nestedness is positively related to the resistance of plant communities to extinction (Verdú & Valiente-Banuet, 2008; Losapio & Schöb, 2017; Losapio, Pugnaire, O'Brien & Schöb, 2018). In this study, however, the nested pattern between adults and seedlings describes a core of adult and seedling species which have the strongest facilitative interactions, and a different core of adult and seedling species which have the strongest competitive interactions. The near reversal of species' roles in the seedling-seedling and adult-seedling network may be a force promoting species coexistence in this community (Gallien *et al.*, 2017), similar to what was suggested in a study finding changes in species competitive rankings at different life stages (Zhang & Lamb, 2012). While facilitation itself will not necessarily promote coexistence (Bulleri, Bruno, Silliman & Stachowicz, 2016), the divergent responses of seedlings to adults may.

Old fields are a novel habitat in eastern North America and exist in their current state because abandoned agricultural fields have been prevalent in this region since the mid 19th century (Foster, Motzkin & Slater, 1998; Hall, Motzkin, Foster, Syfert & Burk, 2002). The native woody species that inhabit old fields in eastern North America were thought to have been restricted to permanently open habitats in the pre-European colonization landscape (Marks, 1983), thus there is no characteristic co-evolved native old field woody plant community. Finding a mixture of structural features that promote and hinder species coexistence should perhaps be expected in a relatively novel habitat with species that have only co-occurred in modern times. In fact, weak intransitivity is a potential mechanism by which stronger network-level patterns can assemble in ecological communities over time (e.g., strong

intransitivity, Gallien *et al.*, 2018).

Using this network-based framework allows for a quantitative comparison of species roles, comparing invasive and native species within the community (n.b., this is not a comparison of invasive and native species more broadly). Notably, the rankings among seedlings apparent by looking only at pairwise effects did not align with the species' roles taking network structure into account. Invasive *Rosa* was overrepresented in the top position of transitive hierarchies, and had strongly asymmetric competitive effects in this position. *Rosa* is an invasive species in northeast and Midwest North America that can become dominant in mid-successional old fields, forest edges, and gaps in forest understories (Banasiak & Meiners, 2009). Unlike the native species that occupied the top position in transitive substructures (*Rhus*), *Rosa* had very weak intraspecific competition. Though *Rhus typhina* is native to eastern North America, it is invasive in central Europe (Möllerová, 2019) and in China (Zhang, Jiang, Zhang, Zhang & Shi, 2009), where its competitive ability may influence its success (Du *et al.*, 2017). While *Berberis* and *Elaeagnus* are pervasive invaders in eastern North America, they were overrepresented in the bottom positions of hierarchical network substructures in interactions among seedlings. However, both species were facilitated by adults. *Berberis* can inhabit fully shaded forest understory (DeGasperis & Motzkin, 2007) and *Elaeagnus* can inhabit partially shaded forest edges (Dornbos, Martzke, Gries & Hesselink, 2016), thus adult species may have facilitated seedlings by microclimate amelioration (creating shade, reducing temperature). In contrast, the other species in this study are not known to be shade tolerant, including invasive *Rosa* (Dlugos, Collins, Bartelme & Drenovsky, 2015). Adult *Rosa* was central in the nested structure of facilitative interactions, facilitating both *Berberis* and *Elaeagnus*. Facilitation among co-occurring invaders could lead to increasing invader impacts (Simberloff & Von Holle, 1999), though the complex network of interactions in which the facilitative interactions occur may buffer these impacts.

