

Plant interaction networks reveal the limits of our understanding of diversity maintenance

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Abstract

Species interactions are key drivers of biodiversity and ecosystem stability. Current theoretical frameworks for understanding the role of interactions make many assumptions which unfortunately, do not always hold in natural, diverse communities. This mismatch extends to annual plants, a common model system for studying coexistence, where interactions are typically averaged across environmental conditions and transitive competitive hierarchies are assumed to dominate. We quantify interaction networks for a community of annual wildflowers in Western Australia across a natural shade gradient at local scales. Whilst competition dominated, intraspecific and interspecific facilitation were widespread in all shade categories. Interaction strengths and directions varied substantially despite close spatial proximity and similar levels of local species richness, with most species interacting in different ways under different environmental conditions. Contrary to expectations, all networks were predominantly intransitive. These findings encourage us to rethink how we conceive of and categorize the mechanisms driving biodiversity in plant systems.

KEYWORDS

coexistence, community ecology, competition, diversity, environmental heterogeneity, facilitation, intransitivity, networks, plant population ecology, species interactions

INTRODUCTION

In nature, life is rarely solitary. Animals, plants and microbes continually interact with one another as they find resources, grow and die. These interactions connect all species belonging to the same ecological community into a complex and dynamic network. The structure of this network and the strength of its interactions determine which species can establish, coexist or go extinct (Ives et al., 2000; May, 1972; Pimm et al., 1991; Ratzke et al., 2020), driving local to regional patterns of diversity

(Allesina & Tang, 2012; Chesson, 2000a; García-Callejas et al., 2018; Michalet et al., 2006; Michalet et al., 2015; Mougi & Kondoh, 2012; Wisz et al., 2013). Unfortunately, our ability to reliably predict diversity patterns from these local interactions remains unrealised.

In response, various theoretical frameworks have delineated the conditions under which species pairs may compete and yet coexist stably over time (e.g. Chesson, 2000a; Gause, 1934; Hutson & Law, 1985; MacArthur & Levins, 1967; Tilman, 1982), often using annual plants as a model system. Traditional approaches

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to understanding the impacts of species interactions on plant diversity emerged from population ecology by studying how species' growth rates or densities vary over time. Interactions with neighbouring species are measured as increases (facilitation) or decreases (competition) in a focal species' growth rate and estimated from field or laboratory experiments (Connell, 1961; Grace & Tilman, 1990). Early research focused almost exclusively on competition (Gause, 1934; MacArthur & Levins, 1967) using the theoretical expectation that environments with a limited number of resources can maintain a limited number of competing species. Under these conditions, trade-offs in resource uptake rates or requirements may increase that number (Tilman, 1982). This framework also dictates that diversity can be maintained when species exhibit negative density dependence (NDD) where individuals of a species compete more strongly with themselves than with individuals of other species (Adler et al., 2018). This led to the development of the 'mutual invasibility criteria', which evaluates whether two species can mutually invade a resident population of the other species and grow from rare (Hutson & Law, 1985; Turelli, 1978). This criteria is viewed as the gold standard for predicting coexistence between plant species over multiple generations (Grainger, Levine, & Gilbert, 2019) and is a foundational element of Modern Coexistence Theory (MCT), a framework which quantifies how pairwise competition can maintain diversity (Chesson, 2000a; Chesson, 2000b). Competitive interactions have thus come to dominate the plant diversity maintenance literature and the way many ecologists think about coexistence (Godwin et al., 2020; HilleRisLambers et al., 2012; Letten et al., 2017), especially in the annual plant community ecology literature. The only non-competitive model of diversity maintenance that has become similarly prominent in the coexistence literature is neutral theory (Hubbell, 2001), which describes the circumstances under which no species interactions, positive or negative, direct or indirect, are involved in diversity maintenance. Though important to our understanding of diversity maintenance at community scales, these two dominant frameworks combined leave major gaps around the role of non-competitive ecological interactions in maintaining diversity.

The body of work on competitive interactions has proven useful to conceptualize how coexistence and thus diversity maintenance might emerge from local interactions in competitive, species-poor systems with relatively simple dynamics (Adler et al., 2010; Barabás et al., 2018; Kraft et al., 2015; Levine et al., 2008; Mayfield & Levine, 2010). These conditions, unfortunately, seldom describe the context in which natural plant communities operate. Most notably, the assumptions that interactions between plants are competitive in nature and constant across heterogeneous environments do not often hold in empirical systems (other than simplified experimental systems; Barabás et al., 2018; Bimler et al., 2018; Maestre

et al., 2005). Despite this, they have become rooted in community ecology theory and the associated tools developed to study population growth and diversity maintenance (Ferrarini, 2011; Simha et al., 2022). For example, evidence that facilitation structures community diversity is growing (McIntire & Fajardo, 2014; Pascual-García & Bastolla, 2017; Wright et al., 2014) yet its role in annual plants (and other non-trophic systems) is still poorly understood; as such it is often ignored in theoretical frameworks or detailed community-level studies (Bimler et al., 2018; Bruno et al., 2003; McIntire & Fajardo, 2014). Likewise, changes in interaction type (e.g. from competitive to facilitative) and magnitude can be caused by environmental variation (Bimler et al., 2018; Germain et al., 2018; Grainger, Letten, et al., 2019; Holmgren et al., 1997) and biotic factors, including indirect multispecies effects (Johnson et al., 2022; Mayfield & Stouffer, 2017), leading to well-documented empirical observations of gradual and sudden changes to interaction outcomes (Brooker, 2006; Choler et al., 2001; Maestre et al., 2005; Mod et al., 2014; Mod et al., 2016). Lastly, while coexistence can theoretically emerge in a multispecies context due to competition, it is typically evaluated between small numbers of plant species (or against a community average) due to the considerable effort and resources necessary to quantify population model-derived interactions in diverse communities. This has limited our understanding of coexistence in more complex and diverse systems.

Efforts to integrate more biological realism into predictions of coexistence are ongoing and tackle various facets of the above issues: facilitation (Koffel et al., 2021; Spaak & De Laender, 2020), variable interactions (Poisot et al., 2015; Saavedra et al., 2015), multiple species (Barabás et al., 2016; De Ruiter et al., 2005; Fowler, 2013; Saavedra et al., 2017) and several issues together (Song et al., 2018, 2020). Our understanding, however, remains largely theoretical and thus incomplete (Chave, 2013; Clark et al., 2019; Hart et al., 2017) as these frameworks are rarely tested empirically beyond the case studies which accompany them. Moreover, these frameworks have emerged as extensions to current dominant theory and are thus built upon a historical foundation of competitive pairwise interactions and mutual invasibility. This approach inherently limits the options for exploring how facilitation, non-linear, non-pairwise interactions and variation in interaction outcomes can lead to coexistence (Simha et al., 2022). Consequently, various limiting assumptions which may not hold in empirical communities still underpin and co-construct current mathematical frameworks for predicting diversity patterns and must be challenged together. These assumptions include: that interactions cannot be facilitative, in the sense that species have important positive effects on their or another species' growth rate (Bruno et al., 2003); that interactions are constant or vary linearly across environments and modelling them as such reliably captures the

relevant processes driving diversity (Bimler et al., 2018); and that diversity can be treated as an extension of coexistence between sets of species pairs (Barabás et al., 2016; Levine et al., 2017), rather than as an emergent process that is not reflective of additive pairwise outcomes alone (Maynard et al., 2017; Zelnik et al., 2022).

