Received: 7 November 2023 | Revised: 12 March 2024 | Accepted: 12 March 2024

DOI: 10.1111/ele.14425

LETTER

ECOLOGY LETTERS cnrs WILEY

Fast–slow traits predict competition network structure and its response to resources and enemies

Caroline Daniel[1] | **Eric Allan**[1,2] | **Hugo Saiz**[1,3] | **Oscar Godoy**[4,5]

[1]Institute for Plant Sciences (IPS), Bern University, Bern, Switzerland

[2]Centre for Development and Environment, University of Bern, Bern, Switzerland

[3]Departamento de Ciencias Agrarias y Medio Natural, Escuela Politécnica Superior, Instituto Universitario de Investigación en Ciencias Ambientales de Aragón (IUCA), Universidad de Zaragoza, Huesca, Spain

[4]Departamento de Biología, Instituto Universitario de Investigación Marina (INMAR), Universidad de Cádiz, Puerto Real, Spain

[5]Estación Biológica de Doñana, EBD-CSIC, Sevilla, Spain

Correspondence
Caroline Daniel, Institute for Plant Sciences (IPS), Bern University, Altenbergrain 21, CH-3013 Bern, Switzerland.
Email: caroline.daniel@ips.unibe.ch

Funding information
European Social Fund Plus (TASTE), Grant/Award Number: PID2021-127607OB-I00; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 310030_185260; Ministerio de Economía y Competitividad

Abstract

Plants interact in complex networks but how network structure depends on resources, natural enemies and species resource-use strategy remains poorly understood. Here, we quantified competition networks among 18 plants varying in fast–slow strategy, by testing how increased nutrient availability and reduced foliar pathogens affected intra- and inter-specific interactions. Our results show that nitrogen and pathogens altered several aspects of network structure, often in unexpected ways due to fast and slow growing species responding differently. Nitrogen addition increased competition asymmetry in slow growing networks, as expected, but decreased it in fast growing networks. Pathogen reduction made networks more even and less skewed because pathogens targeted weaker competitors. Surprisingly, pathogens and nitrogen dampened each other's effect. Our results show that plant growth strategy is key to understand how competition respond to resources and enemies, a prediction from classic theories which has rarely been tested by linking functional traits to competition networks.

KEYWORDS

leaf fungal pathogens, network structure, nitrogen addition, plant–plant interactions, species diversity, specific leaf area

INTRODUCTION

Global changes are dramatically altering ecological communities (Brooker, 2006). These changes can occur through shifts in plant performance (Ahmad et al., 2010) and alterations in plant–plant interactions (Matías et al., 2018; van Dyke et al., 2022). While past research has extensively investigated how resource gradients (e.g. DiTommaso & Aarssen, 1989; Tilman, 1985) or plant consumers can change plant interactions (e.g. Holt et al., 1994), most of the studies have either quantified overall competitive responses of individual species (Dormann & Roxburgh, 2005; Yang et al., 2022), or have examined pairwise interactions among a limited number of species (Chesson, 2000). Consequently, our understanding of how species interactions change within communities of multiple interacting species remains limited (Levine et al., 2017). This knowledge is essential to gain a more mechanistic understanding of global change effects on the assembly, stability and functioning of ecological communities (López-Angulo et al., 2018; Loreau & Hector, 2001; Mayfield & Levine, 2010).

Initial efforts to upscale pairwise interactions to multispecies plant–plant networks were largely theoretical (Allesina & Levine, 2011). Network approaches provide a way to summarise complex systems, however, studies of competition networks have typically focused on quantifying only some aspects of network structure (Gallien et al., 2017; Kinlock, 2019; Saiz et al., 2019; Soliveres et al., 2015). In contrast, classic competition studies have focused on simple metrics like the overall strength or degree of asymmetry in competition. However, to characterise interaction networks in contrasting conditions (Table 1) it is important to consider multiple metrics because they each provide complementary information about how the strength (weak vs. strong) and the sign (negative vs. positive) of species interactions change. Based on ecological theory, we might expect certain aspects to respond more strongly to different environmental drivers (Table 2). Further, many networks have been assembled using co-occurrence data or simple measures of interactions such as visitation rates. Although this information is valuable, it cannot be used to link network structure with the temporal dynamics of communities, because such networks do not contain information on how an increase or decrease in the abundance of one species, impacts the abundance of another species. Consequently, it is important to measure species interactions so that they can be incorporated into a population model to assess the demographic consequences (abundance shifts, local extinction, etc.) of plant–plant interactions and predict long-term outcomes.

Nitrogen addition is a key global change driver that can dramatically change the overall structure of plant–plant interactions. A large body of research has shown that nitrogen addition decreases coexistence opportunities by removing a limiting factor for plant growth (Tilman, 1982) and leads to long-term diversity loss (Crawley et al., 2005; Isbell et al., 2013; Suding et al., 2005). Nitrogen could therefore impact network structure in several ways: removing a limiting factor will

TABLE 1 Network metrics selected for this study, with their definition and ecological meaning.

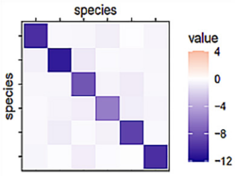
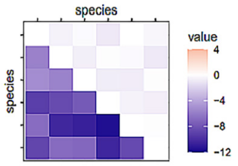
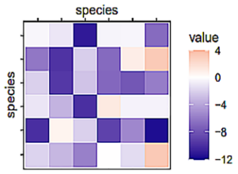
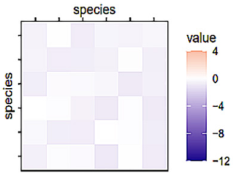
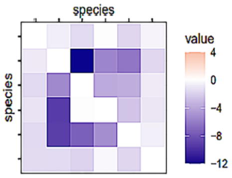
Network metric	Matrice layout	Definition	Ecological meaning
Diagonal dominance (dominance of intraspecific competition over interspecific competition)		Average difference between intraspecific and interspecific competition (Box 1, Equation 1)	Stronger intraspecific than interspecific competition means that species limit themselves more than limit others. This difference results in a higher niche differentiation, and more opportunities for species to coexist (Chesson, 2000).
Asymmetry (asymmetry of competitive effect vs. response)		Overall ratio between competitive effect (higher triangle of the matrix) and response (lower triangle of the matrix) (Box 1, Equation 2)	A high asymmetry between competitive effect and response means some species exert strong effects on others while suffering little competition in return. This could arise from competition for resources that can be easily pre-empted and monopolised, such as light and space (Connolly & Wayne, 1996). A higher asymmetry between competitive effect and response can result in higher fitness differentiation and less opportunities for species to coexist (Chesson, 2000).
Skewness (skewness in the distribution of interaction coefficients)		How skewed is the distribution of the interaction coefficients (towards negative or positive values). Symmetrical networks have a distribution equal to zero (Box 1, Equation 3)	Negative skewness means a few species are highly competitive, while most others are less competitive. We generally expect interaction coefficients to be negatively skewed (Adler et al., 2018) as a positive skew would indicate a small number of highly facilitative interactions and few/no strong competitive interactions. A strong negative skewness indicates some extreme competition coefficients (effect and/or response) which can emerge from a strong hierarchy in the competition between species, that is, one or two species are much more competitive than the others (Goldberg & Landa, 1991).