In this study, I have identified features in the community that represent a mixture of both stabilizing and destabilizing characteristics, given current theoretical understanding

(e.g., [Allesina & Levine, 2011](#); [Gallien *et al.*, 2018](#)). While the interplay of such features may provide a useful explanatory framework for understanding community stability and species coexistence, a direct, causal interpretation of the role these network features have is difficult for several reasons. First, I did not explicitly test for coexistence using invasion analysis (e.g., [Carroll, Cardinale & Nisbet, 2011](#)) or stability analysis (e.g., structural stability analysis, [Saavedra *et al.*, 2017](#)). Also, the networks in this study were composed of interaction indices, which are proxies of per capita competitive effects of species on populations of other species that may not adequately represent population-level responses. Including more species in future studies of plant interaction networks is important. In this study, most interactions among seedlings were moderately strong and competitive (though adults and seedlings had weaker interactions). Weak interactions have been found to promote species coexistence in ecological communities ([McCann, Hastings & Huxel, 1998](#)), and including additional (and rare) species may therefore illuminate additional stabilizing features in plant communities. Only a single community was characterized in this study; similar comparisons of plant interaction substructures and species' roles across communities are necessary to understand whether these features are consistent across contexts. Species' roles have been found to be conserved across temporal, spatial, or phylogenetic contexts in other types of ecological networks ([Stouffer *et al.*, 2012](#); [Baker, Kaartinen, Roslin & Stouffer, 2015](#)), but this is not known for plant interaction networks. Last, the experimental method by which interactions among seedlings were measured may have removed potential stabilizing niche mechanisms (e.g., indirect interactions with co-occurring species not included in the study, or plant-soil feedbacks, [Ke & Wan, 2020](#)) that could occur in a more realistic field setting (but see [Tuck, Porter, Rees & Turnbull, 2018](#)).

Conclusions

I quantified the complex structure of a plant community by measuring interactions among woody plant species at two different life stages, among seedlings and between seedlings and adults, using a series of field and garden experiments. I sought to identify structural features of the seedling-seedling and adult-seedling networks that were associated with community stability, given current theoretical understanding, at different scales of network analysis. Measures of pairwise species-level effects and responses suggested that seedling species could be ranked in a hierarchy of competitive effects and that adult species had similar, weak effects on seedlings. In contrast, the use of a network approach revealed that interactions among seedlings were neither strictly transitive nor intransitive. Though three- and four-species transitive substructures were common, they were not composed of strongly asymmetric interactions and many were weakly intransitive (Gallien *et al.*, 2018). There were both three-species and four-species intransitive loops, and while three-species loops are expected to promote diversity in communities, four-species loops may destabilize species coexistence (Allesina & Levine, 2011; Gallien *et al.*, 2017). In general, future studies of community structure in plant communities should incorporate the nuances of transitive and intransitive substructures, measuring substructures of different sizes and quantifying interaction asymmetry. Interaction patterns between adults and seedlings were also only apparent using a network approach, as adults tended to facilitate or harm seedlings in a nested pattern. Additionally, interactions with adults in the adult-seedling network favoured species that disproportionately occupied the bottom roles in hierarchical substructures in the seedling-seedling network, which is a potential mechanism promoting species coexistence. The careful analysis of the network architecture of plant communities is important for understanding species coexistence, and in this study, network analysis revealed multiple potentially stabilizing features that were not observable when considering pairwise interactions independently.

Acknowledgments

I thank Jessica Gurevitch for guidance and feedback for the duration of this project. The staff, coordinators, and researchers at the Yale Myers Forest, in particular Julius Pasay, Shannon Murray, Marlyse Duguid, Mark Ashton, and Oswald Schmitz, made the fieldwork involved in this study possible. I also thank Stony Brook University greenhouse staff Mike Axelrod and John Klumpp as well as Emily Herstoff for assistance with seedling germination. Alistair Rogers, Stephan Munch, Jennifer Dunne, Drew Jamieson, and members of the Gurevitch lab provided feedback on earlier versions of this manuscript. The Associate Editor, Malyon Bimler, and three anonymous reviewers provided comments that substantially improved this manuscript. I was supported by a Robert R. Sokal Award from the Stony Brook University Department of Ecology & Evolution and a Graduate Council Fellowship from Stony Brook University.

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.76hdr7sttX> (Kinlock, 2020).

