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Research article

Species diversity promotes facilitation under stressful conditions

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Climate change is expected to lead to a drier world, with more frequent and severe droughts, constituting a growing threat to biodiversity, especially in drylands. Positive plant–plant interactions, such as nurse plants facilitating beneficiary communities in their understorey, could mitigate such climate-induced stress. However, testing the real-world relevance of nurse facilitation under drought requires accounting for interactions within the diverse beneficiary communities, which may reduce, or amplify the buffering effect of a nurse. Here, we investigated when and how the interactions among nurse plants and beneficiary community members buffered drought effects in a Mediterranean semiarid abandoned cropland. We transplanted sapling beneficiary communities of either one or three species either under a nurse or in open microsites for different soil moisture levels through watering. Net facilitative effects on survival and biomass were only observed when beneficiary communities were species-diverse and under drought (without watering), meaning that under these conditions, facilitation provided by the nurse had larger positive effects than the negative effects stemming from competition with the nurse and among beneficiary species. Nurses appear to be generating these increases in survival and biomass in drought conditions via two mechanisms commonly associated with watering in open sites: they generate complementarity among the beneficiaries and shift traits to lower stress profiles. Contrasting with watering, which was found to enhance competitive hierarchy, our study shows that nurses appear to alter species dominance, favouring the less competitive species. Our results highlight three mechanisms (complementarity, competitive dominance, and trait plasticity) by which nurse species could mitigate the loss of biodiversity and biomass production due to water stress. Maintaining and supporting nurse species is thus a potentially pivotal approach in the face of projected increase in drought conditions for many drylands across the world.

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Introduction

Climate change has already led to a rise in the frequency of extreme heat and drought events, a trend observed globally over recent decades and projected to persist (Calvin et al. 2023). Such conditions have direct detrimental effects on plants, especially those not adapted to prolonged and frequent periods of water stress, and will likely alter ecosystem structure and functioning in the long term (Müller and Bahn 2022). Changes to ecosystem structure and functioning will certainly arise in part due to changes in plant–plant interactions and plant coexistence (Alexander et al. 2016, Graff and Aguiar 2017). However, plant–plant interactions may also modulate the level of water stress experienced by plants (Maestre et al. 2003), potentially buffering the impacts of increasingly drier conditions (Morcillo et al. 2019). A key example of such buffering arises from the hypothesised positive impacts of nurse plants on others (Callaway 2007). Improving our understanding of how species interactions both respond to and shape responses to drought is critical to predict the future of plant communities in a drier world.

Drylands across the planet exhibit limited water availability for plants and animals. In drylands, plants referred to as 'benefactors' or 'nurses' that facilitate other plants ('beneficiaries') are key drivers of community structure and functioning (Michalet et al. 2006, Anthelme et al. 2007, Maestre et al. 2016). Nurse plants can improve environmental conditions beneath their canopy, e.g. by reducing soil erosion, buffering the daily fluctuations in temperature, and increasing water retention (Callaway 2007). Such positive effects relative to drought conditions correlate with increased species richness (Gross 2008, Cavieres et al. 2014), increased diversity in community composition (Kikvidze et al. 2015), and underpin large scale ecosystem properties such as productivity (Cardinale et al. 2002, Wright et al. 2017), resilience (Kéfi et al. 2007a, b) and the spatial distribution of species in drylands (Kéfi et al. 2007a, b). Nurse plants, by generating these local environmental conditions, could thus mitigate the effects of increasing severity and frequency of drought events on biodiversity and ecosystem functioning.

However, in order to accurately assess the potential of facilitative effects for mitigating the effects of climate change (e.g. droughts, extreme temperatures), one must evaluate nurse effects in biodiverse communities and disentangle the multiple mechanisms by which they operate and contexts in which they arise. We propose to monitor three key mechanisms that arise from trait-based ecology and ecosystem functioning research (Loreau and Hector 2001): complementarity effects (i.e. niche differentiation and facilitation), competitive hierarchy (i.e. selection effects), and plasticity (i.e. trait profile changes). There are independent pieces of evidence for all three of these, which we review below before introducing our experiment and data that address all three simultaneously.

