

Direct and higher-order interactions in plant communities under increasing weather persistence

Simon Reynaert¹, Jonas Lembrechts², Hans De Boeck³, Chase Donnelly⁴, Lin Zi⁵, Lingjuan Li⁵, and Ivan Nijs²

¹University of Antwerp Faculty of Sciences

²University of Antwerp

³Plant and Vegetation Ecology research group

⁴University of Antwerp Department of Mathematics and Computer Science

⁵University of Antwerp Department of Biology

March 29, 2023

Abstract

Climate change is increasing the weather persistence in the mid-latitudes, prolonging both dry and wet spells compared to historic averages. These newly emerging environmental conditions destabilize plant communities, but the role of species interactions in this process is unknown. Here, we tested how direct and higher-order interactions (HOIs) between species may change in synthesized grassland communities along an experimental gradient of increasing persistence in precipitation regimes. Our results indicate that species interactions (including HOIs) are an important determinant of plant performance under increasing weather persistence. Out of the 12 most parsimonious models predicting species productivity, 75 % contained significant direct interactions and 92 % significant HOIs. Inclusion of direct interactions or HOIs respectively tripled or quadrupled the explained variance of target species biomass compared to null models only including the precipitation treatment. Drought dominated the plant responses, with longer droughts increasing direct competition but also HOI-driven facilitation. Despite these counteracting changes, drought intensified net competition. Grasses were generally more involved in competitive interactions whereas legumes had a stronger affinity for facilitative interactions. Under longer drought, species affinity for nutrient rich or wet environments resulted in more negative direct interactions or HOIs, respectively. We conclude that higher-order interactions, crucially depending on species identity, only partially stabilize community dynamics under increasing weather persistence.

Direct and higher-order interactions in plant communities under increasing weather persistence

Abstract

Climate change is increasing the weather persistence in the mid-latitudes, prolonging both dry and wet spells compared to historic averages. These newly emerging environmental conditions destabilize plant communities, but the role of species interactions in this process is unknown. Here, we tested how direct and higher-order interactions (HOIs) between species may change in synthesized grassland communities along an experimental gradient of increasing persistence in precipitation regimes. Our results indicate that species interactions (including HOIs) are an important determinant of plant performance under increasing weather persistence. Out of the 12 most parsimonious models predicting species productivity, 75 % contained significant direct interactions and 92 % significant HOIs. Inclusion of direct interactions or HOIs respectively tripled or quadrupled the explained variance of target species biomass compared to null models only including the precipitation treatment. Drought dominated the plant responses, with longer droughts increasing direct competition but also HOI-driven facilitation. Despite these counteracting changes, drought intensified net competition. Grasses were generally more involved in competitive interactions whereas legumes had a

stronger affinity for facilitative interactions. Under longer drought, species affinity for nutrient rich or wet environments resulted in more negative direct interactions or HOIs, respectively. We conclude that higher-order interactions, crucially depending on species identity, only partially stabilize community dynamics under increasing weather persistence.

Keywords: higher-order interactions, grasslands, facilitation and competition, species interactions, increasing weather persistence, drought

Introduction

Climate warming changes the inter- and intra-annual variability of precipitation regimes in the mid-latitudes (Pendergrass et al., 2017), including shifts towards more persistent summer weather with longer dry and wet spells compared to historic averages (Pfleiderer et al., 2019). With more extreme precipitation regimes (Fig. 1), we expect that ecosystems will be subjected more often to prolonged plant stress-inducing extreme conditions, due to the accompanying changes in soil water and temperature (Felton et al., 2021; Knapp et al., 2008; Reynaert et al., 2021; Zhao & Khalil, 1993), and potential changes in nutrient cycling (Borken & Matzner, 2009). For example, when dry periods become longer, or occur at higher temperatures (Collins et al., 2013), soil water declines more, increasing the chance of crossing mortality thresholds (De Boeck et al., 2018; Knapp et al., 2008). Moreover, longer droughts can increase the risk of nutrient leaching upon rewetting, potentially leading to nutrient shortages in the longer term (Borken & Matzner, 2009; Klaus et al., 2020).

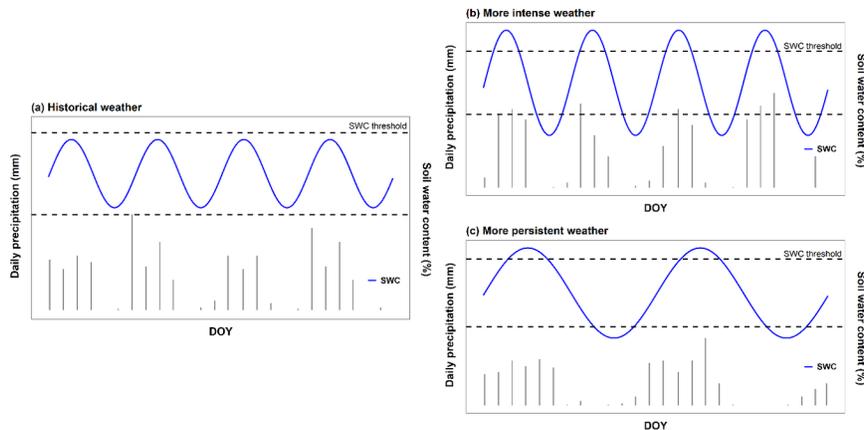


Figure 1. Theoretical framework indicating how increasing precipitation variability can influence soil moisture regimes as an extension of Knapp et al. (2008), who primarily discussed the effects of increased weather intensity (i.e. larger, more irregular event sizes). Grey bars represent daily precipitation. Day of the year and soil water content are abbreviated by DOY and SWC, respectively. Under climate change, we expect an increase in both intensity and persistence of summer weather in the mid-latitudes (Pfleiderer et al., 2019; Spinoni et al., 2018). In all panels, the precipitation totals are equal to historical weather (a). More intense weather (b) results in less frequent but larger rainfall events intermitted with longer dry spells under higher temperatures, which could exacerbate drought/flooding effects. More persistent weather (c) results in prolonged dry and wet periods, which could also lead to more extreme variation in soil water content. In both cases, the chance increases that critical soil moisture thresholds are exceeded, negatively affecting ecosystem functioning (Ciais et al., 2005).

While research has explored how climate shifts may alter selection of species with specific traits (Siepielski et al., 2017), whether interspecific interactions will change, or how species interactions shape community responses to these regime changes remains unclear (Grant et al., 2014). Direct species interactions, i.e. the direct effect of plant A on plant B and vice versa (Fig. 2), are important determinants of ecosystem

functioning (Schmitz et al., 2008). They can be facilitative (positive) or competitive (negative). In grasslands, legumes often facilitate grasses through N-fixation, which increases ecosystem productivity (Ball et al., 2020), in return for improved microclimatic conditions such as wind protection (Walker et al., 2003). Conversely, fast-growing dominant grasses often compete with one another for limited resources, which can result in productivity loss (Corbin & D’Antonio, 2004; Fay et al., 2003). During episodes of extreme abiotic conditions, when water (drought) or oxygen (flooding) become limited, direct interactions between species may become more positive, negative, or not change (Grant et al., 2014; Van den Berge et al., 2014). The net effect of direct interaction changes on ecosystem functioning (e.g., productivity) under such conditions is ecosystem specific and depends on their strength and direction, but also on the affected species. For example, under drought, increased competition between dominant species can exacerbate the productivity decline (Fay et al., 2003; Grant et al., 2014; Suttle et al., 2007).