TABLE 1 (Continued)

Network metric	Matrice layout	Definition	Ecological meaning
Evenness (evenness in the distribution of interaction coefficients)		Evenness in the distribution of interaction coefficients, calculated from the Gini coefficient (bounded between 0 and 1). The Gini coefficient is the deviation from the line of perfect evenness. 1-Gini then represents the evenness (Box 1, Equation 4)	A high evenness in competitive interactions means all species interact similarly, either strongly or weakly. High evenness might occur in neutral communities (Adler et al., 2007), which show functional equivalence among species. In these communities, stochastic events can have a large effect on the population dynamics of interacting species. Importantly, high evenness is impossible when species differ strongly in intra and interspecific competition or if there is high asymmetry between effects and response. High skewness will also make high evenness impossible but skewness close to zero could arise in an even community with no strong interactions or in an uneven community where there is a balance between extreme competition and extreme facilitation.
Modularity (strength of competitive modules)		Average ratio of interaction strength between two species belonging to the same module, versus two species belonging to different modules (Box 1, Equation 5)	High modularity means that species interact strongly with only a few other species in the network, whereas low modularity means that all species interact with all others. High modularity could arise if species share resources or natural enemies. High modularity might indicate that different subsets of species occupy different niches.

Note: Each metric is presented with an example of the matrix layout when the metric is high (i.e. the network is highly diagonal dominant, highly asymmetric, highly even, highly negatively skewed and highly modular). Examples are presented for a species richness of $n=6$ species, for better clarity.

reduce intraspecific interactions relative to interspecific ones (Adler et al., 2018), leading to reduced diagonal dominance in the competition matrix. However, nitrogen addition alone might not strongly reduce niche dimensionality if other resources remain limiting (Harpole et al., 2016). In addition, nitrogen addition often makes plants taller and increases light competition (Eskelinen et al., 2022; Hautier et al., 2009). This is likely to promote competitive superiority for taller species (DeMalach et al., 2017), leading to asymmetry between competitive effects and responses because tall species exert strong effects on, but do not respond to competition from, short species. Overall, nitrogen addition is expected to impact various aspects of plant interaction networks (see Table 2 for detailed information) and determining which measures respond more strongly may shed light on the underlying mechanisms (changes in niche dimensions or light competition) by which nitrogen impacts species interactions.

Consumers, such as herbivores or pathogens, can also alter plant–plant interactions (Chesson & Kuang, 2008). Shared consumers can drive apparent competition among plant species (Holt, 1977) with potentially opposing effects on plant–plant interaction networks. For example, plant enemies, like specialist fungal pathogens, can maintain biodiversity by increasing intraspecific relative to interspecific competition (Bagchi et al., 2014; Connell, 1971; Janzen, 1970), thereby increasing diagonal dominance. Pathogens might also reduce the growth of several of the most competitive species (Alexander & Holt, 1998) causing plant–plant interactions to become weaker. Consequently, network skewness would decrease because of fewer strong competitive effects of dominant species on others, and evenness would increase (Table 2). Alternatively, pathogens could reduce biodiversity by reducing the tolerance of weaker competitors for competition (Mordecai, 2011; Pacala & Crawley, 1992; Parker & Gilbert, 2018). This would result in more extreme competition coefficients as weak competitors suffer more (increased negative skewness), and a decrease in evenness. Because studies on foliar fungal pathogens have found inconsistent effects on plant communities (Allan et al., 2010; Granjel et al., 2023; Liu et al., 2022; Spear & Mordecai, 2018), characterising competition networks with and without pathogens would provide a way to test both alternatives. Finally, fungal pathogens might interact with resources (Allan & Crawley, 2011; Cleland

TABLE 2 Corresponding hypotheses for how each network metric will respond to treatments and growth strategies.

Network metric	Expected changes with N addition	Expected changes with F addition	Expected changes with increasing SLA	Expected changes with increasing SLA variance
Diagonal dominance (D)	Decrease in diagonal dominance with nitrogen addition, as one limiting factor is removed, increasing interspecific competition (Tilman, 1982)	Decrease in diagonal dominance with fungicide addition if leaf fungal pathogens have a strong density-dependent effect and removing them decreases intraspecific competition (Liu et al., 2022)	Decrease in diagonal dominance for higher values of SLA, if fast growing species are less differentiated and have higher intraspecific competition than slow growing species (Adler et al., 2013)	No clear expectations for SLA variance
Asymmetry (A)	Increase in asymmetry with nitrogen addition, due to a shift towards more competition for light (Craine & Dybzinski, 2013)	Increase (or decrease) in asymmetry with fungicide addition if leaf fungal pathogens specifically attack strong (or weak) competitors, and removing them increases their competitive effect (Alexander & Holt, 1998; Pacala & Crawley, 1992)	Increase in asymmetry with higher SLA, if fast growing species compete more asymmetrically for light (Schwinning & Weiner, 1998)	Increase in asymmetry with higher SLA variance, if fast growing species have stronger competitive effects on slow growing species (Schwinning & Weiner, 1998)
Skewness (γ)	Skewness becomes more negative with nitrogen addition, if resource addition favours a small set of species that have a disproportionally strong impact on other species (Tilman, 1982)	Increase (or decrease) in skewness with fungicide, if leaf fungal pathogens attack strong (or weak) competitors (Alexander & Holt, 1998; Pacala & Crawley, 1992)	Skewness becomes more negative for higher values of SLA, if fast growing species compete more than slow growing species (Grime, 2006)	No clear expectations for SLA variance
Evenness ($1 - G$)	Decrease in evenness with nitrogen addition, if resource addition favours a small set of species unevenly increasing their interactions (Tilman, 1982)	Decrease (or increase) in evenness with fungicide, if leaf fungal pathogens attack strong (or weak) competitors (Alexander & Holt, 1998; Pacala & Crawley, 1992)	Decrease in evenness for higher values of SLA, if all fast growing species are competing strongly for the same resources while slow growing species have more possibilities for niche differentiation and compete less strongly (Grime, 2006)	Increase in evenness or decrease in evenness for higher values of SLA variance, depending on whether interaction coefficients are linked respectively to more niche differentiation (Grime, 2006) or more differences in competitive abilities (Kraft et al., 2015)
Modularity (M)	Increase in modularity with nitrogen addition as a small set of favoured species interact more strongly together (Tilman, 1982)	Decrease in modularity with fungicide, if pathogen sharing between a set of species drives formation of modules based on apparent competition (Alexander & Holt, 1998; Pacala & Crawley, 1992)	Decrease in modularity with higher SLA if all fast growing species equally interact together, while slow growing species are competing for soil resources and have more niche differentiation (Grime, 2006), forming better defined modules.	Increase in modularity with higher SLA variance if mixed community form modules of fast growing species on one hand, slow growing species on the other hand (Gross et al., 2009)

Abbreviations: F, fungicide; N, nitrogen; SLA, specific leaf area.