References

- Adler, P.B., Ellner, S.P. & Levine, J.M. (2010) Coexistence of perennial plants: An embarrassment of niches. *Ecology Letters* pp. no–no.
- Allesina, S. & Levine, J.M. (2011) A competitive network theory of species diversity. *Proceedings of the National Academy of Sciences* **108**, 5638–5642.
- Almeida-Neto, M. & Ulrich, W. (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling & Software* **26**, 173–178.
- Armas, C., Ordiales, R. & Pugnaire, F.I. (2004) Measuring plant interactions: A new comparative index. *Ecology* **85**, 2682–2686.

- Armas, C. & Pugnaire, F.I. (2009) Ontogenetic Shifts in Interactions of Two Dominant Shrub Species in a Semi-Arid Coastal Sand Dune System. *Journal of Vegetation Science* **20**, 535–546.
- Baiser, B., Elhesha, R. & Kahveci, T. (2016) Motifs in the assembly of food web networks. *Oikos* **125**, 480–491.
- Baker, N.J., Kaartinen, R., Roslin, T. & Stouffer, D.B. (2015) Species' roles in food webs show fidelity across a highly variable oak forest. *Ecography* **38**, 130–139.
- Banasiak, S.E. & Meiners, S.J. (2009) Long term dynamics of *Rosa multiflora* in a successional system. *Biological Invasions* **11**, 215–224.
- Barabás, G., Michalska-Smith, M.J. & Allesina, S. (2017) Self-regulation and the stability of large ecological networks. *Nature Ecology & Evolution* **1**, 1870–1875.
- Bersier, L.F., Banašek-Richter, C. & Cattin, M.F. (2002) Quantitative descriptors of food-web matrices. *Ecology* **83**, 2394–2407.
- Black, B.L., Fordham, I.M. & Perkins-Veazie, P. (2005) Autumnberry (*Elaeagnus umbellata*): A potential cash crop. *Journal of the American Pomological Society* **59**, 125–134.
- Blüthgen, N., Fründ, J., Vázquez, D.P. & Menzel, F. (2008) What do interaction network metrics tell us about specialization and biological traits? *Ecology* **89**, 3387–3399.
- Bulleri, F., Bruno, J.F., Silliman, B.R. & Stachowicz, J.J. (2016) Facilitation and the niche: Implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology* **30**, 70–78.
- Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: A synthetic approach to interactions in plant communities. *Ecology* **78**, 1958–1965.
- Carroll, I.T., Cardinale, B.J. & Nisbet, R.M. (2011) Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology* **92**, 1157–1165.
- Catford, J.A., Vesk, P.A., Richardson, D.M. & Pyšek, P. (2012) Quantifying levels of biological invasion: Towards the objective classification of invaded and invulnerable ecosystems. *Global Change Biology* **18**, 44–62.
- Cavieres, L.A., Quiroz, C.L. & Molina-Montenegro, M.A. (2008) Facilitation of the non-native *Taraxacum officinale* by native nurse cushion species in the high Andes of central Chile: Are there differences between nurses? *Functional Ecology* **22**, 148–156.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31**, 343–366.
- Chu, C. & Adler, P.B. (2015) Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. *Ecological Monographs* **85**, 373–392.