In this study, we engage in quantitative natural history to describe how species interactions operate in empirical systems when those assumptions are jointly removed. We quantify plant–plant interactions derived from population dynamic models in a species-rich wildflower system, allowing interactions to be competitive or facilitative and to vary with environmental heterogeneity. We examine a large number of interactions across an environmental gradient that has previously been shown to structure diversity in our system: shade (Bimler et al., 2018). We quantify network metrics to evaluate the overall organization of interactions, rather than between isolated pairs or against a community average (Levine & HilleRisLambers, 2009; Wainwright et al., 2018). We ask the following questions: (1) What do species interactions look like when the assumption of ‘competition only’ is removed? (2) How do species interactions (direction and magnitude) vary under different environmental conditions? and (3) What do interaction networks look like in diverse, natural communities of annual plants? Based on the answers to these questions, we discuss how our findings may or may not support the expected assumptions for diversity maintenance as detailed above, and how they may be used to inform future developments of theory which better capture how diversity emerges in complex natural systems. We hope that our approach, when joined with the conceptual advances built by generations of past population ecologists, can serve to broach the gap between empirical and theoretical understandings of how diversity is established and maintained.

METHODS

Data

Study site and experimental design

Data were collected in 2016 from York gum-jam woodlands in West Perenjori Reserve in Western Australia (29°28′01.3″ S 116°12′21.6″ E). The woodlands consist of *Eucalyptus loxophleba* and *Acacia acuminata* trees which form an open canopy, and a diverse annual wildflower understory. One hundred 50 × 50 cm plots were set up in the understory to contain at least one of four common annual plant species: *Goodenia rosea* (Goodeniaceae, native forb), *Arctotheca calendula* (Asteraceae, exotic forb), *Pentameris airoides* (Poaceae, exotic grass) and *Podolepis canescens* (Asteraceae, native forb). Plots were monitored over the length of the full field season (July to October).

Plots were at least 0.5 m apart and grouped into five sampling blocks (20 plots each) with at least 100 m between blocks. Using a fisheye lens, we took an image of the overhead canopy cover and quantified the percent cover using ImageJ (Rueden et al., 2017). Plots experienced a range of natural shade, from open (0%) to 40% canopy cover. A quarter of the plots were thinned to 60% and a quarter thinned to 30% density to mitigate possible confounding effects between plot location and plant density, whilst the remaining half were left unthinned. Thinning did not target any particular species or lower richness (Supplementary Methods S1.1). Plots were mapped using a pantograph (Hill, 1920; Scheiner, 1631) as in Martyn and Mayfield (2023) and all individual plants were located and identified during peak biomass (September). Maps were digitized using GIS software (QGIS Development Team 2016). We collected seed data over 6 weeks (September–October), prioritizing collecting as many observations as possible and covering a wide range of species. Seeds were collected for 11,301 individuals (plot mean = 115.3, min = 17, max = 470). Inflorescences were bagged after they were no longer receptive to pollinators to ensure we could collect seeds before they dispersed. Due to the short collection window, some plants had already dispersed seeds whilst others still had flowers and/or buds which had not yet formed seeds, in those cases we noted the number of open pods, inflorescences or empty bracts in order to estimate total seed production (S. Methods S1.2). Seed production was counted for 68.4% of individual plant observations, estimated for 5.4% observations, and the remaining 26.2% were partially counted and partially estimated.

Environmental categories and networks

In this harsh semi-arid environment, variable coexistence outcomes between annual plant species are common (Mayfield & Stouffer, 2017; Wainwright et al., 2018), particularly in response to shade (Bimler et al., 2018). We defined three environmental categories based on the percent canopy cover present over each plot: open (0–7.9%), intermediate (8–17.9%) and shady (18–40%). We pragmatically binned variation in shade to have similar numbers of plots in each category (35, 33 and 32 plots, respectively), shade is a continuous variable and varied sufficiently between plots for meaningful inference. We do not claim that these categories represent biologically special units, but rather allow for reasonable comparison between species drawn from the same community experiencing different shade extents. Two other main abiotic factors also substantially affect community composition and structure in this system: water availability and soil phosphorus (Dwyer et al., 2015). The effects of water availability operate largely over regional gradients, whereas soil P was measured for sampling blocks, at a coarser grain than canopy cover. Increasing shade

was weakly positively correlated with soil phosphorus ($r = 0.34$) and water availability ($r = 0.28$) (S. Methods S1.1, Table S1.1).

In each category, focal species were selected as those with over 20 observations of seed production, resulting in 21 focal species (Table 1) and over 5500 observations (Table S1.2). Nine focal species were present in all three categories. In total, we had 43 unique focal species \times shade combinations. Focal species were all among the most common species in the reserve, though some common species were omitted from the study due to difficulties collecting seed before dispersal.






















For every observed seed production value, we extracted the identities and abundances of all neighbouring individuals from plot maps within a 3, 4 or 5 cm radius, such that larger focal species had larger neighbourhoods (Table 1). Size of the interaction neighbourhood was defined for each focal species based on average species height and aboveground spread, as determined by personal observation. This assumption unfortunately ignores the size of neighbouring plants, which is also likely to affect the spatial distance at which an interaction is relevant. Certain neighbourhoods between focal individuals overlapped spatially. Neighbouring species which were recorded fewer than 10 times in each category were

grouped as ‘rares’. Our final dataset consisted of three categories of increasing shade, with 12, 14 and 17 focal species and 31, 31 and 36 neighbour species, respectively.

Demographic parameters

To place plant–plant interactions into a population dynamics context, we required measures of seed survival and germination rate for each focal species. Rates for 16 focal species were estimated from a collated set of experiments between 2015 and 2019 where seedbags were placed in the field to estimate germination rates, and ungerminated seeds were evaluated in the lab for survivorship. Mean field rates were assigned to the remaining five focal species. All but one focal species in our sampled plots were annuals; the one perennial (*Austrostipa elegantissima*) dies back every year leaving only a rhizomatous root in the ground. We, therefore, felt justified in treating it as an annual species in our model, with mean field estimates of survivorship and germination equivalent to survivorship of the root and likelihood it grows back the next year. Bimler et al. (2023a) describe the entire design in detail and the data have been publicly archived (Bimler et al., 2023b).

TABLE 1 List of focal species used in analyses and their identifying code, the neighbourhood radius in centimetres, presence/absence in each network and colour as in Figures 1 and 2.

Code	Species	Family	Radius	Open	Inter	Shady	Colour
ARCA	<i>Arctotheca calendula</i>	Asteraceae	5	✓	✓	✓	
CAHI	<i>Calotis hispidula</i>	Asteraceae	3		✓		
GITE	<i>Gilberta tenuifolia</i>	Asteraceae	3		✓		
GOBE	<i>Goodenia berardiana</i>	Goodeniaceae	5		✓	✓	
GOPU	<i>Goodenia pusilliflora</i>	Goodeniaceae	4	✓			
HAOD	<i>Haloragis odontocarpa</i>	Haloragaceae	4			✓	
HYGL	<i>Hyalosperma glutinosum</i>	Asteraceae	3	✓	✓	✓	
HYPO	<i>Hypochaeris glabra</i>	Asteraceae	5			✓	
MEDI	<i>Medicago</i> sp.	Fabaceae	3	✓		✓	
PEAI	<i>Pentameris airoides</i>	Poaceae	3	✓	✓	✓	
PEDU	<i>Petrorhagia dubia</i>	Caryophyllaceae	3			✓	
PLDE	<i>Plantago debilis</i>	Plantaginaceae	3	✓	✓	✓	
POCA	<i>Podolepis canescens</i>	Asteraceae	5	✓	✓	✓	
POLE	<i>Podolepis lessonii</i>	Asteraceae	3		✓	✓	
PTGA	<i>Ptilotus eremita</i>	Amaranthaceae	4	✓	✓	✓	
STPA	<i>Austrostipa elegantissima</i>	Poaceae	5	✓	✓	✓	
TRCY	<i>Trachymene cyanopetala</i>	Araliaceae	4	✓		✓	
TROR	<i>Trachymene ornata</i>	Araliaceae	4			✓	
VECY	<i>Goodenia cynopotamica</i>	Goodeniaceae	4		✓		
VERO	<i>Goodenia rosea</i>	Goodeniaceae	4	✓	✓	✓	
WAAC	<i>Waitzia accuminata</i>	Asteraceae	5	✓	✓	✓	

Note: Focal species present in all three networks are in bold. Neighbourhood radius was determined based on size of the focal species.