Community assembly theory, and specifically the concepts of complementarity and competitive hierarchy, provides key predictions about the outcome of nurse–beneficiary interactions in species-diverse communities. Facilitation can be seen as an expansion of the niche of beneficiary species (Bruno et al. 2003, Koffel et al. 2021), e.g. by making environmental conditions suitable for a larger range of species, such as those that prefer higher moisture. Furthermore, at the microsite scale, nurse plants increase habitat heterogeneity, further extending the niche space available to beneficiary plants (O'Brien et al. 2017). This expanded niche space is likely better exploited by species-rich beneficiary communities that are able to use different aspects of this new resource space, e.g. by having contrasted water use strategies, i.e. higher 'niche complementarity' (Loreau and Hector 2001, Cardinale et al. 2002), or in cases where beneficiaries directly facilitate each other. Previous research identified that facilitation from nurse plants benefits more the least drought resistant species (Liancourt et al. 2005, Graff and Aguiar 2017), and that nurses can alter competitive hierarchy among beneficiary species (Schöb et al. 2013, Michalet et al. 2017), which are coined as 'selection effects' (Loreau and Hector 2001). Previous studies reported that species richness increases complementarity but has contrasting effects on selection (Loreau and Hector 2001, Fargione et al. 2007), such that complementarity effects are responsible for the positive effects of species richness on grassland productivity. Investigating how nurse-provided facilitation affects complementarity (i.e. niche differentiation and facilitation) and selection (i.e. competitive hierarchy) in beneficiary communities can thus help bridge the gap between facilitation and ecosystem functioning research (Wright et al. 2017).

By modifying local environmental conditions, nurse plants may also alter the physiology and resource exploitation strategies of the beneficiary plants via phenotypic plasticity or evolution. The physiological response to variation in environmental conditions can be assessed by using leaf functional traits, such as a lower leaf dry matter content (LDMC) and a higher specific leaf area (SLA) can indicate a decrease of water stress (Galmés et al. 2005, Zhang et al. 2015, Májeková et al. 2021). In harsh environments, previous research identified that beneficiary species located beneath and within a nurse display higher variability in leaf trait composition, but also less-stressed leaf trait syndromes than beneficiary species located in open sites (Schöb et al. 2012, 2013, 2017, Danet et al. 2017, 2018). Accounting for how the presence of the nurse and water stress modulate values of functional traits is therefore a valuable way to further understand the mechanisms by which facilitation operates on beneficiary plants.

Here we report on an in situ experiment set in a semi-arid dryland experiencing a long and severe drought (standard precipitation evaporation index < -1.5 SD over the study period, Supporting information) and designed to test how facilitative effects provided by nurse species in drylands differed for diverse and monospecific beneficiary communities, and how these facilitative effects changed under lower water stress. Our experiment allows us to gather data about the relative importance of complementarity, competitive hierarchy and trait plasticity in shaping patterns of facilitation. To do so, we performed a fully factorial experiment crossing beneficiary species diversity (three species in monoculture and three species communities), presence and absence of nurse species (nurse patch versus open) and water stress (watered versus non-watered). Specifically, with this design, we ask the following four questions. 1) How does species richness of beneficiary communities affect nurse net effects on the survival and biomass of those beneficiary communities? 2) How do nurse plants and water stress interact in driving the response of the beneficiary communities? 3) How do nurse plants affect complementarity and competitive hierarchy in beneficiary communities? 4) How do nurse plants alter the functional traits of beneficiary communities?

Material and methods

Study area

The experiment was conducted in 2016 in the Murcia region, southeastern Spain (37°57′33″N, 1°00′17″W – 172 m a.s.l., Fig. 1a). The climate is semiarid Mediterranean with a very high year to year variability. Mean annual rainfall is 283 mm and mean annual temperature is 18.2°C (Murcia Meteorological Station, period 1960–2017, Paniagua et al. 2019). The experiment was conducted in 2016, within a long drought period in the region that was particularly severe for the years 2013–2016, which received 543.5 mm of total rainfall (64% of the long-term average, i.e. 100 mm less per year than average) and experienced a mean annual temperature of 20°C, almost 2°C above the long-term average (Meteorological State Agency, AEMET). The standardised precipitation evapotranspiration index (SPEI, Vicente-Serrano et al. 2010), a proxy for water balance, was during the experiment 1.5 SD lower than the average over the 1950–2023 period in the region (Supporting information), which can be categorised as severely drought conditions (Slette et al. 2019). Soils are thin (20–50 cm), of silt-loam type (32% sand, 47% silt, 21% clay), and basic (pH = 8.7). The area is a mosaic of moderately steep slopes covered by alpha-grass *Stipa tenacissima* steppes and abandoned agricultural terraces built on the streambeds. The agricultural terraces in the study site were abandoned in the 1980s and 1990s and progressively colonised by forbs and shrubs (Fig. 1b). The extant perennial vegetation is dominated by the shrubs *Artemisia herba-alba*, *Anthyllis cytisoides* and *Pistacia lentiscus*.