In diverse communities, indirect interactions can also emerge, through interaction chains of direct interactions (Wootton, 1993) or through higher-order interactions (HOIs) (Billick & Case, 1994). With interaction chains, apparent indirect interaction effects may appear between two distant plants, due to a shared relationship with a third (e.g., species A modifies performance of species B, in turn affecting performance of species C). Unlike interaction chains, HOIs remain poorly understood, although they play an important role in determining net community dynamics and the stability of complex ecosystems by modifying direct interactions (Bairey et al., 2016; Billick & Case, 1994; Brooker et al., 2008; Grilli et al., 2017; Li et al., 2021; Mayfield & Stouffer, 2017; Singh & Baruah, 2021; Xiao et al., 2020). HOIs can either be defined as the combined effect of two or more neighboring plants on a third target plant (Fig. 2), which is determined by the nature of these neighbors’ own pairwise interaction(s) (Levine et al., 2017; Mayfield & Stouffer, 2017), or, as the effect of one species on the interaction between two others (Billick & Case, 1994). Such interaction effects could arise when a Nitrogen (N)-fixing legume C is introduced into a plant community with scarce resources, reducing N competition between two neighboring grasses (Fig. 2). Recent studies, both theoretical and observational, have indicated that HOIs may mitigate intense direct competitive effects between neighbors, facilitating long-term species coexistence in highly diverse plant communities (Grilli et al., 2017; Li et al., 2021; Singh & Baruah, 2021; Xiao et al., 2020). Thus, Grilli et al. (2017) suggest that HOIs could make communities more robust against ecological perturbations. However, their impact on ecosystem functioning and how they are influenced by shifting climate regimes remains unclear (Bimler et al., 2018; Brooker et al., 2008; Xiao et al., 2020). Elucidating their role is important to better understand climate-driven changes in diverse plant communities.

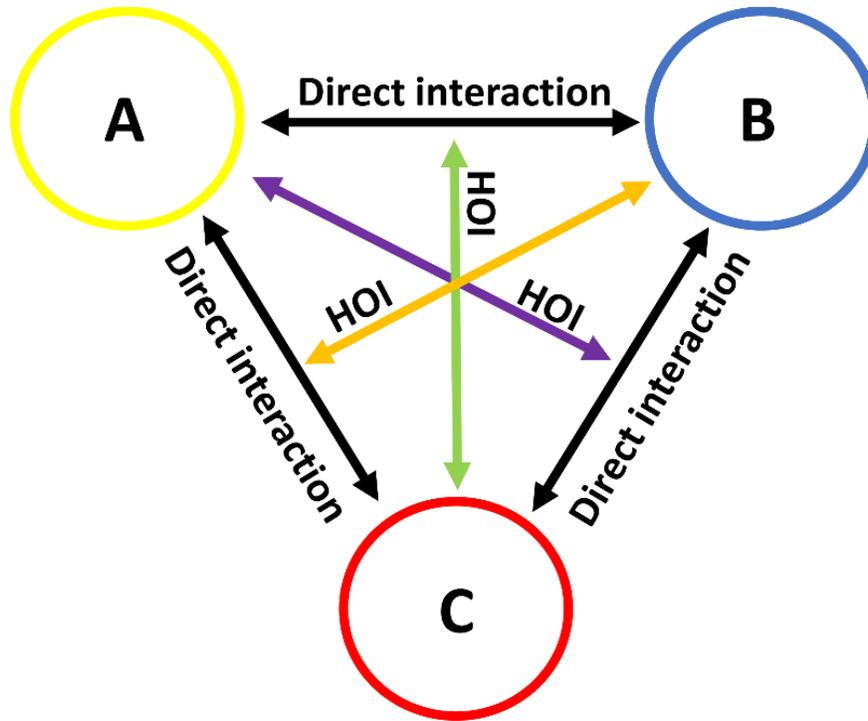


Figure 2. Schematic representation of differences between direct interactions and higher-order interactions (HOIs). Direct interactions involve two plants, a neighbor and a target, while HOIs (in their simplest form), include a neighbor pair and a target plant. For example, although species A (neighbor) may outcompete species B (target) in the absence of species C (negative direct interaction), a mixture also including species C (neighbor), reducing the intensity of competition between A and B (less negative interaction) by supplying a scarce resource to both, may actually benefit (facilitate) the growth of species B (positive HOI).

Exposure to more extreme dry and wet spells may lead to fundamental changes in species interaction networks (Grant et al., 2014; Olsen et al., 2016). The stress-dominance hypothesis predicts that the relative importance of environmental filtering increases while competition decreases along a gradient of environmental stress (Coyle et al., 2014; Weiher & Keddy, 1995). By extension, the stress-gradient hypothesis presumes an increase in the relative importance of facilitation compared to competition along such gradients (Bertness & Callaway, 1994). Despite recent evidence questioning the generality of these hypotheses (De Boeck et al., 2018; Grant et al., 2014; Maestre & Cortina, 2004; Metz & Tielborger, 2016; Singh & Baruah, 2021), directional shifts in mean interactions along environmental gradients have been observed in many ecosystems, indicating important changes in ecosystem functioning (Coyle et al., 2014; De Boeck et al., 2018; Olsen et al., 2016).

We explored if and how increasing persistence in summer precipitation regimes (i.e. precipitation variability) changes the number, strength and directionality of species interactions that influence plant biomass production, including both direct interactions and HOIs. We subjected experimental grassland mesocosms with 12 common C3 species (six grasses, three non-N-fixing forbs, three legumes) to an 8-level gradient of precipitation regimes. These regimes varied the duration of consecutive dry and wet periods from 1 to 60 days while keeping total precipitation constant (Reynaert et al., 2021). Our research questions were whether species interactions, either direct ones or HOIs, determine species biomass under altered precipitation persistence, and whether these interactions change as drought stress intensifies (i.e., the main driver of plant responses to increasing summer precipitation persistence; Reynaert et al. (2021); Reynaert et al. (2022)).

We hypothesized that (1) HOIs would generally counteract direct competitive interactions, weakening net

species interactions and stabilizing community dynamics; (2) species interactions would overall become more positive (or less negative) across the community with increasing drought severity, indicating either a decline in competitive interactions and potentially increased facilitation, or a more prominent role of environmental filtering, leading to increased competitive release; (3) species identity would determine the nature of interactions, with more facilitation in interactions with N-fixing legumes and more competition when considering dominant grasses.