Model

We quantified interactions between focal species and their neighbours for each of the three shade categories using the joint model framework presented in Bimler et al. (2023a). See S. Methods S2.1 for a summary of this approach. This framework regresses the density of neighbouring plants against the performance of focal individuals to estimate the effects of neighbouring species on focal species. We used seed production as our estimate of performance, modelled with a negative-binomial distribution. Due to the large number of parameters in this model, there is potential for overfitting. To minimize this risk, we set informative priors $\mathcal{N}(0, 1)$ on the interaction parameters. Interaction effects between focal species only were transformed into per-capita interaction strengths using a population dynamics model for annual plants with a seed bank (Bimler et al., 2018, 2023a; Levine & HilleRisLambers, 2009; Mayfield & Stouffer, 2017). For clarity, we will henceforth refer to interaction effects as the coefficients that are inferred by the regression model and interaction strengths as the transformed, per-capita values. This transformation step requires the demographic parameters described above and allows us to draw conclusions about population trajectories as a result of changes in density dependent fecundity. As we only had demographic parameters for our focal species, we were unable to transform interaction effects with non-focal neighbours and thus only include interaction strengths between focal species in our subsequent analyses.

The joint model framework was applied in R v.4.0.0 (R Development Core Team et al., 2020) with the rstan package v.2.19.3 (Stan Development Team, 2020) and executed in STAN (Carpenter et al., 2017), using the code available on GitHub at <https://github.com/malbion/JointModelFramework>. We ran one model for each shade category, using 4 chains of 10,000 iterations each with a burn-in of 8000. We modified the *adapt_delta* and *max_treedepth* arguments to achieve optimal convergence for each model (S. Methods S2.2). Whilst convergence for the intermediate and shady categories was unproblematic ($\hat{R} < 1.01$), convergence was more difficult for certain parameters in the open environment (4.3% parameters with $\hat{R} > 1.1$, 21.7% with $\hat{R} > 1.01$). This was not unexpected as Bimler et al. (2023a) had similar difficulties when evaluating the model on the overall dataset with all categories grouped together, indicating problematic geometries in the shape of certain posteriors. We refer to the S. Methods S2.2 for further details and why we are confident our estimates are still informative despite imperfect convergence for a small number of parameters. Posterior predictive checks were conducted to verify our model assumptions, and overall, our models predicted values of seed production which matched observations (S. Methods S2.3). We also compared the cumulative log-posterior of the models run on each separate shade

category to the log-posterior of a model run on all the data at once.

Each model returned regression coefficients as distributions of possible values rather than single point estimates. We took 1000 samples from the posterior distributions of each coefficient and transformed interaction effects between focal species into interaction strengths for each sample (S. Methods S2.1) to create posterior distributions of values for each interaction strength. Whilst many of these distributions overlapped 0, this does not necessarily signify that the interaction is unimportant (Bimler et al., 2023a). We thus include all interaction strengths in our analyses and networks. Each interaction network for each shade category is thus described by a posterior distribution of 1000 network samples which account for uncertainty in our estimates and maintain any covariance between returned parameters.

Analysis

Results were analysed from the above interaction strengths and network samples. Unless otherwise noted, we report medians with the 80% equal-tailed credibility interval given in square brackets. Significance tests were not performed as the large number of samples renders the number of 'observations' meaningless and artificial (S. Methods S4.4). For each focal species in each network, we calculated the sum of competitive and facilitative interspecific interaction strengths they received as a focal (input) and emitted as a neighbour (output) separately. Out-strength is the sum of all emitted interspecific interaction strengths for a species, competitive and facilitative. We quantified both absolute and relative (i.e. divided by species richness) versions of these measures, the patterns were not found to differ so we refer to absolute measures in the text.

Interaction loops were based on reciprocal interaction strengths between pairs of focal species. An interaction loop was categorized as cooperative (+/+) when species *i* and *j* had facilitative effects on one another, competitive (-/-) when *i* and *j* competed with one another, and asymmetric (+/- or -/+) when *i* and *j* had opposing effects on one another. Interaction loops were limited to two species to make our results tractable and we did not investigate loops involving three species or more.

The inferred community interaction matrices (networks) were weighted, non-symmetrical, non-sparse, with positive and negative values. Unfortunately, few methods have yet been developed for analysing the properties of such networks (Delmas et al., 2019). For each network sample, we quantified the level of competitive hierarchy or intransitivity. In a competitive hierarchy, a dominant species emerges and outcompetes all others, with the next in line out-competing all species save for the first, and so on. In intransitive systems, species form loops likened to the game rock-paper-scissors, where

species A outcompetes B, B outcompetes C and C outcompetes A. We calculated the variance in species competitive rank with the Relative Intransitivity index (RII), where 0 indicates high intransitivity and 1 indicates a fully hierarchical network as in Laird & Schamp, 2006 (S. Methods S2.5.1). We measured weighted connectance as in Ulanowicz and Wolff (1991) and Kinlock (2019), where high values indicate a more even distribution of interaction strengths (S. Methods S2.5.2). We calculated modularity as in Traag and Bruggeman (2009) using the *cluster_singlass* function from the *igraph* package (Csárdi & Nepusz, 2006) (S. Methods S2.5.3), where high values indicate the network is strongly clustered into modules where species predominantly facilitate one another but compete with species from other modules. All three properties are relative to species richness, allowing for direct comparison between networks of different sizes.

RESULTS

We estimated the interaction effects using data from each shade category, resulting in three networks capturing all pairwise interaction strengths between 12, 14 and 17 focal species in open, intermediate and shady environmental conditions, respectively (Table 1). Whilst shade is an environmental factor previously determined to structure diversity and interaction strengths in this system (Bimler et al., 2018; Dwyer et al., 2015), plot-level species richness and evenness metrics were not significantly affected by percent canopy cover (S. Methods S1.1) and there was a substantial overlap in species identity, with a mean β diversity of 0.76 between shade categories (Table S1.1). As noted in the Methods, shade is a continuous variable and these categories were selected to categorize this gradient and are not reflective of inherently distinct micro-environments. However, the cumulative log-posterior of all three models was smaller than the log-posterior of a model run on all data at once (Figure S3.1), suggesting that this environmental grouping does capture important distinctions in how species interact across the whole range of shade experienced in the system.

Interaction strengths varied between species

Competition was the dominant interaction type between species, accounting for 60.6% [56.1–65.2%], 64.8% [59.9–68.7%] and 55.9% [52.2–59.9%] of all interspecific interaction strengths under open, intermediate and shady conditions, respectively. The distributions of each interaction strength often overlapped 0 and thus included both positive and negative values, though the credibility intervals of 28%, 34.1% and 16.9% of interspecific interaction strengths were of the same sign in the open, intermediate and shady categories, respectively (Figure S3.2).