BOX 1 Equations for calculating network metrics

With the matrices of species interactions obtained in the previous step, we calculated the following metrics at the community level (Table 1):

- The global ratio of intraspecific versus interspecific competition (D)

$$D = \frac{1}{n} \sum_{i=1}^{n} \left(\left| \alpha_{ii} \right| - \sum_{j \neq i}^{n} \left| \alpha_{ij} \right| \right) \tag{1}$$

where D is a measure of the diagonal dominance of the matrix, n is the total number of species in the matrix, α_{ii} is the intraspecific competition coefficient (contained in the diagonal) and α_{ij} is the interspecific effect of species j on species i (contained in the off diagonal). If $D \geq 0$, then species suffer stronger intraspecific competition than the sum of all possible interspecific competition coefficients. Reciprocally, if $D \leq 0$, the sum of interspecific competition is larger than intraspecific competition. This continuous measure is conceptually close to the binary measure of quasi diagonal dominance (QDD) which has been related to network stability (Liang & Wu, 1998).

- The degree of asymmetry (A) in competition

$$A = \frac{\sum_{i \neq j}^{n} \left| \alpha_{ij} \right| - \left| \alpha_{ji} \right|}{n} \tag{2}$$

where A measures the difference between the competitive effect of species i on species j (α_{ij}), versus the effect of j on i (α_{ji}), averaged across all pairs of species (Vázquez et al., 2007). A greater value of A implies larger asymmetry within the community.

- The distribution of interaction coefficients measured as skewness (γ)

$$\gamma = \frac{\overline{\alpha} - M_d}{\mathrm{SD}} \tag{3}$$

where $\overline{\alpha}$ is the mean of all interaction coefficients α_{ij} within the network, M_d the median and SD the standard deviation of the coefficients. The skewness, by comparing the mean to the median, describes to the extent to which interaction coefficients are skewed to either negative or positive values, that is, if there are some extremely low or high values. Greater skewness values indicate a distribution of interaction coefficients with larger tails.

- The distribution of interaction coefficients measured as the Gini coefficient of evenness (G)

$$G = \frac{\sum_{i=1}^{n} \sum_{j \neq i}^{n} \left| \alpha_{ij} - \alpha_{(i+1)(j+1)} \right|}{2n^2 \, \overline{\alpha}} \tag{4}$$

where n is the number of species, $\overline{\alpha}$ is the mean of every interaction coefficient α_{ij}. The Gini coefficient describes the degree of inequality in the distribution of the interaction coefficients. It ranges between 0 and 1 where 0 is perfect equality and 1 is total inequality (Gini, 1912), we use $1 - G$ here so that high values indicate high evenness. Because interspecific interactions coefficients were both positive and negative, we used a correction of G which separates positive and negative values, then reassembles them in a single value of evenness (Raffinetti et al., 2015).

- The modularity (M)

Modularity (M) is computed as a ratio that compares the average strength of the links between two nodes, or vertex, that belong to the same module, versus links between two nodes of different modules. Consequently, optimising modularity corresponds to grouping the nodes, that is, the species, to maximise the strength of interactions (interaction coefficients are used as weights) within a module, while minimising the strength of interactions between modules. This creates the smallest number of groups of similarly behaving species. Modularity was computed using absolute values of interaction coefficients, following the formula from Clauset et al. (2004):

$$M = \frac{1}{2m} \sum_{i,j} \left(A_{ij} - \gamma \frac{k_i k_j}{2m} \right) \delta\left(c_i, c_j\right) \tag{5}$$

BOX 1 (Continued)

where m is the number of edges, A_{ij} is the adjacency matrix (weighted by the magnitude of their corresponding interactions α_{ij}), γ is the resolution parameter weighing for the size of the modules ($\gamma = 1$ here, as standard), k_i is the degree of connection going out from the node, k_j the one coming to the node, $\delta\left(c_i, c_j\right)$ is equal to 1 if both vertex are belonging to the same module, 0 otherwise. By weighing the adjacency matrix by the interaction magnitude and not sign, we assume that a strong positive link is of the same importance as a strong negative link. Negative values of modularity mean that interactions are stronger between than within modules, while positive values indicate the opposite (Clauset et al., 2004; Reichardt & Bornholdt, 2006).

& Harpole, 2010), and they might amplify or dampen each other's effects, depending on whether they favour the same set of species or not. Only experiments crossing nitrogen addition and enemy removal can address these potential interactions.

Plant–plant interactions might also vary depending on plants resource-use strategies. A key axis of plant functional variation separates fast growing, resource acquisitive species from slow growing, conservative species with high levels of defence against consumers (Coley et al., 1985; Poorter et al., 1990). Fast growing species rapidly acquire resources and are competitive for light, whereas slow growing species are adapted to low-resource conditions and may be more competitive for soil resources. Several traits relate to the resource economics spectrum, and specific leaf area (SLA) is one of the most commonly measured (Díaz et al., 2016; Funk et al., 2017; Kunstler et al., 2016). Previous studies linking traits to competition have considered that trait differences (i.e. variation in SLA) affect network structure. For example, if competitive ability depends on SLA (Kraft et al., 2015), we should expect high evenness and low response-effect asymmetry between species which are similar in SLA versus low evenness and high asymmetry in networks with high variation in SLA (van Dyke et al., 2022). Moreover, classic ecological theories would predict that fast and slow growing plants interact differently, however, studies have not tested whether mean traits (e.g. mean SLA of a community) affect plant–plant interactions, that is, whether slow–slow competition is different from fast–fast competition. Networks of fast growing plants (high mean SLA) competing for light might have higher response-effect asymmetry, be less even and more skewed, with some highly competitive species and many weaker competitors (DeMalach et al., 2017). In contrast, networks of slow growing species competing for different soil resources might be more symmetrical, more even, less skewed and show greater differences between intra and interspecific competition (Tilman, 1982). As fast and slow species are expected to respond differently to pulses of resources and enemies attack (Grigulis et al., 2013; Loranger et al., 2012), traits like SLA could also predict the response of competition networks to resources and enemies. For instance, fast species are likely to benefit more from nutrient addition (da Silveira Pontes et al., 2010) and a reduction in enemies (Cappelli et al., 2020; Coley et al., 1985). Many studies have compared interactions between high- and low-resource environments but they have not distinguished whether plant–plant interactions change because the resources and enemy levels change, or because functional composition changes (from slow to fast species).