Methods & materials

Data collection

From July to November 2019, a 120-day open air precipitation manipulation experiment was conducted in Flanders, Belgium (51°09'41"N, 04deg24'9"E). In total, 256 mesocosms (29.5 cm inner diameter and 50 cm depth), each containing the same synthesized grassland plant community with three individuals of 12 common C3 species (36 plants per community; Fig. S1), were evenly distributed across eight identical plots of 3 m diameter and subjected to a gradient of increasingly longer dry-wet period alternations (Reynaert et al., 2021). The precipitation persistence gradient contained eight different regimes of dry-wet period alternations, ranging from 1 to 60 consecutive days with or without precipitation and starting with either a dry or a wet period. This yielded 16 regimes in total, including 1, 3, 6, 10, 15, 20, 30 and 60 consecutive days dry/wet. All regimes had a total of 60 days with and 60 days without precipitation. Historically, Belgian weather patterns following 1-day dry-wet alternations are most common (KMI, 2019; Reynaert et al., 2021). The precipitation regimes were created by blocking out ambient precipitation with rainout screens which were automatically deployed only during rain, and applying dripper irrigation (Reynaert et al., 2021). Precipitation was equal in all regimes on each irrigation day (6.87 L/m², being 1.5 times the Belgian daily average of a rainy day to compensate for excess evapotranspiration in mesocosms) as well as in total across the experimental period. Mesocosms had holes in the bottom, allowing free drainage and preventing flooding (Reynaert et al., 2021). Per regime, a total of 16 replicate mesocosms was evenly distributed across 4 plots. The position of these replicates was different in every plot to account for potential edge effects.

The 12 grassland species represented a broad gradient in plant functional traits (Table S1) and included six grasses (*Agrostis capillaris* L. (AC), *Anthoxanthum odoratum* L. (AO), *Deschampsia cespitosa* (L.) P. Beauv. (DC), *Phleum pratense* L. (PHP), *Poa pratensis* L. (POP), *Holcus lanatus* L. (HL)); three N-fixing forbs (*Lotus corniculatus* L. (LC), *Trifolium pratense* L. (TP), *Trifolium medium* L. (TM)); and three non-N-fixing forbs (*Centaurea jacea* L. (CJ), *Lychnis flos-cuculi* L. (SF), *Plantago lanceolata* L. (PL)). Seeds were obtained from a seed company in the Netherlands (Cruydt-Hoeck) and sown in separate seedling containers at the start of April 2019. By May, viable seedlings of similar size per species were transplanted directly into the mesocosms (Reynaert et al., 2021). We maximized interspecific interactions by planting them in a hexagonal grid where each individual had different neighbors at 4.5 cm interspace, and avoiding clumping (Fig. S1). The spatial configuration in our containers was aimed at representing each species pair at the most comparable extent possible, with 92% of the 66 possible pairs occurring either one or two times (Table S2). Species positions and north-south orientation were equal in all mesocosms. Mesocosms were weeded regularly over the course of the experiment to prevent (re)colonization.

Average volumetric soil water content (SWC) over 0-30 cm depth was recorded half-hourly in two to four mesocosms per precipitation regime by a CS6650-DS Reflectometer (Campbell(r) Scientific INC., Logan, Utah, USA). Because the impact of increasing weather persistence was shown to be mainly related to drought in the 2019 growing season (Reynaert et al., 2021), the daily averages of mean SWC values per regime were utilized to calculate different drought indices which represented the persistency of the precipitation regime. These included drought stress intensity (at relative extractable water (REW) of 0.4, 0.2 and 0.1), total time below permanent wilting point, and the length of the longest consecutive period below permanent wilting point (Reynaert et al., 2021; Reynaert et al., 2022; Vicca et al., 2012). Following Vicca et al. (2012), drought stress intensity was calculated by determining a soil moisture threshold, and integrating the duration and extent to which soil moisture declined below it over the experimental period.

At the end of the experiment, all standing dead and live biomass above 4.5 cm height was harvested per species per mesocosm, in 12 out of the 16 replicate mesocosms per regime (all available individuals of the same species per mesocosm per paper bag). Dead biomass was included since death at the time of measurement, does not indicate a lack of previous interact with its neighbors. In half of these 12 mesocosms, one third of the individuals per species was randomly removed for another study. We corrected for this by multiplying the plant mass in these bags by 1.5 (per regime, every species was discarded twice in every unique position; Fig. S1). Combining the biomass of all harvested individuals per species in a mesocosm accounted for variation caused by differences in local neighbor setting. Biomass bags were oven-dried at 70 degC for >72 h and immediately weighed with 0.01 g accuracy. To achieve dry plant mass per species per mesocosm, we subtracted the average mass of 58 oven-dried empty bags (SD = 0.08 g). Plants that had little or no biomass above 4.5 cm height because they remained too small during the experiment (< 17 %, n = 2281) were given a mass of 0.01 to account for being below our detection limit (Lubbe et al., 2021).

Statistical analysis

All statistical analyses were performed in R version 4.0.2 (R Core Team, 2019). Significance was assumed for p-values < 0.05. Graphs were constructed utilizing the packages dplyr (Wickham et al., 2015), igraph (Csardi & Nepusz, 2006) and ggplot2 (Wickham, 2016).

To model direct interactions and HOIs, we adapted the approach from Mayfield and Stouffer (2017), which allows the use of biomass data. Their methodology suggests to construct models with the characteristic of interest of a target species in the community (here: biomass) as response variable and (the biomass of) all neighboring species and their statistical interactions as explanatory variables, after which all significant terms from the most parsimonious equivalent models (e.g., $\Delta \text{AIC} < 2$) per target species are of interest. The estimates of significant model terms can then be utilized to obtain information about species interactions, direct ones and HOIs, in the studied plant community. Because biomass data was pooled per species per mesocosm in our experiment, we did not focus on the role of individual plant position but rather on species identity. Our central question was if and how the growth performance of a target species, expressed as accumulated dry biomass over the growing season, was affected by the growth performance of neighboring species under increasingly persistent precipitation regimes in diverse grassland communities.

As described earlier, we opted to represent our treatments in the models by a drought index. Out of all calculated drought indices (section 3.1), the length of the longest consecutive period below permanent wilting point captured species biomass effects caused by increasingly persistent summer precipitation regimes the best (lowest AIC, adj. $R^2 = 0.56$; Table S3), allowing us to more accurately linearize the biomass responses (Fig. S2 & S3) and model the wet and dry start regimes along a common dimension (Reynaert et al., 2021).

First, we normalized all biomass data by taking the natural logarithm of each biomass observation divided by the mean biomass per species across all regimes. This approach is similar to the log-response ratio, a technique often applied in meta-analysis, where values >0 indicate above average plant performance, and values <0 below average (Van Sundert et al., 2021). By doing so, effect sizes become comparable among species with distinct intrinsic characteristics, i.e. the coefficients of models with different target species are standardized and directly comparable. Since all effects become relative, they can be interpreted as the extent to which a change in mass of a neighbor species (relative to its mean size) affects the mass of a target species (relative to its mean size). We then created multiple linear models of all possible species combinations including every species as response variable (target) and all others (neighbors), the drought index and their two-way interactions as explanatory variables (Fig. 2; Eqn. 1).

$$? (BM_{A,i}) = \text{Intercept} + \alpha_1 BM_{B,i} + \alpha_2 BM_{C,i} + \alpha_3 BM_{B,i} BM_{C,i} + \gamma \text{Index} + \beta_1 BM_{B,i} \text{Index} + \beta_2 BM_{C,i} \text{Index} + \beta_3 BM_{B,i} BM_{C,i} \text{Index} + \dots + \epsilon_i \text{ (Eqn 1)}$$

With ? (BM_{A,i}) the expected standardized total dry biomass (BM) of target species A in a specified mesocosm i, BM_{B,i} and BM_{C,i} the standardized total dry biomass of neighbor species B and C, respectively, in that mesocosm, Index the length of the longest consecutive period below permanent wilting point, α and β the species interaction (model) coefficients and ϵ_i the errors. Model terms including only one species (BM_{B,i}

or $BM_{C,i}$) represent direct interactions. Model terms including both species ($BM_{B,i}BM_{C,i}$) indicate HOIs.