Species varied widely in how they affected others and typically exerted both competitive and facilitative effects on neighbours (upper panels Figure 1), which varied according to neighbour identity and environmental conditions (see Figure S3.3). In the open and shady categories, we observed a positive correlation between the summed strength of competitive and facilitative interactions a species might emit towards neighbours, this relationship was much weaker under intermediate shade. On the receiving end, species also experienced both competitive and facilitative effects from their neighbours (lower panels Figure 1), which also varied from one environment to the next (Figure S3.4). There was little to no correlation between the summed strength of facilitation and competition a species could receive from its focal neighbours.

Whilst competition was also the dominant type of intraspecific interaction, some focal species also facilitated themselves, with four [± 1], three [± 1] and five [± 2] species facilitating themselves in the open, intermediate and shady conditions, respectively. Some intraspecific interaction strengths also had distributions which contained both competitive and facilitative values, though this was to a lesser degree than for interspecific interaction strengths. In the open, intermediate, and shady categories, the credibility intervals of all intraspecific interaction strengths did not overlap 0 for six, nine and six species, respectively. Intraspecific interaction strength was not correlated to a species' overall effect on neighbours (Figure 2), nor was it correlated with density or frequency. The ratio of median intraspecific to median interspecific interaction strength varied widely between species, when pooled across all species it was highest under open and shady conditions (1.55 and 3.38, respectively) but was roughly equal under intermediate shade (0.96).

Interaction strengths varied among networks

Out of the 21 focal species in our dataset, nine were present in all three categories and interaction strengths between those nine focal species typically varied in sign and magnitude from one category to the next. Figure 3 shows a subset of interaction strengths occurring between an exotic *Asteraceae* (HYGL), a native grass (PEAI) and a native *Asteraceae* (POCA). Changes in interaction sign and magnitude were difficult to quantify but Figure 3 illustrates various patterns: directional change (row 3, column 3), directional change including a change in sign (row 2, column 2), non-directional change (row 2, column 1) and little to no change (row 3, column 1). Out of the 81 pair-specific interaction strengths which were measurable under all shade conditions, 49 had their median value switch sign at least once between categories (Figure S3.5).

We also investigated the proportion of asymmetric, competitive and cooperative interaction loops each of

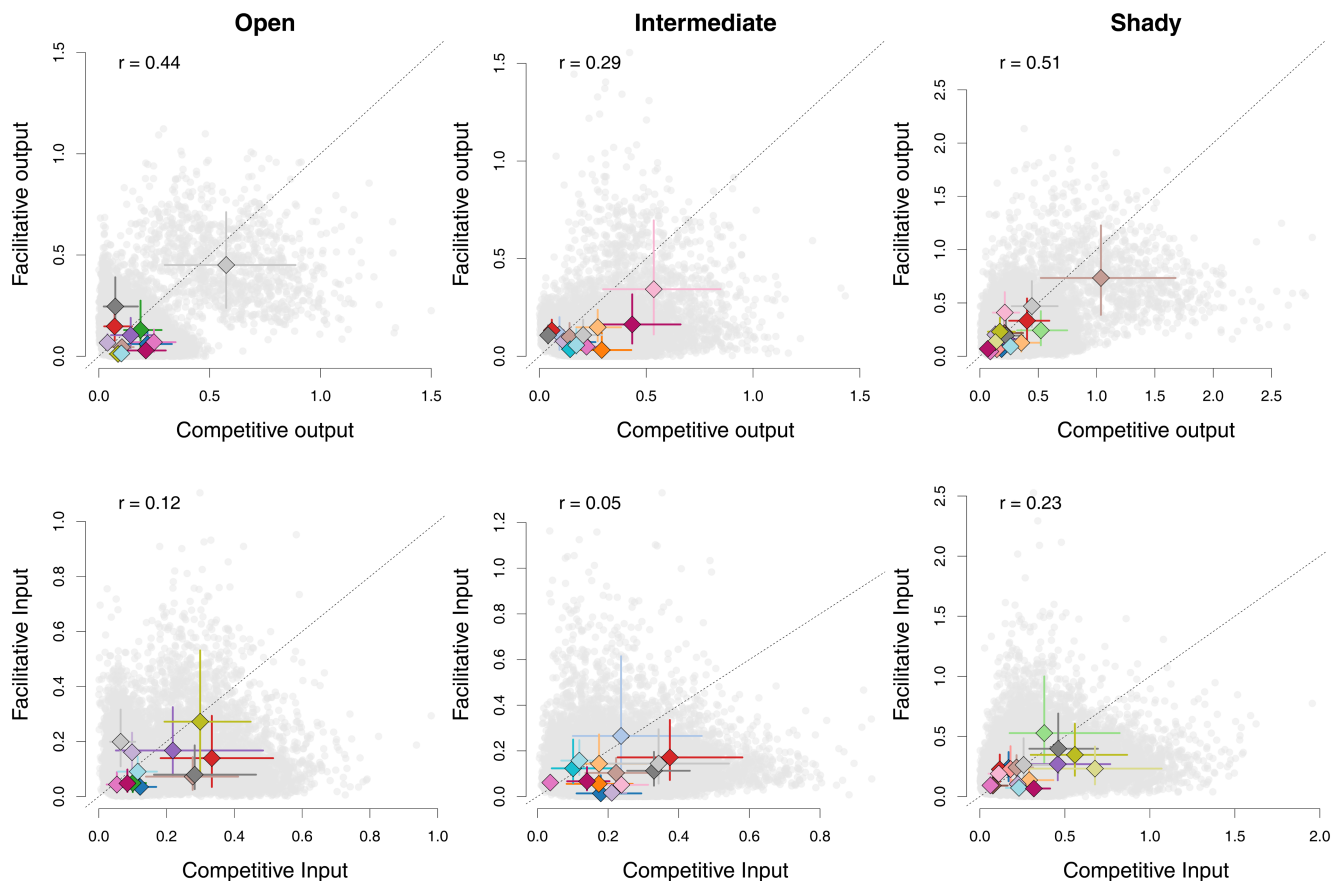


FIGURE 1 Focal species exhibited both competitive and facilitative interactions. Here we show the sum of competitive and facilitative interactions emitted (output) by each focal species (upper panels) and the sum of competitive and facilitative interactions received (input) by each focal species (lower panels). Intraspecific interactions are not included. Values are given as the absolute sum of scaled per-capita interaction strengths, either competitive (x -axis) or facilitative (y -axis), note that the scales of each axis differ between graphs. Diamonds represent species medians within each network and each of the 21 focal species is assigned a unique colour (Table 1), the coloured lines cover the 80% quantile of all samples for that species and network. Grey dots show values for unique samples. The dashed line indicates where the sum of competitive and facilitative interactions are equal. Pearson's correlation coefficient is reported in the top left corner of each graph. See Figures S3.3 and S3.4 for a further breakdown of this figure by species and shade category.