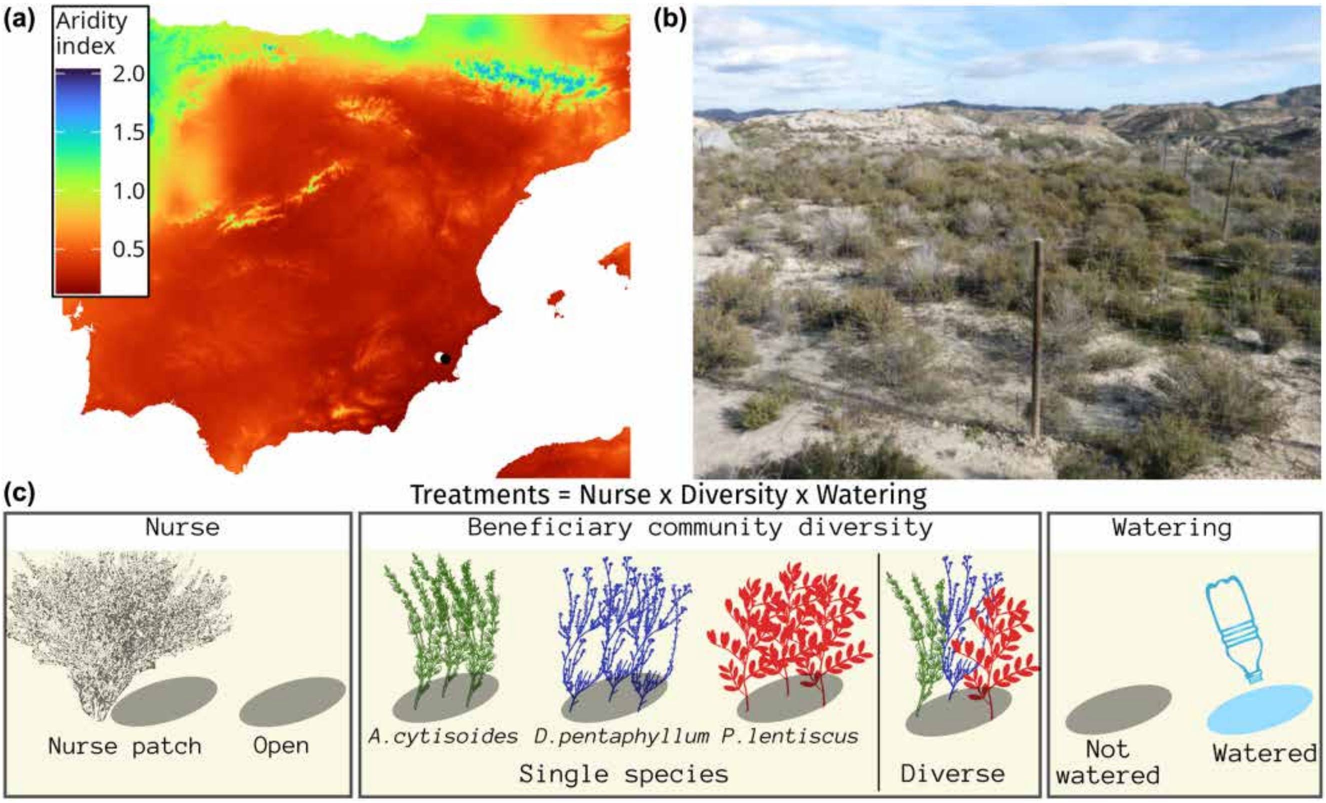

Figure 1. Study site and experimental treatments. (a) Average aridity index (annual precipitation over evapotranspiration) at 30 arc-seconds resolution over the 1970–2000 period. Data from Zomer et al. (2022). White and black dots (aridity index resp. 0.17 and 0.18) display respectively the location of Murcia and of the experimental site. (b) *Artemisia herba-alba* shrubs (nurse species) in one of the three terraces. (c) The microsites were located either under a nurse plant or in open interpatch areas, occupied by a single species beneficiary community or a three species beneficiary community, and watered regularly or not.

Experimental design

To assess the nursing effects on beneficiary communities, we set the beneficiary communities either under the canopy of a nurse plant, *Artemisia herba-alba*, or in open microsites. *Artemisia herba-alba* is a pioneer and common non-palatable species in drylands, known for extending its grazing protection toward palatable plants (Alados et al. 2006, Verwijmeren et al. 2014, 2019). *Artemisia herba-alba* was also reported to increase soil moisture after high rainfall events but to decrease it after small rain events (Verwijmeren et al. 2019). Furthermore, a closely related species *Artemisia tridendata* was previously shown to positively alter microclimate (Callaway et al. 1996, Ryel et al. 2003). It was reported to be partially phytotoxic, producing strong anti-germination compounds affecting both its own and other species, which however were not reported to affect negatively sapling growth (Arroyo et al. 2018).