- Cirtwill, A.R., Roslin, T., Rasmussen, C., Olesen, J.M. & Stouffer, D.B. (2018) Between-year changes in community composition shape species' roles in an Arctic plant-pollinator network. *Oikos* **127**, 1163–1176.
- Cirtwill, A.R. & Stouffer, D.B. (2015) Concomitant predation on parasites is highly variable but constrains the ways in which parasites contribute to food web structure. *Journal of Animal Ecology* **84**, 734–744.
- Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* **111**, 1119–1144.
- DeGasperis, B.G. & Motzkin, G. (2007) Windows of opportunity: Historical and ecological controls on *Berberis thunbergii* invasions. *Ecology* **88**, 3115–3125.
- Dlugos, D.M., Collins, H., Bartelme, E.M. & Drenovsky, R.E. (2015) The non-native plant *Rosa multiflora* expresses shade avoidance traits under low light availability. *American Journal of Botany* **102**, 1323–1331.
- Dormann, C.F. (2011) How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology* **1**, 1–20.
- Dormann, C.F., Frund, J., Bluthgen, N. & Gruber, B. (2009) Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. *The Open Ecology Journal* **2**, 7–24.
- Dormann, C.F., Gruber, B. & Fründ, J. (2008) Introducing the bipartite Package: Analysing Ecological Networks. *R News* **8**, 8–11.
- Dornbos, D.L., Martzke, M.R., Gries, K. & Hesselink, R. (2016) Physiological competitiveness of autumn olive compared with native woody competitors in open field and forest understory. *Forest Ecology and Management* **372**, 101–108.
- Du, N., Tan, X., Li, Q., Liu, X., Zhang, W., Wang, R., Liu, J. & Guo, W. (2017) Dominance of an alien shrub *Rhus typhina* over a native shrub *Vitex negundo* var. *heterophylla* under variable water supply patterns. *PLOS ONE* **12**, e0176491.
- Durrett, R. & Levin, S. (1998) Spatial Aspects of Interspecific Competition. *Theoretical Population Biology* **53**, 30–43.
- Ehrenfeld, J.G. (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics* **41**, 59–80.
- Foster, D.R., Motzkin, G. & Slater, B. (1998) Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. *Ecosystems* **1**, 96–119.
- Gallien, L. (2017) Intransitive competition and its effects on community functional diversity. *Oikos* **126**, 615–623.

- Gallien, L., Landi, P., Hui, C. & Richardson, D.M. (2018) Emergence of weak-intransitive competition through adaptive diversification and eco-evolutionary feedbacks. *Journal of Ecology* **106**, 877–889.
- Gallien, L., Zimmermann, N.E., Levine, J.M. & Adler, P.B. (2017) The effects of intransitive competition on coexistence. *Ecology Letters* **20**, 791–800.
- Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical science* **7**, 457–511.
- Godoy, O., Bartomeus, I., Rohr, R.P. & Saavedra, S. (2018) Towards the integration of niche and network theories. *Trends in Ecology & Evolution* **33**, 287–300.
- Godoy, O. & Levine, J.M. (2014) Phenology effects on invasion success: Insights from coupling field experiments to coexistence theory. *Ecology* **95**, 726–736.
- Godoy, O., Stouffer, D.B., Kraft, N.J. & Levine, J.M. (2017) Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences. *Ecology* **98**, 1193–1200.
- Goldberg, D.E. & Fleetwood, L. (1987) Competitive effect and response in four annual plants. *The Journal of Ecology* **75**, 1131.
- Goldberg, D.E. & Werner, P.A. (1983) Equivalence of competitors in plant communities: A null hypothesis and a field experimental approach. *American Journal of Botany* **70**, 1098.
- Hall, B., Motzkin, G., Foster, D.R., Syfert, M. & Burk, J. (2002) Three hundred years of forest and land-use change in Massachusetts, USA. *Journal of Biogeography* **29**, 1319–1335.
- Howard, T.G. & Goldberg, D.E. (2001) Competitive response hierarchies for germination, growth, and survival and their influence on abundance. *Ecology* **82**, 979–990.
- Ke, P.J. & Wan, J. (2020) Effects of soil microbes on plant competition: A perspective from modern coexistence theory. *Ecological Monographs* **90**.
- Keddy, P.A. (2001) *Competition*, vol. 26 of *Population and Community Biology Series*. Kluwer, Dordrecht, 2nd edn.
- Keddy, P.A. & Shipley, B. (1989) Competitive hierarchies in herbaceous plant communities. *Oikos* **54**, 234.
- Keddy, P.A., Twolan-Strutt, L. & Wisheu, I.C. (1994) Competitive effect and response rankings in 20 wetland plants: Are they consistent across three environments? *The Journal of Ecology* **82**, 635.
- Kinlock, N.L. (2019) A meta-analysis of plant interaction networks reveals competitive hierarchies as well as facilitation and intransitivity. *The American Naturalist* **194**, 640–653.