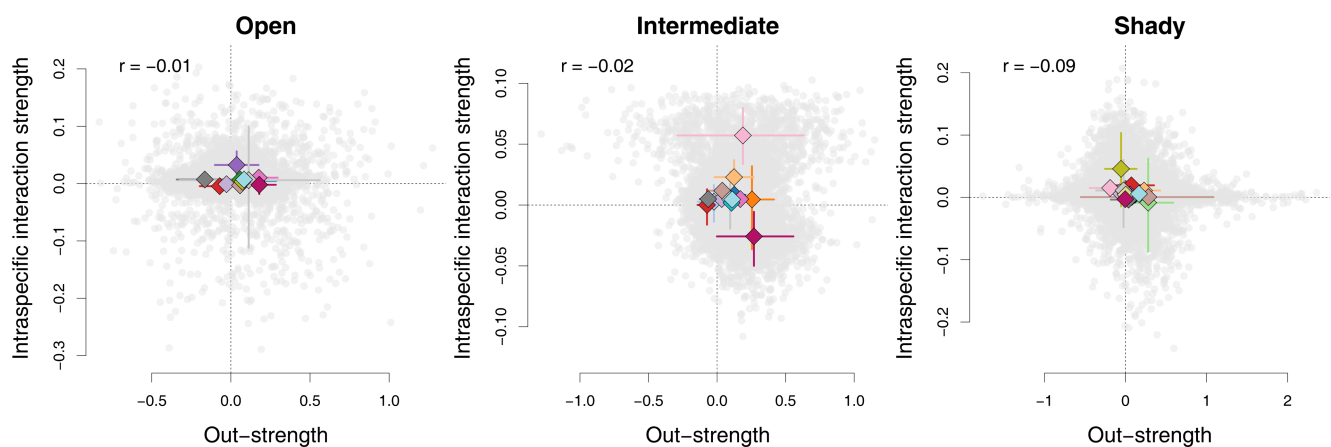


FIGURE 2 Focal species exhibited both competitive and facilitative intraspecific interactions, whose magnitude and direction did not correlate with their overall effect on neighbours. On the x -axis, out-strength is the sum of all interaction strengths from a focal species on its heterospecific neighbours. The y -axis shows intraspecific interaction strength. For both axes, values greater than 0 indicate competition and values lesser than 0 indicate facilitation, note that the scales of each axis differ between graphs. Diamonds represent species medians within each network and each focal species is assigned the same unique colour as in Figure 1. Coloured lines cover the 80% quantile of all samples for that species and network and grey dots show values for unique samples. Readers will notice a light grey diamond and quantile lines in the leftmost graph which are unusually wide on the y -axis, this corresponds to *Austrostipa elegantissima* for which our model returned a particularly wide intraspecific interaction posterior distribution. Pearson's correlation coefficient is reported in the top left corner of each graph.

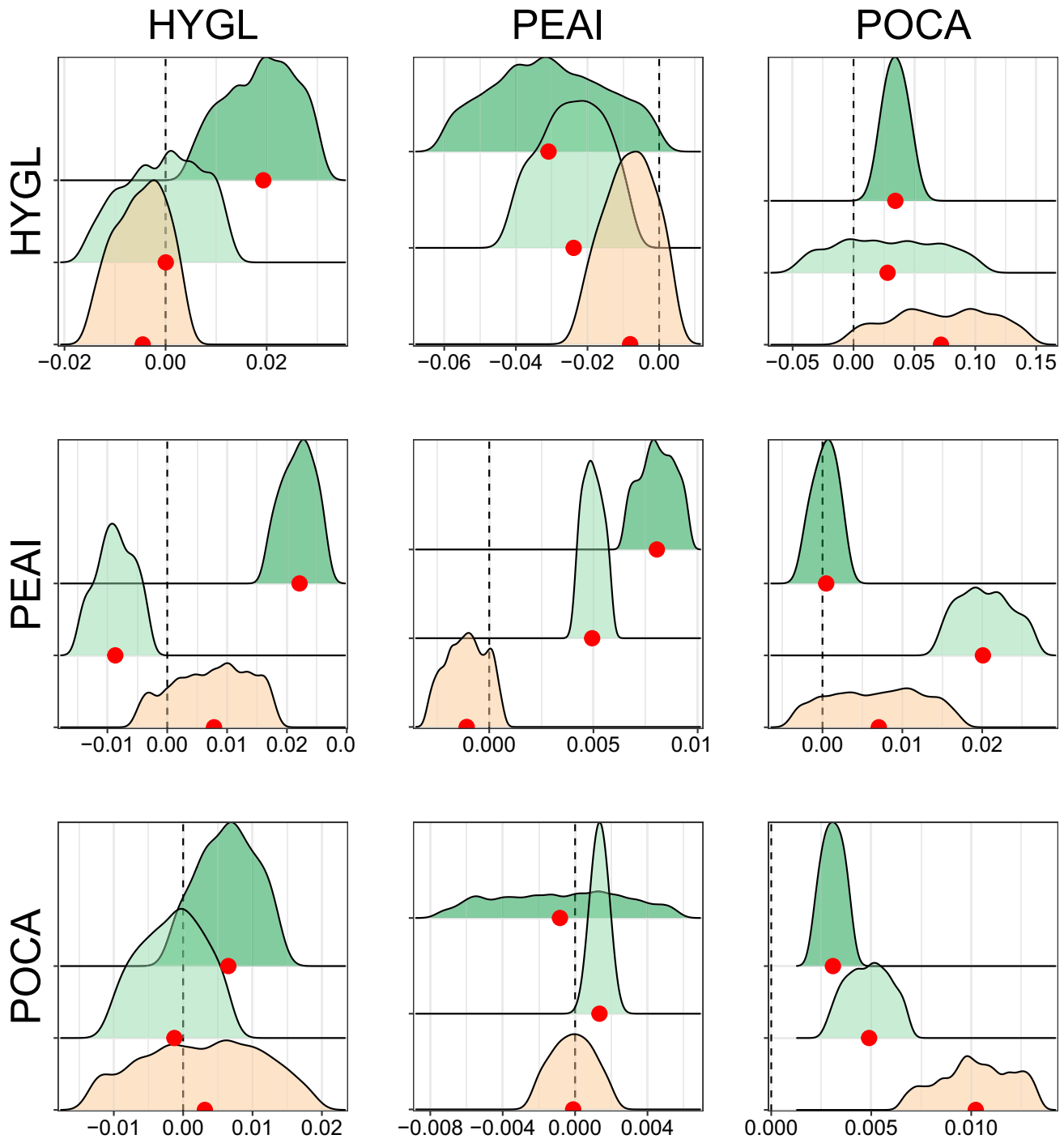


FIGURE 3 Interactions between three representative species from our study vary in direction and magnitude from one shade category to the next. Each graph plots the density distributions of the 80% credibility intervals of an interaction strength across all three networks (shady=dark green, intermediate=light green, open=yellow). Rows indicate the species being affected by the interaction, columns are the species which are emitting the interaction. The diagonal shows intraspecific interaction strengths. Values greater than 0 indicate competition and values lesser than 0 indicate facilitation. The red dots mark the median value of each distribution. Note the scale of the x-axis varies for each graph. We show a subset of interactions only for readability, see [Figure S3.5](#) to see the distributions of all 81 interaction strengths which were quantified across all three networks.

these nine species engaged in within each category. Some species participated in similar proportions of each interaction loop type across all environments whilst others did not ([Figure 4](#)). Most species, however, participated in different proportions of each interaction loop type in

each category ([Figure S3.6](#)). Though some species always maintained an overall competitive or facilitative effect, species often switched between overall competitive and overall facilitative roles in different shade conditions ([Figures S3.3–S3.4](#)). Individual species could, therefore,