To avoid overfitting and other issues related to insufficient data (Martyn et al., 2021), we only included the simplest, i.e. the three-way, HOIs (Fig. 2). Intraspecies interactions were excluded from the models because we pooled the species biomass for the three individuals per mesocosm, which accounts for variation caused by individual plant position. Following Grant et al. (2014), we interpret the general variation in interspecies interactions knowing that distant (i.e. non-direct neighbor; Fig. S1) intraspecies effects may also contribute to the estimated interaction coefficients. Because plant density and positions are the same in all mesocosms we assume that found model coefficients primarily reflect variation in plant performance related to changes in interspecies interactions and drought effects. Per response variable (target species), we then compared full models with direct-interaction only and null models (only including the drought index as explanatory variable), retaining only the most parsimonious model per target species ($\Delta AIC < 2$). In the remnant models, the strength and direction of the interaction(s) was determined by the model estimates of the explanatory variable(s). Significant model coefficients excluding the drought index (α coefficients; Eqn 1) represent interaction strengths at a drought length of zero. All other significant model coefficients (β coefficients; Eqn 1) indicate a change of interaction strength along the gradient of increasing drought length. To calculate interaction strengths at maximum drought index, the maximum index value (39), was used to fill in Eqn 1. If the model coefficient was not significant, the interaction strength was assumed to be zero. By doing so, we were able to isolate the most important direct interactions and three-way HOIs per target species in the plant community.

Although our models suggest the capacity to detect unidirectional effects of species on each other and thus causation (influenced species as dependent variable or target, influencing species as independent variables or neighbors in Eq. 1), they can actually only detect the balance of these unidirectional effects, and thus correlation. We therefore considered every found interaction coefficient as the bidirectional outcome of the (potential) unidirectional effects, regardless of whether the species of interest was included as target or neighbor in the model.

Utilizing the interaction coefficients obtained in this way, we then calculated the total number of interactions that involved this species (either as target or neighbor in the models). This was done separately for direct interactions and HOIs. Direct interaction coefficients between the same species pair originating from different models were only counted once per species. Other coefficients represented unique and equally relevant 3-way HOIs and were all counted per species. Next, we calculated the mean direct interaction and HOI strengths by averaging all positive and negative interactions per species, again utilizing the mean values of coefficients between the same species pairs for direct interactions and all coefficients for HOIs. We then visualized species interaction networks for direct interactions, HOIs, net interactions (sum of direct interactions and HOIs per species pair) and their changes along the drought gradient. Finally, to test if species characteristics determined any of the observed patterns, we conducted various non-parametric Spearman correlation tests, utilizing mean interaction strengths and total number as response variables and average species biomass (at zero or maximum drought index) as well as Ellenberg nutrient and moisture indices as explanatory variables.

Results

Species interactions (including HOIs) played an important role in determining species performance, expressed as aboveground biomass production, under changing precipitation regimes. Out of the 12 most parsimonious models ($\Delta AIC < 2$), 75% contained significant direct interactions and 92% significant HOIs (Table S4). Null models, which only included the drought index as explanatory variable, explained 10% of the variance in species biomass on average (Table S4). Inclusion of direct interactions increased the variance explained to 28% on average (Table S4). Full models, also including HOIs, explained 43% of variance in target species biomass on average (Table S4).

At zero drought index, the majority of direct interactions (75%, $n = 24$) (stacked bars above zero; Fig 3a) were positive compared to only half of the HOIs (50%, $n=108$) (Fig. 3b). Although a larger proportion of significant direct interactions became more negative (50%, $n = 12$) (stacked bars below zero; Fig. 3c)

with increasing drought length (i.e., index change), there were still more positive mean direct interactions at maximum drought index overall (72%, $n = 11$; Fig. 4c). For HOIs, the total number of positive and negative interactions stayed similar (52% positive, $n = 75$) (Fig. 3d), though on average, more species were involved in facilitative HOIs at maximum drought index (58%, $n = 12$; Fig. 4d). Whereas opposite interaction effects generally neutralized each other at zero drought index, overall, competition and facilitation became more pronounced with intensifying drought stress (Fig. 4). As such, average direct competition increased in strength and prevalence along the drought gradient while more HOIs became facilitative (Fig. 4). Despite these opposite changes, mean direct interaction and HOI strength did not inversely correlate at either side of the drought gradient (Fig. S4).

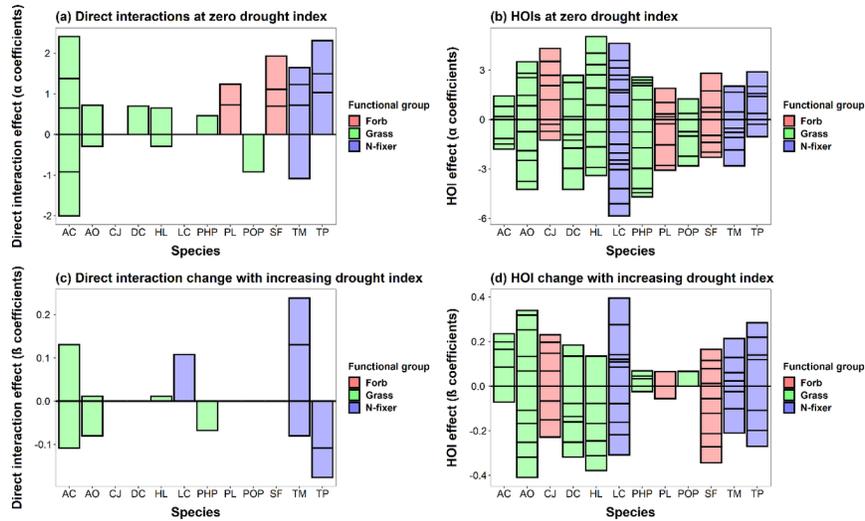


Figure 3. Direct interaction and higher-order interaction (HOI) effects grouped per species (as target or neighbor) at zero drought index (a, b; α coefficients in Eqn 1) and their change (c, d; β coefficients in Eqn 1) with increasing length of the longest consecutive period below permanent wilting point (PWP). Positive values indicate facilitative effects, while negative values indicate competitive effects. The number of interactions (number of blocks inside each bar) indicates how often a species is involved in a direct interaction or HOI with a different species or species pair. Direct interactions between the same species pairs from different models were averaged. The size and orientation of individual boxes indicates the size and direction (+/-) of effects (standardized effect sizes). Colors refer to functional group of the species (red: non-N-fixing Forb, green: Grass, blue: N-fixer). Non-significant interactions were excluded. For full species names, see methods section 3.1.