Here we investigate how nitrogen enrichment and foliar fungal pathogen removal (with fungicide) alter interaction networks of plants differing in resource economics strategy. Networks were built from pairwise intra and interspecific effects among 18 perennial plant species, differing strongly in SLA, planted as focal individuals (phytometers) and measured in a large grassland experiment (PaNDiv Experiment, Switzerland). We quantified 18 × 18 species competition networks in control, nitrogen, fungicide and combined nitrogen and fungicide treatments, in late spring and late summer. Environmental conditions are highly variable throughout the season (especially water availability), so we tested how consistent the patterns were across seasons. We therefore investigated: (1) what attributes of the whole plant network (Tables 1 and 2) varied most with nitrogen addition, pathogen removal and their interaction; and (2) whether networks composed of either slow growing, fast growing or a mix of fast and slow growing species (i.e. differing in the variance and mean of SLA) responded differently to nitrogen and foliar pathogens.

MATERIALS AND METHODS

Experimental set-up

We conducted our study within the PaNDiv experiment in Bern, Switzerland. PaNDiv experiment was set up in October 2015 and contains 336 plots of 2 m × 2 m with different numbers and compositions of 20 perennial grass and herb species, selected to vary in their SLA and leaf nitrogen content and therefore in resource use strategy (Table S1). In total, 80 monoculture plots and 256 mixture plots were established, varying in functional composition and species richness (for more information, see Pichon et al., 2020). Species richness and functional composition are crossed with four treatments: control (C), nitrogen addition (N), fungicide addition (F) and combined nitrogen and fungicide addition (NF). Fertilised plots received nitrogen in the form of urea twice a year in April and late June, for an annual addition of 100 kg N ha^{-1} year^{-1}. Two fungicides ('Score Profi', 23.5% Difenoconazol 250 g L^{-1} and 'Heritage Flow', 22.8% Azoxystrobin 400 g L^{-1}) were sprayed four times a year (early April, early June, late July and September) to reduce foliar pathogens. Water was sprayed simultaneously on the untreated plots. The experiment was weeded three times a year to maintain the diversity and composition treatments. Plots were mown twice a year, in mid-June and mid-August, which corresponds to intermediate to extensive grassland management (Blüthgen et al., 2012).

Phytometer experiment to estimate species interactions

We took advantage of this experimental design to estimate species interactions as pairwise intra and interspecific effects. We used a phytometer approach, which involved measuring biomass production of individuals planted in neighbourhoods differing in density (from no neighbours to crowded neighbourhoods) and relative frequency of different species (with conspecific or heterospecific neighbours), across the four treatments. These neighbours could belong to several species including the phytometer species. Neighbourhoods were defined as all plants within a 20-cm radius of the phytometer (Granjel et al., 2023). We obtained phytometers by germinating commercially supplied seeds (UFA Samen in Switzerland and Rieger Hoffmann in Germany) in an experimental greenhouse (Ostermundigen, Switzerland August 2019). We planted phytometers in the field in September 2019 when they had grown to 3–5 cm tall. Because they were seedlings, our study allows us to understand how perennial plants interact across life stages from early seedlings to maturity, when they flower in summer. Two of the 20 species, *Anthriscus sylvestris* and *Heracleum sphondylium*, did not germinate well enough, and were not included, but they also did not establish well on the experiment (Cappelli et al., 2022). The remaining 18 species were each planted into 10 different intraspecific neighbourhoods varying in density, using monoculture plots and into three different neighbourhoods for each heterospecific competitor. Three species, *Poa trivialis*, *Anthoxanthum odoratum* and *Rumex acetosa*, did not occur in high density neighbourhoods, although they were present in some neighbourhoods for each phytometer. Finally, we grew phytometers of all species in plots with no neighbours, to estimate growth without any other individuals present. These phytometers were planted 20 cm apart in 2 × 2m plots covered with landscape fabric to prevent weed growth and received all combinations of nitrogen and fungicide (as applied on PaNDiv). They were cut at the same time as the field was mown. Overall, we planted a total of 4248 phytometers for all species, which corresponded to 3240 heterospecific neighbourhoods (3 replicates × 4 treatments × 18 species × 15 neighbourhoods), 720 conspecific neighbourhoods (10 replicates × 4 treatments × 18 species) and 288 no competition neighbourhoods (4 replicates × 4 treatments × 18 species). We measured phytometers in June 2020 2–3 weeks before the mowing, and again in August 2020 after their regrowth. All species are perennials and regrow following cutting. We started with 4248 phytometers planted in September 2019, and recovered 3888 (91.5%) in June 2020 and 2722 (64.1%) in August 2020.

Statistical approach to estimate species interactions

With the phytometer data, we assessed the strength of negative (competition) or positive (facilitation) interactions that occur when the phytometer biomass of a species i is reduced (or increased) as the neighbourhood density of species j increases. Although the neighbourhoods included multiple species, the model allowed us to statistically tease apart these interactions at the pairwise level (including intraspecific effects). More specifically, for each of the 18 focal species, we fitted a model with a negative binomial function ('GLMMTMB' package, version 1.1.2.3, Brooks et al., 2017). This function was selected because it allowed us to quantify with equal probability both competition and facilitation. In our analyses, the response variable (phytometer biomass as dry weight in mg) was related to the (1) cover of each of the 18 neighbour species, including conspecifics (each species cover was included as an independent variable, i.e. 18 variables), (2) treatment (control, nitrogen, fungicide and combined nitrogen and fungicide) and (3) sampling time (June or August). We also included as a covariate the (4) cover of weeds, that is, neighbouring plants different from the 18 target species, however, it was generally low (5.39% on average). The model also included all interaction effects between treatment, sampling period and neighbour species, except for the interaction between sampling period and treatment, which was not estimated due to convergence issues. The level of experimental replication was sufficient to independently estimate each interspecific pairwise interactions from neighbourhoods in which several competitors co-occurred, however some interspecific coefficients, particularly those between species that were rare in the experiment, were estimated with more error. To account for this uncertainty, we divided each interaction coefficient by its standard error, so that poorly estimated coefficients became close to 0. We therefore estimated all intraspecific effects (α_{ii}, the per capita effect of one species on itself) and pairwise interspecific effects (α_{ij}, the per capita effect of species j on species i) across treatments and sampling times. In total, we built eight matrices (4 treatments × 2 sampling times) of 18×18 species, with $4 \times 2 \times 18^2 = 2592$ interaction coefficients. These coefficients were used to compute several network metrics (Table 1). All analyses were done using R version 4.1.0.

Computation of network metrics

We selected five different network metrics that represent different facets of plant competition (Table 1). These five metrics were calculated using Equations (1)–(5) respectively (Box 1). Skewness (γ) was calculated with the skewness function of the package 'moments' (version 0.14.1, Komsta & Novomestky, 2015). The Gini coefficient (G) was calculated with the function Gini_RSV of the package 'GiniWegNeg' (version 1.0.1, Raffinetti et al., 2015). Modularity (M) was calculated with the modularity function of the 'igraph' package 1.3.1. on the modules determined with the cluster_optimal function (Csardi, 2013), using the absolute values of the coefficients ($\sum_{i \neq j}^{n} \left|\alpha_{ij}\right|$) as weights of the edges (Reichardt & Bornholdt, 2006).