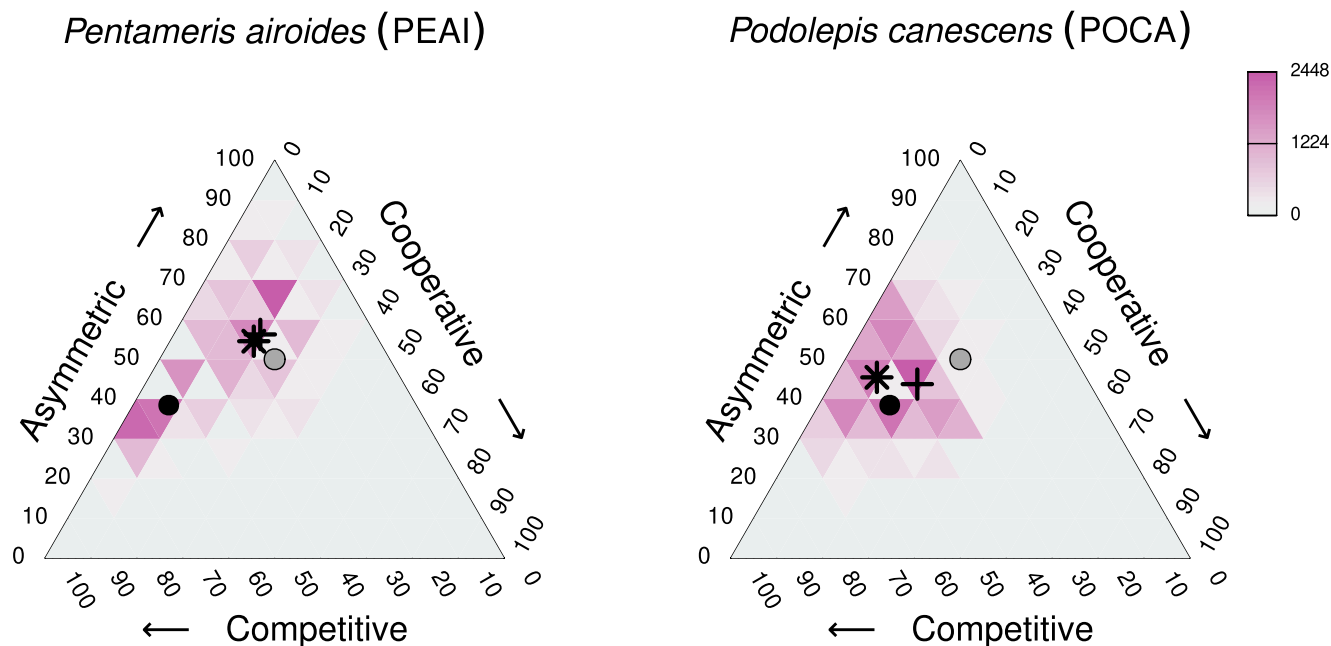


FIGURE 4 Two examples of how species showed variable (*P. airoides*) or consistent (*P. canescens*) interaction strategies across habitats. Axes represent the proportion of cooperative (+/+), competitive (-/-) and asymmetric (+/- or -/+) pairwise interaction loops. *P. airoides* and *P. canescens* engaged in all of these interactions across the study, we show the median for each shade category: a black asterisk (*) for the open network, a circle (●) for the intermediate network and a cross (+) for the shady network. The background colour indicates the density of values across all samples, going from light grey (low density) to magenta (high density), the scale is given at 10 levels per axis. The grey circle centred in the top half of each plot serves as a reference point, indicating where a species would be placed if it engaged in 25% cooperative loops, 25% competitive loops and 50% asymmetric loops. Graphs for the 19 other focal species are presented in [Figure S3.6](#).

vary in how they interacted between categories, and overall showed a weak consistency in response to changing environmental and biotic conditions.

Network properties

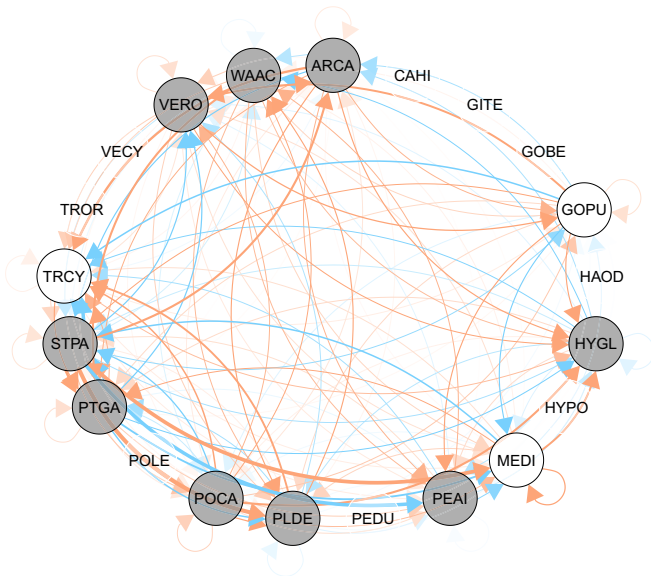
Network properties were fairly consistent across shade categories ([Figure 5](#)). Networks for all three shade conditions showed high degrees of intransitivity, with a median RII of 0.329 [0.203–0.469] under open conditions, 0.349 [0.253–0.464] under intermediate conditions and 0.191 [0.123–0.265] under shade. Median weighted connectance was fairly high for all networks, sitting at 0.539 [0.502–0.574] for the open category, 0.601 [0.564–0.638] for the intermediate category and 0.486 [0.455–0.517] for the shady category. Modularity was overall low at 0.21 [0.144–0.276], 0.231 [0.181–0.28] and 0.263 [0.22–0.304] under open, intermediate and shady conditions, respectively.

At the network level, interaction loops under open and shady conditions were predominantly asymmetric with a median of 45.4% [36.4–54.5%] and 50% [37.5–50%] of all interaction loops, respectively. Interaction loops were equally divided between competitive (42.3% [34.6–50%]) and asymmetric (42.3% [30.8–50%]) in the intermediate category. Cooperative loops were in the minority across all environments, sitting at 13.6% [9.1–18.2%], 11.5% [7.7–15.4%] and 18.8% [12.5–25%] in the open, intermediate and shady categories, respectively.

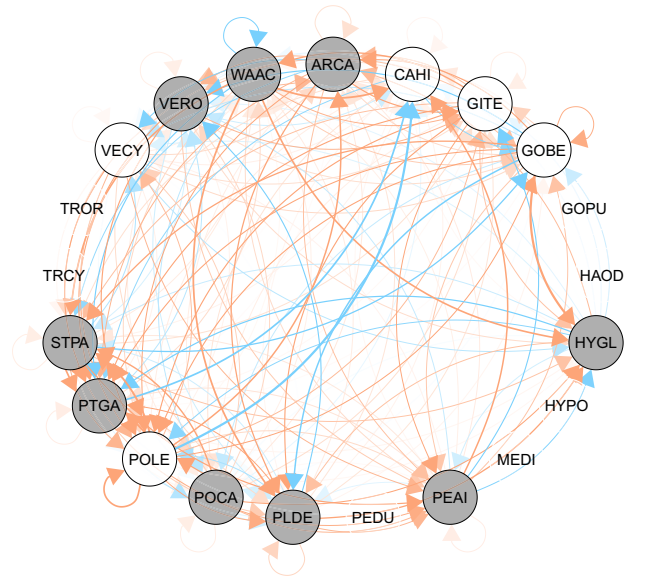
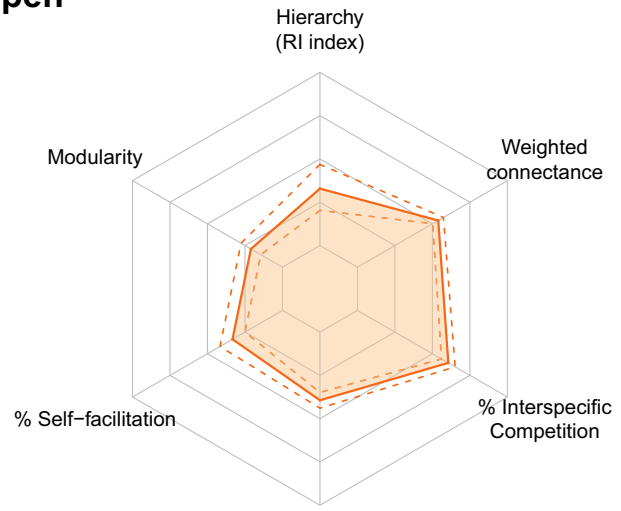
An increased participation in cooperative loops under shady conditions was matched with a decreased participation in competitive loops (31.3%, [25–37.5%]), rather than asymmetric ones.