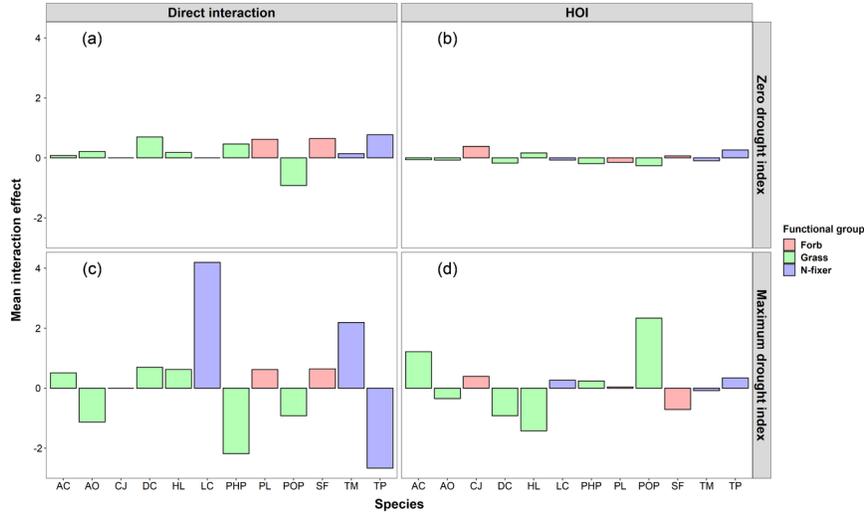


Figure 4. Mean direct (a, c) and higher-order interaction (b, d) effects grouped per species in the most parsimonious models at zero and maximum drought index. To calculate mean direct interactions, the average of bidirectional direct interactions is taken. Positive values indicate facilitative effects, while negative values indicate competitive effects. Colors refer to functional group of the species (red: non-N-fixing Forb, green: Grass, blue: N-fixer). Higher-order interaction is abbreviated by HOI. Non-significant interactions were excluded. For full species names, see methods section 3.1.

Species identity determined the nature of interactions. Out of the four species involved in competitive interactions on average at maximum drought index, three were grasses in both direct interactions and HOIs (Fig. 4c,d). Forbs (incl. N-fixers) were on average more involved in facilitation relative to their species number, especially at maximum drought index (Fig. 4). Furthermore, Ellenberg’s moisture and nutrient indices correlated with average interaction effects. At maximum drought index, direct interactions became more negative with increasing affinity to nutrient rich environments ($p = 0.02$; Fig. S5b), while HOIs became more negative with increasing hydrophilicity ($p = 0.04$; Fig. S5a). No correlations were found between average interaction strength or number and average species biomass (Fig. S6, Table S5).

Interaction networks became stronger and more negative at maximum drought index (Fig. 5). Net interactions (sum of direct interactions and HOIs) were generally most positive on average for N-fixers, more negative for non-N-fixing forbs and most negative for grasses (Table 1). Moreover, the majority of net interactions became negative for grasses and non-N-fixing forbs at maximum drought index, while the majority of net N-fixer interactions remained facilitative. Both at zero and maximum drought index, N-fixers were proportionally most involved in net interactions, followed by forbs and grasses (Table 1). Average net interaction strengths did not change noticeably with increasing drought index within functional groups (Table 1).

Table 1. Number and average strength of all significant positive and negative net interactions (sum of direct interactions and HOIs) involving grasses, (non-N-fixing) forbs or N-fixers at zero and maximum drought index, respectively. Non-significant interactions were excluded. See Figure 5 for the complete network overview.

	At zero drought index	At zero drought index	At zero drought index	At maximum drought index
	Grass	Forb	N-fixer	Grass
# (+) interactions	20	14	15	21
# (-) interactions	19	7	10	23

	At zero drought index	At zero drought index	At zero drought index	At maximum drought index
mean interaction effect	-0.23	-0.08	0.11	-0.23

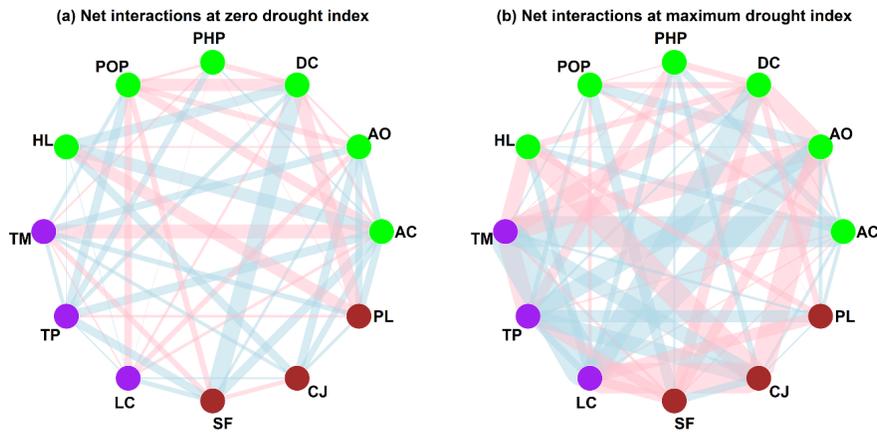


Figure 5. Species networks indicating the net strength of interactions (sum of direct interactions and higher-order interactions per species pair) in the most parsimonious models ($\Delta AIC < 2$) at zero (a) and at maximum (b) drought index. The color of the network links indicates whether the net interaction is positive (blue) or negative (red). The color of the species relates to its functional group including grasses (green), non-N-fixing-forbs (brown) and N-fixers (purple). When multiple interactions were found between the same species pair in different models, their strengths were averaged. The thickness of the connections indicates net interaction strength. Non-significant interactions were excluded. For full species names, see methods section 3.1.

Discussion

Inclusion of species interactions (including HOIs) increased the accuracy of plant performance models along the drought gradient compared to models only including the drought effect. Direct interactions improved the explanatory power of models more on average compared to HOIs, though the latter were present in a larger number of the most parsimonious models (Table S4). This finding affirms the necessity to include at least some HOIs to improve net species interaction estimates in complex and diverse ecological networks (Li et al., 2020; Li et al., 2021; Martyn et al., 2021; Mayfield & Stouffer, 2017). Particularly in plant communities subjected to drought, where species interactions can change drastically (Grant et al., 2014; Van den Berge et al., 2014), facilitation and/or competition may be overestimated without inclusion of HOIs, limiting our ability to predict ecosystem trajectories (Brooker et al., 2008). Incorporating HOI approaches in more studies could thus improve the predictability of species performance under climate change.