Effects of nitrogen, fungicide and species resource use on plant–plant network properties

A central aim of our work was to use network metrics to understand how plant interactions varied with nitrogen and fungicide treatments and whether fast and slow growing species responded differently (Table 2). To address this, we focused on subnetworks of five species because this is the average number of species found in interspecific neighbourhoods (mean = 5.19 species). We estimated the network metrics described above (Table 1; Box 1) for all 68,916 five species networks composed from the 18 species, in each of the four treatments and two sampling periods. We characterised the growth strategy of these networks using the mean and variance in SLA between the species (Supplementary Method 1). We then fitted models to estimate the network metrics for the 55,1328 networks using: (1) nitrogen addition, fungicide addition and their combination, (2) the sampling period (June and August), (3) the mean and variance in community SLA and (4) interactions between mean and variance in SLA and the treatments and seasons. The networks of five species are not fully independent since they share species, so we used multi-membership models to correct for the degree of similarity between networks inside the random effects of the mixed model (Supplementary Method 2).

In the last step of the analyses, we tested whether previous results based on five species would differ if larger networks were considered. Accordingly, we computed all metrics for every possible network containing 5, 7, 11 and 15 species, resulting in a total of $n = 292{,}128$ networks. To make this analysis comparable across species richness levels, we focused on networks containing mixed resource use strategies (at least one fast and one slow growing species). This is because networks with 11 or 15 species necessarily include both strategies, as there are eight fast and 10 slow growing species, and the range in mean and variance of SLA would therefore be lower in these larger networks. For this last analysis, we also fitted multi-membership models (Supplementary Method 2), but we only included interactions measured in June.

RESULTS

We estimated 324 pairwise interaction coefficients for each sampling period and treatment, that is, 2592 interaction coefficients in total. Although we observed some facilitation, negative interactions (i.e. competitive interactions) were prevalent (84%, min = 81%, max = 90%), and their average strength was −1.55 (min = −10.86, max = 3.00, Figure 1 for June and Figure S1 for August). A competitive interaction of −1.55 corresponds to a reduction of around 26% of the phytometer biomass when competitor cover increases from 0% to 20%. Among all 18 species, *Holcus lanatus* (Hl) had particularly large competitive effects on all others (Figure S2). In contrast, *R. acetosa* (Ra) and *Daucus carota* (Dc) were fairly insensitive to competition (low competitive response, Figure S3).

Nitrogen and fungicide addition had significant impacts on almost all network metrics (Figures 2 and 3; Table S2). As we analysed a very large number of networks, effects were typically significant and we therefore focused on effects that we defined as 'strong', that is, with standardised coefficients >0.1 or <−0.1. Fungicide had the strongest effects and impacted all metrics except asymmetry. Fungicide strongly increased evenness, reduced modularity and negative skewness. Nitrogen addition strongly reduced the diagonal dominance of the networks, increased asymmetry and negative skewness. However, nitrogen also strongly increased evenness and modularity. Nitrogen and fungicide interacted with each other and often dampened each other's effects. We analysed whether such dampening was due to different species responding to the two treatments but found no consistent pattern (Figures S4 and S5). Season primarily affected modularity and networks were strongly modular in August (Figures S6 and S7).

Communities with different mean SLA often responded in opposing ways to the treatments. Asymmetry increased with nitrogen addition in low SLA networks but was reduced with nitrogen in networks with high SLA. Conversely, fungicide reduced modularity in low SLA networks, but led to more modular networks in high SLA communities. A triple interaction was also observed for skewness between mean SLA, nitrogen and fungicide addition. As such, skewness was increased by

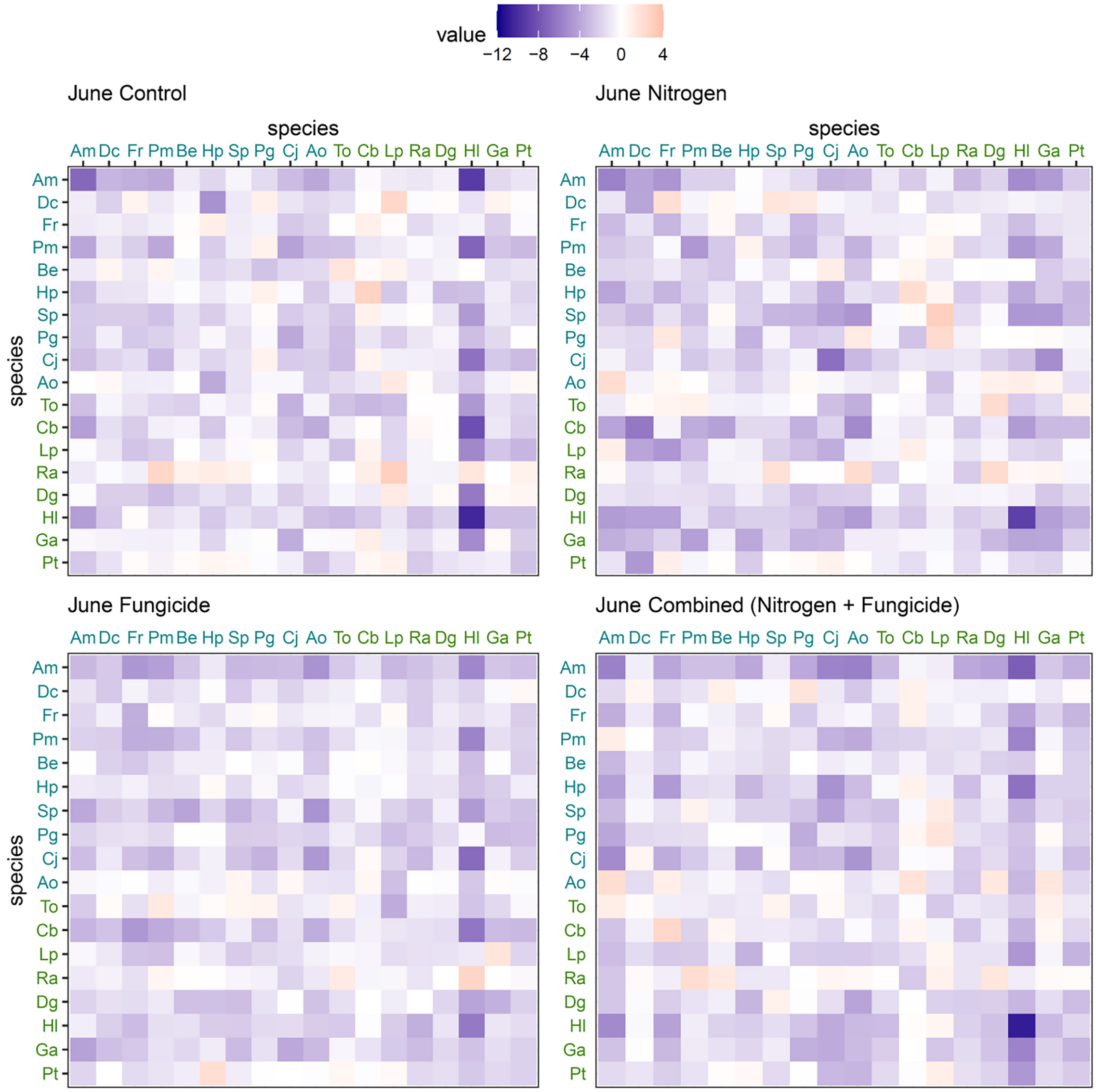


FIGURE 1 Matrices of pairwise interactions between the 18 species sampled in our experiment in June. August matrices for each treatment are included in Figure S1. Each cell shows a pairwise interaction, colours show the sign and the magnitude of the interaction. Species names in blue are slow growing species, green are fast growing species. Columns show species effects on others while rows show species response to competition from others. For instance, row 2 column 1 shows the response of Salvia pratensis to competition from *Achillea millefolium* and row 1 column 2 shows the effect of Sp on Am. See Table S1 for species names abbreviation.