DISCUSSION

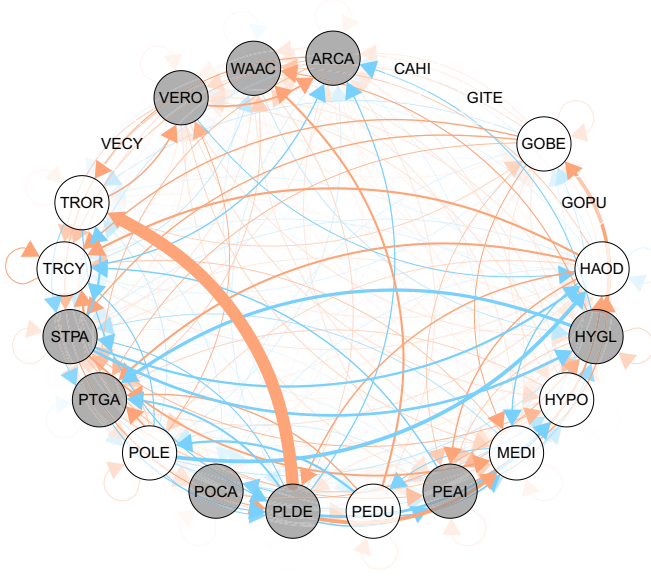
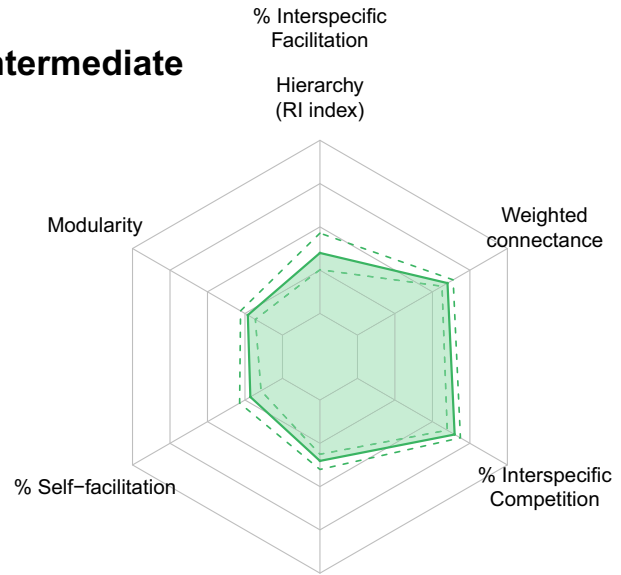
Our study reveals that plant–plant interactions and associated interaction networks vary non-linearly across an environmental gradient in ways that are distinct from patterns of diversity and composition. We first discuss how key aspects of these interactions and the networks we described differed from current dominant theoretical frameworks conceptualizing how diversity is maintained in non-trophic systems, namely the presence of interspecific and intraspecific facilitation and intransitivity. These results suggest that the processes maintaining diversity in this system are not operating according to competition-based expectations (Keddy & Shipley, 1989; Shipley, 1993), highlighting the need for alternative frameworks of diversity maintenance. Secondly, we examine how our results provide essential foundational information for laying out expectations for coexistence in circumstances when the assumptions of current frameworks do not hold. Though our findings in no way diminish competition as an important pathway to maintaining diversity, they give insight into avenues ripe for further investigation and potential



Open



Intermediate



Shady

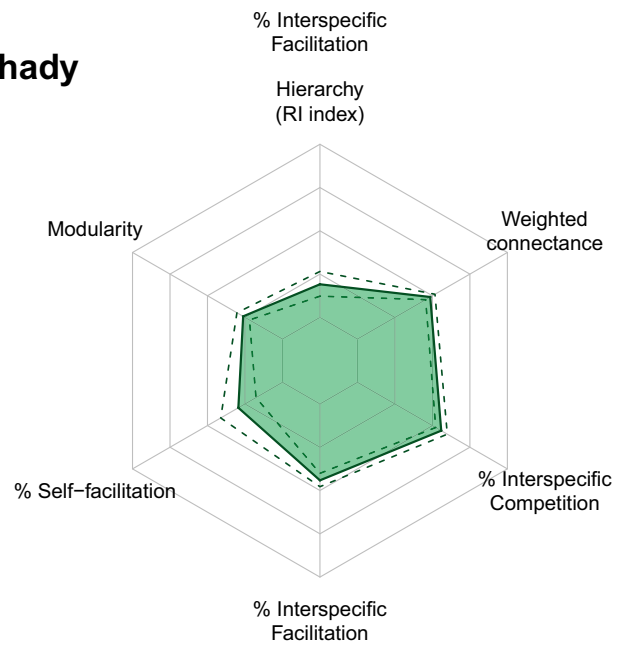


FIGURE 5 (Caption for previous page.) In the left column, we show median scaled interaction networks for each shade category. All 21 focal species are presented in each network to facilitate comparison, identified by their four-letter species code (Table 1 to match species codes to their name). The nine grey nodes indicate species which are present in all three networks, whereas species codes without a border indicate species that are absent from that network, and thus not interacting with other species. Competitive interactions are shown in orange, and facilitative interactions are blue. Each line represents an interaction strength with the arrow pointing to the species receiving the interaction and line thickness increasing with absolute interaction strength. Note that because median strength was close to 0 for many interactions these may not be strongly visible, but this does not imply they are absent. In the right column, we show how various network properties differ between networks. The solid line denotes the median across 1000 network samples, and the dashed lines indicate the 80% quantile across those same samples. The top three axes go from 0 to 1 and the bottom three from 0 to 100. Hierarchy (RI index) is given as in S. Methods S2.5.1, where a low value indicates intransitivity. Weighted connectance is given as in S. Methods S2.5.2, a lower value indicates the presence of many weak interactions and few strong interactions. % Interspecific Competition and Facilitation are the percentages of interspecific interactions which are competitive and facilitative, respectively. % Self-facilitation gives the percentage of intraspecific interactions which are facilitative. Modularity is given as in S. Methods S2.5.3. See Figure S3.7 for scatterplots of the covariance between these properties.

inclusion into more generalisable frameworks of diversity maintenance.

Challenges to current expectations of diversity maintenance

Though competition was the most common type of interaction observed in our study, facilitation was ubiquitous across species and environments. Current theory expects competition to dominate plant–plant interactions (Adler et al., 2010; Chesson, 1994; Went, 1973), whilst facilitation is relegated to extremes of abiotic stress (Bertness & Callaway, 1994) or specific life histories and stages (Choler et al., 2001; He et al., 2013; Losapio et al., 2018; Verdú & Valiente-Banuet, 2008). We did not find evidence of such restrictions: whilst some species had predominantly competitive or facilitative effects, many exerted and received a mix of both such that generalizing species into ‘competitors’ or ‘facilitators’ was impractical. Moreover, as interaction strengths often switched sign from one environmental category to the next, the majority of common species in our system experienced some degree of facilitation at some point along the naturally occurring shade gradient. Potential mechanisms driving facilitation in this system are numerous and include micro-environmental modification (Holmgren et al., 1997), plant–soil feedbacks (Ke & Wan, 2020) and pollinator attraction (Loy et al., 2015). Whilst these are currently being investigated, disentangling their relative contributions is complicated by the diversity, context-dependency and covariations of such processes (Callaway, 1995). Nonetheless, our findings support increasing evidence that facilitation is a pervasive and dynamic phenomenon which many species experience across their realized environmental ranges.