Contrasting with the stress gradient hypothesis (Bertness & Callaway, 1994), more net interactions became negative on average along the drought gradient. This occurred because direct interactions predominantly shifted to more negative with longer drought, while HOIs were doing the opposite, albeit without fully neutralizing intensified competition (Fig. 4). In line with Xiao et al. (2020) and Li et al. (2021), these findings indicate that HOIs may influence community stability by partially counteracting increased direct competitive effects under increasing precipitation variability. While Xiao et al. (2020) argue that especially intraspecific HOIs play a stabilizing role, our experimental findings suggest that interspecific HOIs may also contribute to stabilizing community dynamics (Bairey et al., 2016; Grilli et al., 2017; Singh & Baruah, 2021). Hence, persistence of highly diverse communities under increasing drought stress could be promoted by interspecies HOIs counteracting stronger direct competitive effects, thus stabilizing community dynamics, and preventing dominance of one single species group (Brooker et al., 2008). Since such stabilizing HOIs are

more likely to be generated in multi-species assemblages (Grilli et al., 2017), this observation may also point at an additional mechanism through which more diverse communities could be better equipped to withstand climate extremes (Brooker et al., 2008; De Boeck et al., 2018).

In terms of directionality, the majority of HOIs showed a shift towards stronger facilitation (or weaker competition) along the drought gradient on average (positive values in Fig. 3d), in line with the stress gradient and dominance hypotheses (Bertness & Callaway, 1994; Coyle et al., 2014). However, three additional species exerted direct competitive pressures at maximum drought index on average (Fig. 4c), and more net interactions became competitive (Fig. 5; Table 1). Hence, while the majority of direct competitive interactions was weakened by positive HOIs, the strengthening of some competitors may have led to a destabilized system where more species were being outcompeted under longer drought (Table 1; Fig. 5). This is in agreement with some studies (Maestre et al., 2005; Olsen et al., 2016; Saccone et al., 2009), but contradicted by others (Brooker et al., 2008; He et al., 2013). Having more species in negative direct interactions (and more net competitive interactions) under longer drought indeed suggests that some species (e.g. *Phleum pratense*) could become more competitive under water shortage because of, for example, favorable resource acquisition traits (Kraft et al., 2015; Olsen et al., 2016).

In that regard, we observed that direct interactions became more negative with increasing Ellenberg’s nutrient indices under longer drought (Fig. S5b), indicating that species with an affinity for resource rich environments became involved in more direct competitive interactions. Hence, increasing weather persistence seemed to not only affect species interaction networks directly through intrinsic negative responses to changes in soil water availability (i.e. Ellenberg’s moisture indices; Fig. S5a), but also indirectly through effects of drought on nutrient availability. These intensified direct competitive effects may thus also reflect differences in plant resilience during post-drought rewetting and recovery phases, when the flush of nutrients related to Birch effects induces transient periods of high nutrient availability (Birch, 1958; Borken & Matzner, 2009), allowing rapid recovery of more resilient species.

However, positive interactions still made up half of all interactions under extreme drought (Fig. 5b), and the average strength of net interactions per functional group did not change noticeably with drought (Table 1). Together with the striking productivity declines (Fig. S2 & S3) and diversity losses related to the intrinsic drought sensitivity of individual species (Reynaert et al., 2021), these observations may indicate a primary role of environmental filtering (i.e. drought), and only to a lesser extent shifts in species interactions as the primary cause for aboveground productivity declines under drought (Coyle et al., 2014; Elst et al., 2017). Following Maestre et al. (2009), we pose that under extreme environmental stress (e.g., prolonged drought), species could potentially also stop growing due to exceedance of intrinsic ecological thresholds, mostly independently of the community dynamics (i.e. facilitative or competitive interactions) in their growing environment (De Boeck et al., 2018; Reynaert et al., 2021; Soliveres et al., 2015). The non-linearity in survival responses (Fig. S5; Reynaert et al. (2021)), could indeed suggest such a mechanism. Similar negative threshold responses of aboveground plant productivity have been observed in many terrestrial ecosystems, particularly in relation to the duration of dry spell anomalies (Felton et al., 2021). Taken together, these results indicate that both intrinsic responses to increasing drought and intensifying interspecific competitive effects (Olsen et al., 2016) lead to the observed changes in community dynamics by the end of the first 120 days of the experiment.

In line with our third hypothesis, forbs (particularly N-fixers) tended to be more involved in facilitative interactions on average, while grasses seemed the strongest competitors (Table 1; Fig. 5). This role of species identity (Martyn et al., 2021; Weigelt et al., 2002) was confirmed by the relationships with Ellenberg’s moisture and nutrient indices at maximum drought index, with species with an affinity for wetter and more resource rich environments experiencing or exerting more negative HOIs or direct interactions on average, respectively (Fig. S5a,b). Additionally, the disproportionate contribution of N-fixers to positive interactions and grasses to negative interactions suggests that some species (or species groups) are crucial in defining the dynamics of complex species networks (Singh & Baruah, 2021). With the available information, we cannot fully determine whether N-fixer importance is because of active facilitative traits (e.g., improving water or

nutrient supply), or due to passive competitive release as these smaller species rapidly disappeared with increasing drought stress (i.e. were more susceptible to environmental filtering), or because they prevent other more competitive neighbors from colonizing (e.g., via vegetative propagation) (Maestre et al., 2003).

Some aspects of this study’s methodology should be considered. First, the presented direct vs three-way higher-order counteracting interaction system may not fully reveal the nature of net community dynamics. Inclusion of HOIs beyond simple three-way terms may shed more light on the overall strength of facilitation and competition, but was not feasible in this study because of insufficient data (Martyn et al., 2021). Nonetheless, previous studies have indicated that inclusion of more complex (i.e., 4-way, 5-way, etc.) HOIs leads to progressively diminished returns in explaining community dynamics (Li et al., 2021), highlighting the importance of the modelled interactions. Second, the exclusion of intraspecific and density effects likely perturbed the estimation of interaction coefficients, since intraspecific interactions (both direct and HOIs) and competitor density influence net community dynamics in diverse ecosystems (Chesson, 2000; Li et al., 2021; Xiao et al., 2020). However, because individuals of the same species were never planted directly next to one-another and the initial planting density was identical in every mesocosm, we believe that the observed changes primarily reflect plant responses in function of neighbor performance and drought (Grant et al., 2014). Finally, the species interactions investigated here represent short-term responses to altered persistence in summer precipitation (Reynaert et al., 2021). Since we already observed strong differences in species performance related to the extremity of the precipitation regime, later assessment of interactions would likely disproportionately reflect the effects of only a few single species since many had died already under extreme summer drought after 120 days (Reynaert et al., 2021). Consequently, the identified interactions likely represent the most important ones that contributed to the observed declines of species under the imposed climate trend.

Conclusion

Modelling and disentangling the role of HOIs in community dynamics remains challenging because of their complexity, extensive dataset requirements and a lack of widely applicable methodologies. More targeted manipulation experiments filtering out the environmental noise that perturbs the estimation of interaction coefficients could aid in bridging the gap between theoretical modelling and meaningful ecological understanding of diverse communities. We took a first step in that direction, by experimentally demonstrating that species interactions, including HOIs, can significantly change along a gradient of increasingly persistent precipitation regimes. Inclusion of HOIs did not only improve model explanatory power, but also shed more light on potential stabilizing mechanisms for increasing competition under drought. Hence, HOI approaches could further improve the accuracy of species performance models under rapidly changing environmental conditions, an imperative prerequisite for targeted and efficient ecosystem management.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The corresponding data of this study will be made publicly available online in a Zenodo repository at [INSERT DOI] and in the previously published Dryad repository at <https://doi.org/10.5061/dryad.k98sf7m52>.