all treatments in low SLA communities, but it was reduced or not affected by the treatments in high SLA communities. The variance of SLA within communities also strongly affected network metrics response to both nitrogen and fungicide addition (Table S2). Overall, communities with high variance in SLA were more negatively skewed and modular than those with low variance in SLA (Figures 2 and 3; Table S2). However, both nitrogen and fungicide addition reduced diagonal dominance and increased skewness in communities with high variance in SLA, whereas the treatments had no effect at low variance in SLA. In contrast, evenness was increased by nitrogen and fungicide and modularity was reduced, in communities with high variance in SLA (Figure 2). Asymmetry was also increased by nitrogen, in communities with low variance in SLA, and reduced by nitrogen at high variance in SLA.

Finally, we observed that network metrics changed as we increased the number of species in the network from 5 to 15. However, the treatment effects and interactions between treatments, mean and variance of SLA remained qualitatively the same (Figures S8 and S9; Table S3).

DISCUSSION

We found that resource addition and enemy removal strongly impacted the structure of plant–plant interaction networks. Nitrogen addition and the removal of foliar fungal pathogens generally reduced the dominance

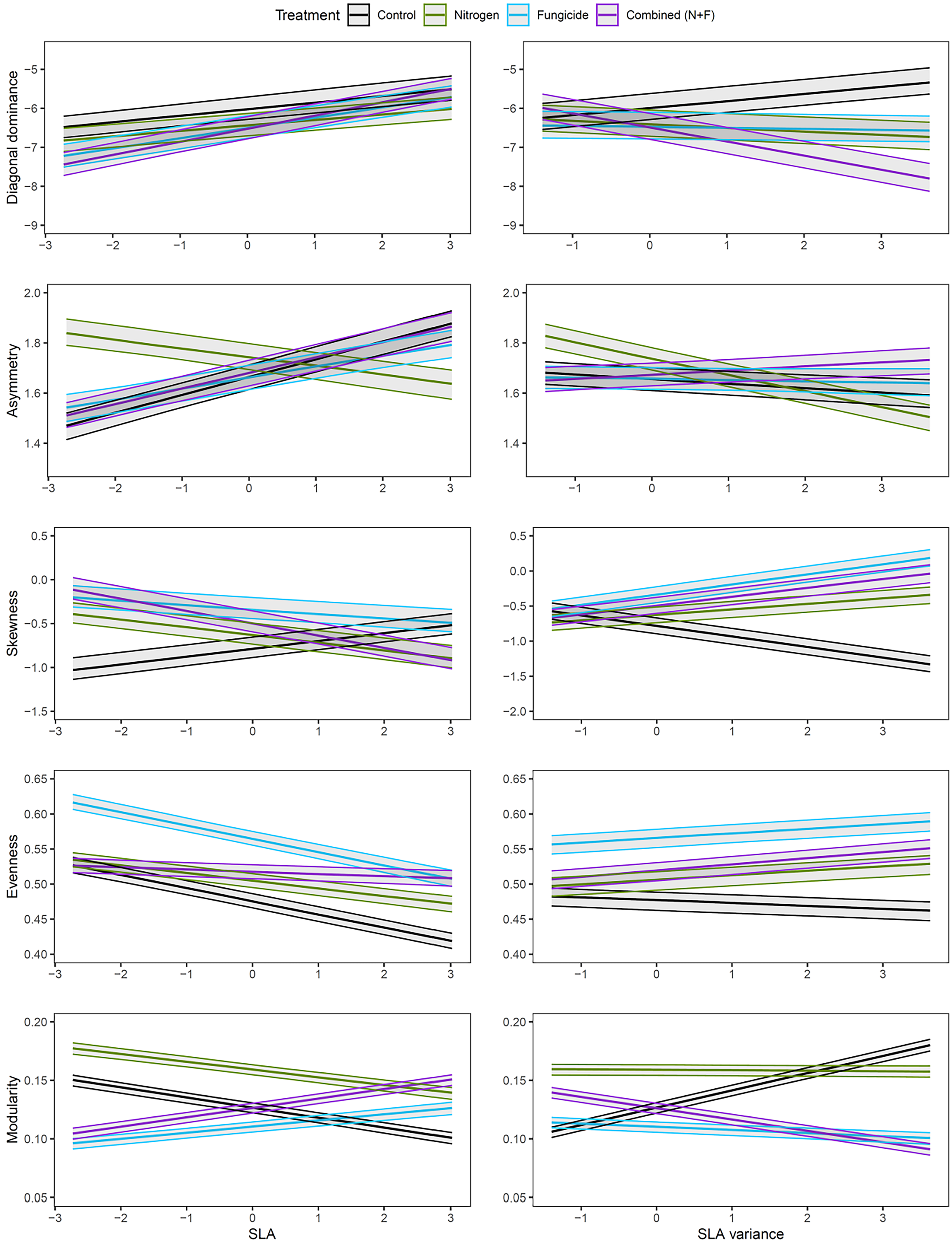


FIGURE 2 Impact of SLA (left panels), SLA variance (right panels) and treatments on network metrics for communities of five species over the two sampling seasons. For each network metric, colours determine treatments, and model predictions are shown in the form of predicted mean (bold lines) and confidence intervals (upper and lower lines). SLA and SLA variance were scaled for comparison. F, fungicide; N, nitrogen; SLA, specific leaf area.

of intraspecific interactions over interspecific interactions. Nitrogen addition also made interspecific interactions more asymmetric. Both effects are in line with theoretical expectations that resource limitation and enemies maintain diversity by increasing self-limiting effects and equalising competitive ability between species (Buche et al., 2022; Chesson, 2000). However, nitrogen and fungicide also affected other facets of plant