- Kinlock, N.L. (2020) Data from: Uncovering structural features that underlie coexistence in an invaded woody plant community with interaction networks at multiple life stages. Dryad Digital Repository. <https://doi.org/10.5061/dryad.76hdr7stt>.
- Kuebbing, S.E., Nuñez, M.A. & Simberloff, D. (2013) Current mismatch between research and conservation efforts: The need to study co-occurring invasive plant species. *Biological Conservation* **160**, 121–129.
- Laird, R.A. & Schamp, B.S. (2006) Competitive intransitivity promotes species coexistence. *The American Naturalist* **168**, 182–193.
- Levine, J.M., Bascompte, J., Adler, P.B. & Allesina, S. (2017) Beyond pairwise mechanisms of species coexistence in complex communities. *Nature* **546**, 56–64.
- Levine, J.M., Vila, M., Antonio, C.M.D., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B: Biological Sciences* **270**, 775–781.
- Lortie, C.J. & Turkington, R. (2008) Species-specific positive effects in an annual plant community. *Oikos* **117**, 1511–1521.
- Losapio, G., Montesinos-Navarro, A. & Saiz, H. (2019) Perspectives for ecological networks in plant ecology. *Plant Ecology & Diversity* **12**, 87–102.
- Losapio, G., Pugnaire, F.I., O'Brien, M.J. & Schöb, C. (2018) Plant life history stage and nurse age change the development of ecological networks in an arid ecosystem. *Oikos* **127**, 1390–1397.
- Losapio, G. & Schöb, C. (2017) Resistance of plant-plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. *Functional Ecology* **31**, 1145–1152.
- Marks, P.L. (1983) On the origin of the field plants of the northeastern United States. *American Naturalist* pp. 210–228.
- Maron, J.L. & Connors, P.G. (1996) A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* **105**, 302–312.
- Maron, J.L. & Marler, M. (2008) Field-based competitive impacts between invaders and natives at varying resource supply. *Journal of Ecology* **96**, 1187–1197.
- Mayfield, M.M. & Stouffer, D.B. (2017) Higher-order interactions capture unexplained complexity in diverse communities. *Nature Ecology & Evolution* **1**, 0062.
- McCann, K., Hastings, A. & Huxel, G.R. (1998) Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798.
- Mersch, D.P. (2016) The social mirror for division of labor: What network topology and dynamics can teach us about organization of work in insect societies. *Behavioral Ecology and Sociobiology* **70**, 1087–1099.

- Meyer, W.H. & Plusnin, B.A. (1945) *The Yale Forest in Tolland and Windham Counties, Connecticut*. No. 55 in Yale University School of Forestry Bulletin Series, Yale University, New Haven.
- Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. & Alon, U. (2002) Network motifs: Simple building blocks of complex networks. *Science* **298**, 824–827.
- Möllerová, J. (2019) Notes on invasive and expansive trees and shrubs. *Journal of Forest Science* **51**, 19–23.
- Montoya, J.M. & Yvon-Durocher, G. (2007) Ecological networks: Information theory meets Darwin’s entangled bank. *Current Biology* **17**, R128–R130.
- Patefield, W.M. (1981) Algorithm AS 159: An Efficient Method of Generating Random $R \times C$ Tables with Given Row and Column Totals. *Applied Statistics* **30**, 91.
- Pinheiro, R.B.P., Felix, G.M.F., Dormann, C.F. & Mello, M.A.R. (2019) A new model explaining the origin of different topologies in interaction networks. *Ecology* **100**.
- Plummer, M. (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing* (eds. K. Hornik, F. Leisch & A. Zeileis), pp. 20–22, Technische Universität Wien.
- R Core Team (2018) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Saavedra, S., Rohr, R.P., Bascompte, J., Godoy, O., Kraft, N.J. & Levine, J.M. (2017) A structural approach for understanding multispecies coexistence. *Ecological Monographs* **87**, 470–486.
- Saccone, P., Pagès, J.P., Girel, J., Brun, J.J. & Michalet, R. (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.
- Saiz, H., Gómez-Gardeñes, J., Borda, J.P. & Maestre, F.T. (2018) The structure of plant spatial association networks is linked to plant diversity in global drylands. *Journal of Ecology* **106**, 1443–1453.
- Saiz, H., Le Bagousse-Pinguet, Y., Gross, N. & Maestre, F.T. (2019) Intransitivity increases plant functional diversity by limiting dominance in drylands worldwide. *Journal of Ecology* **107**, 240–252.
- Schöb, C., Michalet, R., Cavieres, L.A., Pugnaire, F.I., Brooker, R.W., Butterfield, B.J., Cook, B.J., Kikvidze, Z., Lortie, C.J., Xiao, S., Al Hayek, P., Anthelme, F., Cranston, B.H., García, M.C., Le Bagousse-Pinguet, Y., Reid, A.M., le Roux, P.C., Lingua, E., Nyakatya, M.J., Touzard, B., Zhao, L. & Callaway, R.M. (2014) A global analysis of bidirectional interactions in alpine plant communities shows facilitators experiencing strong reciprocal fitness costs. *New Phytologist* **202**, 95–105.