References

- Bairey, E., Kelsic, E. D., & Kishony, R. (2016). High-order species interactions shape ecosystem diversity. *Nat Commun*, 7 (1), 12285. doi:10.1038/ncomms12285
- Ball, K. R., Power, S. A., Brien, C., Woodin, S., Jewell, N., Berger, B., & Pendall, E. (2020). High-throughput, image-based phenotyping reveals nutrient-dependent growth facilitation in a grass-legume mixture. *PLoS One*, 15 (10), e0239673. doi:10.1371/journal.pone.0239673

- Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends Ecol Evol*, 9 (5), 191-193. doi:10.1016/0169-5347(94)90088-4
- Billick, I., & Case, T. J. (1994). Higher order interactions in ecological communities: what are they and how can they be detected? *Ecology*, 75 (6), 1529-1543. doi:/10.2307/1939614
- Bimler, M. D., Stouffer, D. B., Lai, H. R., & Mayfield, M. M. (2018). Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency. *Journal of Ecology*, 106 (5), 1839-1852. doi:10.1111/1365-2745.13030
- Birch, H. (1958). The effect of soil drying on humus decomposition and nitrogen availability. *Plant and soil*, 10 (1), 9-31.
- Borken, W., & Matzner, E. (2009). Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biology*, 15 (4), 808-824. doi:10.1111/j.1365-2486.2008.01681.x
- Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., . . . Michalet, R. (2008). Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, 96 (1), 18-34. doi:10.1111/j.1365-2745.2007.01295.x
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, 31 (1), 343-366. doi:DOI 10.1146/annurev.ecolsys.31.1.343
- Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., . . . Valentini, R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, 437 (7058), 529-533. doi:10.1038/nature03972
- Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichet, T., Friedlingstein, P., . . . Krinner, G. (2013). Long-term climate change: projections, commitments and irreversibility. In *Climate Change 2013-The Physical Science Basis: Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1029-1136): Cambridge University Press.
- Corbin, J. D., & D'Antonio, C. M. (2004). Competition between native perennial and exotic annual grasses: Implications for an historical invasion. *Ecology*, 85 (5), 1273-1283. doi:10.1890/02-0744
- Coyle, J. R., Halliday, F. W., Lopez, B. E., Palmquist, K. A., Wilfahrt, P. A., & Hurlbert, A. H. (2014). Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in eastern North American tree communities. *Ecography*, 37 (9), 814-826. doi:10.1111/ecog.00473
- Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, complex systems*, 1695 (5), 1-9.
- De Boeck, H. J., Bloor, J. M. G., Kreyling, J., Ransijn, J. C. G., Nijs, I., Jentsch, A., . . . Wardle, D. (2018). Patterns and drivers of biodiversity-stability relationships under climate extremes. *Journal of Ecology*, 106 (3), 890-902. doi:10.1111/1365-2745.12897
- Elst, E. M., De Boeck, H. J., Vanmaele, L., Verlinden, M., Dhliwayo, P., & Nijs, I. (2017). Impact of climate extremes modulated by species characteristics and richness. *Perspectives in Plant Ecology Evolution and Systematics*, 24 , 80-92. doi:10.1016/j.ppees.2016.12.007
- Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M., & Collins, S. L. (2003). Productivity responses to altered rainfall patterns in a C-4-dominated grassland. *Oecologia*, 137 (2), 245-251. doi:10.1007/s00442-003-1331-3
- Felton, A. J., Knapp, A. K., & Smith, M. D. (2021). Precipitation-productivity relationships and the duration of precipitation anomalies: An underappreciated dimension of climate change. *Glob Chang Biol*, 27 (6), 1127-1140. doi:10.1111/gcb.15480

- Grant, K., Kreyling, J., Heilmeyer, H., Beierkuhnlein, C., & Jentsch, A. (2014). Extreme weather events and plant-plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. *Ecological Research*, *29* (5), 991-1001. doi:10.1007/s11284-014-1187-5
- Grilli, J., Barabas, G., Michalska-Smith, M. J., & Allesina, S. (2017). Higher-order interactions stabilize dynamics in competitive network models. *Nature*, *548* (7666), 210-213. doi:10.1038/nature23273
- He, Q., Bertness, M. D., & Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. *Ecol Lett*, *16* (5), 695-706. doi:10.1111/ele.12080
- Klaus, V. H., Friedritz, L., Hamer, U., & Kleinebecker, T. (2020). Drought boosts risk of nitrate leaching from grassland fertilisation. *Sci Total Environ*, *726*, 137877. doi:10.1016/j.scitotenv.2020.137877
- KMI. (2019). Klimatologisch jaaroverzicht, jaar 2019. [WWW document] URL https://www.meteo.be/resources/climatology/pdf/klimatologisch_jaaroverzicht_2019.pdf [accessed 5 October 2021].
- Knapp, A. K., Beier, C., Briske, D. D., Classen, A. T., Luo, Y., Reichstein, M., . . . Weng, E. (2008). Consequences of More Extreme Precipitation Regimes for Terrestrial Ecosystems. *BioScience*, *58* (9), 811-821. doi:10.1641/B580908
- Kraft, N. J., Godoy, O., & Levine, J. M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proc Natl Acad Sci U S A*, *112* (3), 797-802. doi:10.1073/pnas.1413650112
- Levine, J. M., Bascompte, J., Adler, P. B., & Allesina, S. (2017). Beyond pairwise mechanisms of species coexistence in complex communities. *Nature*, *546* (7656), 56-64. doi:10.1038/nature22898
- Li, Y., Bearup, D., & Liao, J. (2020). Habitat loss alters effects of intransitive higher-order competition on biodiversity: a new metapopulation framework. *Proc Biol Sci*, *287* (1940), 20201571. doi:10.1098/rspb.2020.1571
- Li, Y., Mayfield, M. M., Wang, B., Xiao, J., Kral, K., Janik, D., . . . Chu, C. (2021). Beyond direct neighbourhood effects: higher-order interactions improve modelling and predicting tree survival and growth. *Natl Sci Rev*, *8* (5), nwaa244. doi:10.1093/nsr/nwaa244
- Lubbe, S., Filzmoser, P., & Templ, M. (2021). Comparison of zero replacement strategies for compositional data with large numbers of zeros. *Chemometrics and Intelligent Laboratory Systems*, *210*, 104248. doi:10.1016/j.chemolab.2021.104248
- Maestre, F. T., Bautista, S., & Cortina, J. (2003). Positive, negative, and net effects in grass-shrub interactions in mediterranean semiarid grasslands. *Ecology*, *84* (12), 3186-3197. doi:10.1890/02-0635
- Maestre, F. T., Callaway, R. M., Valladares, F., & Lortie, C. J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, *97* (2), 199-205. doi:10.1111/j.1365-2745.2008.01476.x
- Maestre, F. T., & Cortina, J. (2004). Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271* (suppl.5), S331-S333. doi:10.1098/rsbl.2004.0181
- Maestre, F. T., Valladares, F., & Reynolds, J. F. (2005). Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology*, *93* (4), 748-757. doi:10.1111/j.1365-2745.2005.01017.x
- Martyn, T. E., Stouffer, D. B., Godoy, O., Bartomeus, I., Pastore, A. I., & Mayfield, M. M. (2021). Identifying "Useful" Fitness Models: Balancing the Benefits of Added Complexity with Realistic Data Requirements in Models of Individual Plant Fitness. *Am Nat*, *197* (4), 415-433. doi:10.1086/713082