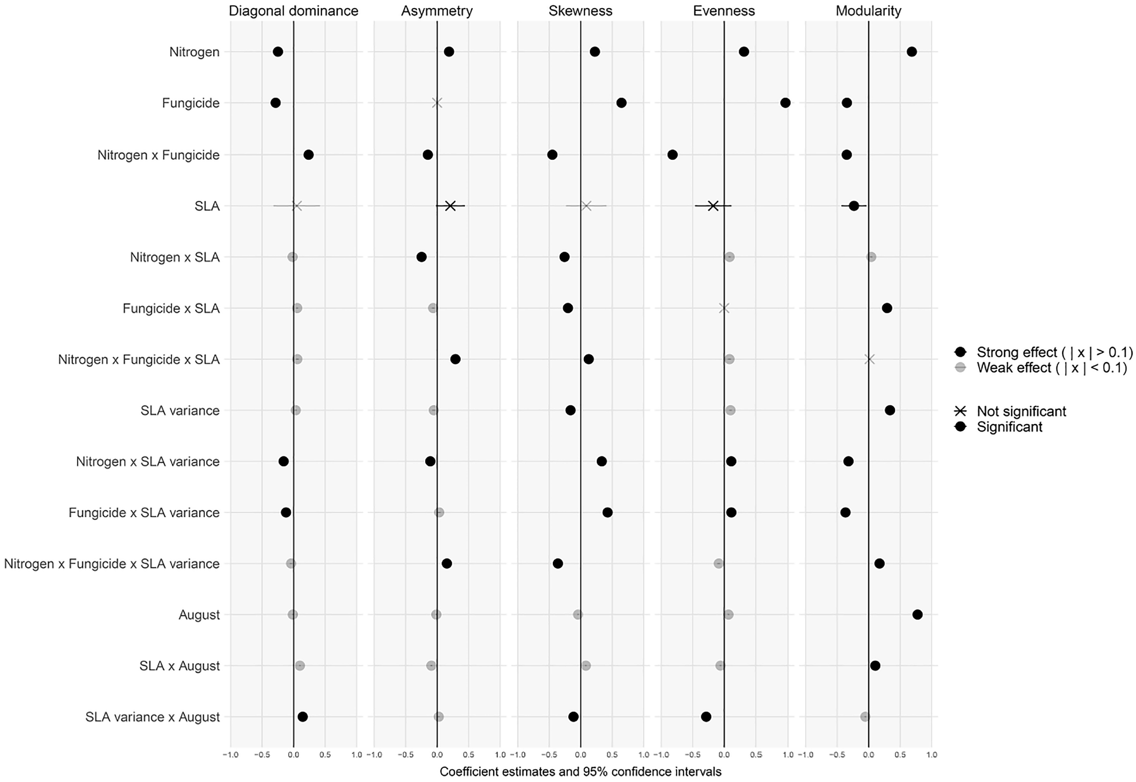


FIGURE 3 Estimates of fixed effects from multi-membership LMER models showing the effects of nitrogen addition, fungicide addition, SLA, SLA variance and season on functionally mixed communities of five species. All network metrics, SLA and SLA variance were scaled for comparison. Importantly, most variables (except SLA) displayed extremely small confidence intervals due to the high number of networks computed (n=55,1328), which is why 'strong' versus 'weak' effects were highlighted. SLA, specific leaf area.

competition in multispecies communities, in ways which did not always agree with major theories (Alexander & Holt, 1998; Tilman, 1982). Nitrogen and fungicide made communities more even and less negatively skewed, which was counter to our expectations, and they typically dampened each other's effects, rather than acting in a similar way. Some of these unexpected results arose because the impacts of nitrogen and fungicide depended on the mean and variance of SLA between species in the networks (Figure 2). Studies linking traits and competition have looked at effects of trait differences but not effects of mean traits (Adler et al., 2018). However, our results indicate that overall fast–slow resource strategy is a key driver of plant–plant interactions and determines how they respond to changes in resources and enemies. This idea is implicit in some classic theories (Grime, 1979; Tilman, 1982) but has rarely been addressed in studies linking functional traits to competition networks.

Effects of nitrogen addition on competition networks strongly depended on the growth strategy of the constituent species. We expected plants to grow taller and compete more for light following nitrogen addition (Eskelinen et al., 2022), which would result in more asymmetric interactions, as tall species strongly affect their neighbours (strong competitive effect) but are only weakly affected by smaller neighbours (weak competitive response). Many studies have looked at traits determining overall competitive effect and response (Goldberg & Landa, 1991; Schwinning & Weiner, 1998; Wang et al., 2010), and some have identified increased asymmetry as a major mechanism causing species loss following nitrogen enrichment (DeMalach et al., 2017; Xiao et al., 2021), however, few have looked at how the asymmetry between competitive effects and responses changes with nitrogen addition. We found that nitrogen did increase response-effect asymmetry in networks composed only of slow growing species, mostly due to increased competitive effects of species such as *D. carota*, *Prunella grandiflora* and *Plantago media* (Figure S4), and not due to decreases in their responses. However, we observed the opposite outcome in fast growing and mixed fast–slow communities, where nitrogen led to more even and symmetrical competition networks. Nitrogen only increased competitive effects for a few fast growing species, like *Gallium album*, while it reduced extreme competitive effects and increased the competitive response of many others, such as *H. lanatus* (Figure S4). Indeed, adding nitrogen alone could shift resource limitation to phosphorus or water, rather than light (Dong et al., 2019; Li et al., 2016; Lü et al., 2018), and slow growing species may be very competitive for phosphorus or water. Alternatively, several fast growing species may be very uncompetitive without nitrogen, leading to highly uneven competition networks under resource-limited conditions. Although more work is needed to test these possibilities, these network changes align with the fact that adding nitrogen shifts our communities towards lower values of SLA over time, which suggests that slow species are more competitive on N fertilised plots (Supplementary Method 3; Figure S10). Overall, these results indicate that the species with different growth strategies may compete in fundamentally different ways with consequences for how their competition networks change in response to resource addition.

Removal of foliar fungal pathogens had a large effect on the network metrics evaluated in our study but they contradicted our main hypotheses (Table 2). Fungicide addition reduced both negative skewness (fewer extreme values) and modularity and increased the evenness of interaction coefficients (Figure 3), that is, it made competition among species more similar. The evenness increase occurred in all networks and seemed to be caused by fungal pathogens reducing the growth of weak competitors, as these species strongly increased in cover when fungicide was applied (Figure S11). However, the decrease in skewness and modularity was more pronounced in slow only, or mixed fast–slow networks. Fast growing species are more affected by pathogens (Cappelli et al., 2020) and may become more competitive against slow species with fungicide, which would make mixed networks less skewed and modular. Parallel to this effect, foliar fungal pathogens did also increase intraspecific competition (since removing them with fungicide decreased diagonal dominance), which should stabilise the dynamics of interacting species. This agrees with the large literature suggesting that pathogens drive stabilising effects through Janzen–Connell mechanisms (Adler & Muller-Landau, 2005; Bagchi et al., 2014; Comita et al., 2014; Liu et al., 2022). Therefore, our results collectively indicate that pathogens can reduce diversity by targeting some fast growing species (*Crepis biennis*, *Lolium perenne* and *R. acetosa*) that were weak competitors in our experiment (Figure S11), but they can also maintain diversity by increasing conspecific negative density dependence.