In competitive systems, intraspecific interactions are expected to be more strongly competitive than interspecific interactions for diversity to be maintained (Adler et al., 2018), a relationship which received only partial support in our study likely due to the inclusion of facilitation. How this expectation translates to systems where both competition and facilitation

jointly operate is not clear in the theoretical literature. Surprisingly, we also found recurring evidence of intraspecific facilitation across all shade conditions. Intraspecific facilitation is particularly problematic for predicting coexistence, summarily because species that self-facilitate have unstable population dynamics in monoculture and can experience runaway growth and over-abundance if not checked by competition (Barabás et al., 2017). It is thus incompatible with the ‘mutual invasibility criteria’ which underpins competitive theories of diversity maintenance even when these are extended to include interspecific facilitation (e.g. Ellner et al., 2019; Ke & Letten, 2018; Koffel et al., 2021; Rohr et al., 2014; Spaak & De Laender, 2020), and it is thus argued to be detrimental to coexistence (Schreiber et al., 2019; Yodzis, 1981).

When competition dominates, species are traditionally expected to form hierarchies of increasing competitive dominance (Shiple, 1993). We found that all networks were instead predominantly intransitive, where species interact like in a game of rock-paper-scissors (species A outcompetes B, B outcompetes C and C outcompetes A; Laird & Schamp, 2006). Intransitivity remains largely ignored from studies of coexistence (Soliveres & Allan, 2018) and whether it is common or rare is a contested matter (Godoy et al., 2017; Shiple, 1993; Soliveres et al., 2015; Soliveres & Allan, 2018), but it is perhaps promoted by facilitation and can yield coexistence under certain circumstances (Gallien et al., 2017; Godoy et al., 2017; Soliveres & Allan, 2018).

Overall, our results suggest that competition, negative density dependence (NDD) and competitive hierarchies are likely overestimated by traditional frameworks of coexistence (Detto et al., 2019) and provide increasing empirical evidence that non-trophic facilitative interactions and intransitivity are not rare occurrences likely to average out across spatial variation, but may be significantly more important than typically thought for maintaining observed diversity (Brooker et al., 2008; Cavieres & Badano, 2009; Coyte et al., 2015). It is likely a mix of competition and facilitation which maintains diversity (Wright et al., 2014) in this particular annual plant system. The effects of facilitation on diversity are complex (Bertness & Callaway, 1994; Bruno et al., 2003;

Callaway, 1995) and how it interacts with competition and intransitivity are ongoing research topics (Gross, 2008; Hart, 2023; Stouffer et al., 2018), but the development of these expectations remain rooted in theory initially developed for competitive systems with simple dynamics. Empirical systems are undoubtedly more complex and nuanced than the idealized ‘null models’ described by MCT, neutral theory and other commonly used frameworks of diversity maintenance and continuing to apply them to empirical cases which do not fit the underlying assumptions unfortunately restricts our ability to develop more inclusive theory.

Informing the development of a more generalisable theory of coexistence

By evaluating interactions between multiple species simultaneously and allowing for some degree of environmental heterogeneity, we can begin to form hypotheses about how diversity may be maintained in more complex and variable cases where the assumptions of current theory do not apply. Though some variability in interaction networks may arise due to changing environmental and biotic conditions, we expect those network properties which are crucial to diversity and stability to be relatively robust to environmental heterogeneity (Borrelli et al., 2015; Kinlock, 2019, but see Maynard et al., 2018). Despite differences in species composition and idiosyncratic and non-linear variation in interaction strengths, networks in this wildflower community were consistently intransitive, with high weighted connectance, low modularity, a higher proportion of facilitative interactions than expected and few cooperative loops across all environmental categories.

Intransitivity is thought to be more likely and more important to diversity maintenance under heterogeneous environmental conditions (Allesina & Levine, 2011; Saiz et al., 2019) as experienced by the annual plants in this system (Stouffer et al., 2018). High weighted connectance describes networks where species are densely and evenly connected to one another and our results align with records of other plant networks (Kinlock, 2019). Connectance also appears to confer some degree of stability (Altena et al., 2016) especially when strongly and weakly self-regulating species are connected to each other (Haydon, 2000). It may thus be an important indicator of stable diversity maintenance in systems such as ours composed of elements which vary widely in their degree of self-regulation (NDD). Modularity can also have a stabilizing effect on diversity but this effect is context-dependent (Grilli et al., 2016). A module as defined by our metric describes a group of species which strongly facilitate one another but compete strongly with non-module members (Traag & Bruggeman, 2009). The low modularity recorded here indicates that species did

not organize into groups of facilitators which preferentially interact with one another. This is supported by the low proportion of cooperative loops. Communities with asymmetric loops (+ / -) have been found to be the most stable (Allesina & Tang, 2012) whilst cooperative (+ / +) and competitive (- / -) loops destabilize systems (Coyte et al., 2015, 2021). Under certain conditions, however, cooperative loops can increase system stability and species persistence (Qian & Akçay, 2020) and some evidence suggests that a mix of cooperative and competitive loops can also maintain coexistence (Mougi & Kondoh, 2012). Moreover, when a time delay in species responses to interactions is introduced, it is communities with a mix of interaction loop types that are the most stable (Yang et al., 2023). Given the existence of a seed bank in our system, it is plausible that it fits this latter category, and the mix of interaction loops that we observed might help maintain system stability.

Clearly, which network properties promote diversity maintenance depends on other features of the community in question, including whether interactions are positive or negative (Grilli et al., 2016). Unfortunately our small sample size does not allow us to empirically test relationships between network properties and diversity. Given the lack of large, population dynamics-based interaction networks in the existing plant literature, our findings still provide crucial insights into how interactions may be organized when both facilitation and competition are included. Generalizing these results to other systems, spatial and temporal scales are crucial steps in furthering the development of more generalisable theory of plant diversity maintenance (Kinlock, 2019; Losapio et al., 2019, 2021; Verdú & Valiente-Banuet, 2008). Moreover, whilst averaging interactions within each environmental category as opposed to across the entire gradient remains only a partial and imperfect solution to the issue of context-dependency, our results illustrate that ignoring environmental heterogeneity likely masks the complexity of species interactions and emergent processes that maintain diversity. We should embrace these challenges and put further efforts into characterizing how diversity is maintained in natural systems, allowing natural history to guide us in developing new theoretical frameworks that better reflect the reality of multi-species coexistence (Travis, 2020).

AUTHOR CONTRIBUTIONS

M.D.B. designed the methodology, carried out analyses and led the drafting of the manuscript. D.B.S. helped design the methodology and interpret analyses and critically revised the manuscript. T.E.M. led the field study and data collection. M.M.M. helped design the field study, collected data, contributed to the interpretation of analyses and critically revised the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14376>.

DATA AVAILABILITY STATEMENT

The data used in this study are available in the Dryad digital repository <https://doi.org/10.5061/dryad.3tx95x6nf>. The code and scripts used to run the models, analyses and figures are available in the GitHub repository <https://github.com/malbion/PlantInteractionNetworks>.

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