- Mayfield, M. M., & Stouffer, D. B. (2017). Higher-order interactions capture unexplained complexity in diverse communities. *Nat Ecol Evol*, *1* (3), 62. doi:10.1038/s41559-016-0062
- Metz, J., & Tielborger, K. (2016). Spatial and temporal aridity gradients provide poor proxies for plant-plant interactions under climate change: a large-scale experiment. *Functional Ecology*, *30* (1), 20-29. doi:10.1111/1365-2435.12599
- Olsen, S. L., Topper, J. P., Skarpaas, O., Vandvik, V., & Klønnerud, K. (2016). From facilitation to competition: temperature-driven shift in dominant plant interactions affects population dynamics in seminatural grasslands. *Glob Chang Biol*, *22* (5), 1915-1926. doi:10.1111/gcb.13241
- Pendergrass, A. G., Knutti, R., Lehner, F., Deser, C., & Sanderson, B. M. (2017). Precipitation variability increases in a warmer climate. *Sci Rep*, *7* (1), 17966. doi:10.1038/s41598-017-17966-y
- Pfleiderer, P., Schleussner, C. F., Kornhuber, K., & Coumou, D. (2019). Summer weather becomes more persistent in a 2 degrees C world. *Nature Climate Change*, *9* (9), 666-+. doi:10.1038/s41558-019-0555-0
- R Core Team. (2019). *R: a language and environment for statistical computing*, *R v.3.6.1*. Vienna, Austria: R Foundation for Statistical Computing. [WWW document] URL <https://www.R-project.org> [accessed 5 October 2021].
- Reynaert, S., De Boeck, H. J., Verbruggen, E., Verlinden, M., Flowers, N., & Nijs, I. (2021). Risk of short-term biodiversity loss under more persistent precipitation regimes. *Glob Chang Biol*, *27* (8), 1614-1626. doi:10.1111/gcb.15501
- Reynaert, S., Zi, L., AbdElgawad, H., De Boeck, H. J., Vinduskova, O., Nijs, I., . . . Asard, H. (2022). Does previous exposure to extreme precipitation regimes result in acclimated grassland communities? *Sci Total Environ*, *838* (Pt 3), 156368. doi:10.1016/j.scitotenv.2022.156368
- Saccone, P., Delzon, S., Pages, J. P., Brun, J. J., & Michalet, R. (2009). The role of biotic interactions in altering tree seedling responses to an extreme climatic event. *Journal of vegetation science*, *20* (3), 403-414. doi:10.1111/j.1654-1103.2009.01012.x
- Schmitz, O. J., Grabowski, J. H., Peckarsky, B. L., Preisser, E. L., Trussell, G. C., & Vonesh, J. R. (2008). From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. *Ecology*, *89* (9), 2436-2445. doi:10.1890/07-1030.1
- Siepielski, A. M., Morrissey, M. B., Buoro, M., Carlson, S. M., Caruso, C. M., Clegg, S. M., . . . MacColl, A. D. (2017). Precipitation drives global variation in natural selection. *Science*, *355* (6328), 959-962. doi:10.1126/science.aag2773
- Singh, P., & Baruah, G. (2021). Higher order interactions and species coexistence. *Theoretical Ecology*, *14* (1), 71-83. doi:10.1007/s12080-020-00481-8
- Soliveres, S., Smit, C., & Maestre, F. T. (2015). Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biol Rev Camb Philos Soc*, *90* (1), 297-313. doi:10.1111/brv.12110
- Spinoni, J., Vogt, J. V., Naumann, G., Barbosa, P., & Dosio, A. (2018). Will drought events become more frequent and severe in Europe? *International Journal of Climatology*, *38* (4), 1718-1736. doi:10.1002/joc.5291
- Suttle, K. B., Thomsen, M. A., & Power, M. E. (2007). Species interactions reverse grassland responses to changing climate. *Science*, *315* (5812), 640-642. doi:10.1126/science.1136401
- Van den Berge, J., Naudts, K., De Boeck, H., Ceulemans, R., & Nijs, I. (2014). Do interactions with neighbours modify the above-ground productivity response to drought? A test with two grassland species. *Environmental and Experimental Botany*, *105*, 18-24. doi:10.1016/j.envexpbot.2014.04.002

- Van Sundert, K., Arfin Khan, M. A. S., Bharath, S., Buckley, Y. M., Caldeira, M. C., Donohue, I., . . . Vicca, S. (2021). Fertilized graminoids intensify negative drought effects on grassland productivity. *Glob Chang Biol* . doi:10.1111/gcb.15583
- Vicca, S., Gilgen, A. K., Serrano, M. C., Dreesen, F. E., Dukes, J. S., Estiarte, M., . . . Granier, A. (2012). Urgent need for a common metric to make precipitation manipulation experiments comparable. *New Phytologist*, *195* (3), 518-522. doi:10.1111/j.1469-8137.2012.04224.x
- Walker, L. R., Clarkson, B. D., Silvester, W. B., & Clarkson, B. R. (2003). Colonization dynamics and facilitative impacts of a nitrogen-fixing shrub in primary succession. *Journal of vegetation science*, *14* (2), 277-290. doi:DOI 10.1111/j.1654-1103.2003.tb02153.x
- Weigelt, A., Steinlein, T., & Beyschlag, W. (2002). Does plant competition intensity rather depend on biomass or on species identity? *Basic and Applied Ecology*, *3* (1), 85-94. doi:Doi 10.1078/1439-1791-00080
- Weiher, E., & Keddy, P. A. (1995). Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos* , 159-164.
- Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. New York, NY, USA: Springer.
- Wickham, H., Francois, R., Henry, L., & Müller, K. (2015). dplyr: A grammar of data manipulation. [WWW document] URL <https://dplyr.tidyverse.org/> [accessed 5 October 2021].
- Wootton, J. T. (1993). Indirect Effects and Habitat Use in an Intertidal Community - Interaction Chains and Interaction Modifications. *American Naturalist*, *141* (1), 71-89. doi:10.1086/285461
- Xiao, J. L., Li, Y. Z., Chu, C. J., Wang, Y. S., Meiners, S. J., & Stouffer, D. B. (2020). Higher-order interactions mitigate direct negative effects on population dynamics of herbaceous plants during succession. *Environmental Research Letters*, *15* (7), 074023. doi:10.1088/1748-9326/ab8a88
- Zhao, W. N., & Khalil, M. A. K. (1993). The Relationship between Precipitation and Temperature over the Contiguous United-States. *Journal of Climate*, *6* (6), 1232-1236. doi:10.1175/1520-0442(1993)006<1232:Trbpat>2.0.Co;2