We found strong interactions between nitrogen and fungicide on multiple network metrics. We expected nitrogen and fungicide to have similar effects, to promote dominance and reduce evenness (Mitchell et al., 2003). However, this was not the case in our experiment as nitrogen and fungicide typically dampened each other's effects (Figure 3). We initially thought nitrogen and fungicide each favoured a different set of species, but it seems instead that individual pairwise competition coefficients changed in different ways in response to nitrogen versus fungicide (see highlighted examples in Figure S5). This often led to similar competitive effects for individual species in the control and combined treatment. For example, nitrogen and fungicide alone increased the competitive effects of the weakest competitor (*C. biennis*) and decreased the competitive effects of the strongest competitor (*H. lanatus*) but they had similar competitive effects in the control and combined treatments (Figure S4). Contrary to Wang et al. (2010), we found that overall, our treatments altered competitive effects more than responses. Competitive response is directly related to species persistence over time (Godoy et al., 2014), so it may be selected to be more stable, while competitive effects could vary more with environmental conditions. Our results show that resource addition and enemy removal can interact in complex ways to affect competition and they highlight the value of characterising different aspects of competition network structure to reveal these effects.

Seasonality had a comparatively small impact on network metrics, indicating that our results are robust and not driven by responses measured at a single time point (Figure 3). Modularity was higher in August, which hints towards different growth strategies during drier months, perhaps because plants suffer from more resource and water limitation (Fischer et al., 2015; Grime, 2006). Interestingly, we also found an interaction effect between SLA variance and seasonality, as mixed communities were more even in June, and less even in August (Figure S7). Therefore, mixing functional strategies could positively impact diversity in June, but negatively in August. Field management (cutting in mid-June) could explain the negative impact in the second half of the growing season, as mowing might favour species with higher disturbance tolerance and ability to resprout (Bellingham & Sparrow, 2000).

Having characterised how species interaction structure changes with resources and enemies, the next step would be to assess the system dynamics, that is, which growth strategies will decline or go extinct (losers), while others increase and become dominant (winners). We could not rigorously evaluate whether less diagonally dominant, more negatively skewed, asymmetric and uneven structures, observed for slow species under nitrogen addition, maintain lower diversity. Nevertheless, we have observed that the PaNDiv communities treated with nitrogen are shifting towards lower values of SLA (Figure S10), suggesting that slow species are more competitive with nitrogen, and we also found a relationship between cover change in fungicide plots and species competitive effects (Figure S11). Therefore, these preliminary data may indicate an empirical connection between the network structure of the interactions and shifts in species abundance. We only modelled change in biomass of our phytometers, from seedling to adult after 1 year of growth, in response to the cover of their neighbours. Our approach therefore uses the simplest approximation to understand the competitive networks among perennial plants, assuming that interactions do not change with ontogeny (Cardinaux et al., 2018). Nevertheless, previous work has shown the importance of life-stage dynamics for plant–plant interactions (Kinlock, 2021; Schiffers & Tielbörger, 2006), and future work should explore how ontogeny affects competitive plant networks.

In conclusion, we show that resources and enemies have large impacts on different aspects of multispecies plant competition networks, and importantly, these impacts depend on plant fast–slow growth strategy. These results suggest that incorporating trait-based approaches into the study of multispecies plant interactions provide a way to systematically scale-up from individual species responses to changes at the entire community level. This was an aim recently highlighted in the literature that remains poorly addressed (Levine et al., 2017; Losapio et al., 2019). Our results further show that the species with different growth strategies might interact and coexist in fundamentally different ways, which is an idea that has not been typically considered by studies linking traits to competition (Adler et al., 2018). Quantifying all pairwise interactions in highly diverse ecosystems across contrasting environmental conditions is extremely challenging. However, our results show that this effort is worthwhile to better mechanistically understand how nitrogen addition and pathogen removal, two of the most common drivers of global change, affect the population dynamics of complex communities. Taken together, our work highlights the necessity of combining a network and a trait-based perspective to progress in our understanding of the effects of global change drivers on diverse plant communities.

AUTHOR CONTRIBUTIONS

EA designed the PaNDiv Experiment and obtained the necessary funding, OG, EA and CD developed the ideas for this study, CD collected the data in PaNDiv experiment, analysed the data and wrote the manuscript with substantial inputs from OG, EA and HS. All authors contributed substantially to revisions.

ACKNOWLEDGEMENTS

We are grateful to the whole PaNDiv team, especially Sylvain Chartier, Mervi Laitinen, Hugo Vincent and many helpers, for maintaining the experiment. We also thank Seraina Cappelli and Noémie Pichon for their role in setting up the PaNDiv experiment. Several people helped with collecting the plant cover data, in particular: Vera Alessandrello, Hannah Bratschi, Eli Bucher, Tala Bürki, Géraldine Chavey, Chiara Durrer, Matthieu Gauvrit, Benjamin Herren, Fabian Heussler, Vinciane Horner, Sandy Kalaydjian, Nadia Maaroufi, Olivier Magnin, Dmitry Maryasov, Anja Michel, Thu Zar Nwe, Barryette Oberholzer, Scarlett Peréz Gordillo, Valentin Pulver, Georges Saumier, Nynke Van Duijin, Joseph Volery and Lia Zehnder. The project was funded by the Swiss National Science Foundation (Award 310030_185260). Oscar Godoy acknowledges financial support provided by the Spanish Ministry of Economy and Competitiveness (MINECO) and by the European Social Fund through the TASTE (PID2021-127607OB-I00) project. Hugo Saíz is supported by a María Zambrano fellowship funded by the Ministry of Universities and European Union-Next Generation plan. Open access funding provided by Universitat Bern.

FUNDING INFORMATION

European Social Fund Plus (TASTE), Grant/Award Number: PID2021-127607OB-I00; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 310030_185260; Ministerio de Economía y Competitividad.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14425.

DATA AVAILABILITY STATEMENT

All data and R code is available in a public GitHub repository at this address: https://github.com/cardaips/PaNDiv_competition_networks, a webpage deployment is also available at this address: https://cardaips.github.io/PaNDiv_competition_networks. A dryad repository containing data linked with this study can be found at: https://doi.org/10.5061/dryad.ncjsxkt34.

ORCID

Caroline Daniel https://orcid.org/0000-0002-7168-2411
Eric Allan https://orcid.org/0000-0001-9641-9436
Hugo Saiz https://orcid.org/0000-0002-7568-2996
Oscar Godoy https://orcid.org/0000-0003-4988-6626

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SUPPORTING INFORMATION

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How to cite this article: Daniel, C., Allan, E., Saiz, H. & Godoy, O. (2024) Fast–slow traits predict competition network structure and its response to resources and enemies. *Ecology Letters*, 27, e14425. Available from: https://doi.org/10.1111/ele.14425