- Silander, J.A. & Klepeis, D.M. (1999) The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. *Biological Invasions* **1**, 189–201.
- Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: Invasional meltdown? *Biological invasions* **1**, 21–32.
- Soliveres, S. & Allan, E. (2018) Everything you always wanted to know about intransitive competition but were afraid to ask. *Journal of Ecology* **106**, 807–814.
- Stouffer, D.B. & Bascompte, J. (2010) Understanding food-web persistence from local to global scales. *Ecology Letters* **13**, 154–161.
- Stouffer, D.B., Camacho, J., Jiang, W. & Nunes Amaral, L.A. (2007) Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences* **274**, 1931–1940.
- Stouffer, D.B., Sales-Pardo, M., Sirer, M.I. & Bascompte, J. (2012) Evolutionary Conservation of Species’ Roles in Food Webs. *Science* **335**, 1489–1492.
- Su, Y.S. & Yajima, M. (2015) *R2jags: Using R to Run 'JAGS'*. R package version 0.5-7.
- Tecco, P.A., Diaz, S., Gurvich, D.E., Perez-Harguindeguy, N., Cabido, M. & Bertone, G.A. (2007) Facilitation and interference underlying the association between the woody invaders *Pyracantha angustifolia* and *Ligustrum lucidum*. *Applied Vegetation Science* **10**, 211–218.
- Tuck, S.L., Porter, J., Rees, M. & Turnbull, L.A. (2018) Strong responses from weakly interacting species. *Ecology Letters* **21**, 1845–1852.
- Vandermeer, J. (2011) Intransitive loops in ecosystem models: From stable foci to heteroclinic cycles. *Ecological Complexity* **8**, 92–97.
- Vázquez, D.P. & Aizen, M.A. (2003) Null model analyses of specialization in plant–pollinator interactions. *Ecology* **84**, 2493–2501.
- Veech, J.A. (2012) Significance testing in ecological null models. *Theoretical Ecology* **5**, 611–616.
- Verdú, M. & Valiente-Banuet, A. (2008) The nested assembly of plant facilitation networks prevents species extinctions. *The American Naturalist* **172**, 751–760.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems: Ecological impacts of invasive alien plants. *Ecology Letters* **14**, 702–708.
- Vilà, M. & Weiner, J. (2004) Are invasive plant species better competitors than native plant species?—evidence from pair-wise experiments. *Oikos* **105**, 229–238.
- Waters, J.S. & Fewell, J.H. (2012) Information processing in social insect networks. *PLoS ONE* **7**, e40337.

- Web Soil Survey (2017) Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. <https://websoilsurvey.sc.egov.usda.gov/>.
- Zhang, S. & Lamb, E.G. (2012) Plant competitive ability and the transitivity of competitive hierarchies change with plant age. *Plant Ecology* **213**, 15–23.
- Zhang, Z., Jiang, C., Zhang, J., Zhang, H. & Shi, L. (2009) Ecophysiological evaluation of the potential invasiveness of *Rhus typhina* in its non-native habitats. *Tree Physiology* **29**, 1307–1316.