To assess how nurse effects varied with the species richness of the beneficiary communities, we transplanted three plants under the nurse and in open microsites: either one beneficiary species growing in monoculture, or a mix of three species (Fig. 1c). We selected three different beneficiary species, so we had four different understorey community types in total (three monocultures and one mixture). We selected three common shrub species of the Mediterranean steppes as beneficiary species, namely *Anthyllis cytisoides*, *Dorycnium pentaphyllum* and *Pistacia lentiscus*, which are commonly found to co-occur in the same communities (Amat et al. 2015). Saplings of those three species were already reported growing under other shrub species in the region (Maestre et al. 2004, Sánchez-Martín et al. 2023). All those species have characteristics that are considered to be adaptations to the semiarid climates. *Anthyllis cytisoides* is a drought-avoider and sheds its leaves during summer, thereby decreasing the transpiring area (Haase et al. 2000). *Pistacia lentiscus* is a late successional evergreen shrub which can develop a dense root system at the sapling stage within one year after transplantation (Maestre et al. 2003). It can also increase the water storage in its leaves during the hot and dry season (Maestre et al. 2004), and the thick cuticle of its leaves (Coste 1937) limits the loss of water by evapotranspiration. *Dorycnium pentaphyllum* is a low-growing species known for its resistance to water stress (Caravaca et al. 2003). Its pinnate leaves, divided into narrow leaflets, decrease the transpiration surface and allow a more efficient regulation of the transpiration rate (Vogel 2009).

To assess how the level of water stress interacted with the nurse effects on beneficiary communities, we manipulated soil moisture by supplementing beneficiary communities with 1.5 litre of water per planting microsite and compared with control (not watered) beneficiary communities. Because of the naturally-droughted ambient conditions, we treat the 'not-watered' treatment as water-stressed conditions and the 'watered' treatment as non-water-stressed conditions. This naturally-droughted approach overcomes the potential limitations and artefacts associated with experimentally induced drought (Kreyling et al. 2017, Kröel-Dulay et al. 2022). We watered the planting microsites eight times during 2016 at around 6 p.m. to avoid the strongest evapotranspiration, once a month in spring and summer (i.e. March, April, May, June, July and August) and every two months otherwise (i.e. January and October). We did so by emptying one water bottle per microsite. We measured soil moisture 16 h after watering in January and June using a hand-held TDR sensor (Supporting information).

We used a fully factorial design that included three treatments with two levels each: microsite (nurse patch/open), assemblage diversity (monospecific/diverse), and watering (yes/no), with three types of monospecific assemblages, one per each target beneficiary species, resulting in 16 combinations of treatments and assemblages, each of them replicated 20 times. The treatment combinations were distributed among three terraces so that treatments were replicated 6 to 7 times per terrace. Because of the abundance of grazers in the area (mainly rabbits), every terrace was fenced with 1.80 m height wire fences and reinforced by chicken wire extending from about 60 cm above ground to 20 cm below ground.

Experimental setting and measurements

The transplantation of beneficiary communities was done between 23 October and 4 November 4 2015, into planting holes (beforehand and hereafter named 'microsite', Fig. 1) of approximately 25 × 25 × 25 cm dug manually. Each hole received one beneficiary community. The holes benefiting from the nurse plant effect (hereafter named 'nurse patch') were located below the canopy of the benefactor, about 20 cm apart from the main stem of the plant, and oriented northward to maximise the shading effect. We selected mature nurse plants, which were relatively homogeneous in canopy size. When a nurse was part of a patch, we located the microsite such that mainly one plant influenced it. Each nurse received one hole only (i.e. one beneficiary community). One week before planting saplings, the area received about 40 mm of natural rainfall (affecting all terraces equally), which provided excellent initial moisture conditions for the planted saplings. The holes were randomly attributed to the different treatments. The saplings composing the beneficiary communities were about 6 months at the time of transplantation and were grown from a local seed bank in the open air in a nursery (Viveros Muzalé S. L., www.viverosmuzale.com). They were grown in controlled wet conditions in 200 ml containers with a mixture of peat and coconut fibre, containing several individuals of the same species. Plants were bought in small pots. Each hole received one beneficiary community of three plants. We planted three pots per hole, following a triangular arrangement in which the plant pots were equally distant from each other (approximately 10 cm). To exclude the initial variation in the number of individuals per microsite, we only considered holes in which at least one individual from the original container survived in January, and removed supernumerary individuals by cutting their stems at their basis.

In order to estimate the total biomass of the beneficiary plants during the experiment, we estimated the allometric relationship linking total biomass to basal diameter and maximal height with a species effect (Catchpole and Wheeler 1992, Nafus et al. 2009). We put aside twelve individuals of each species in November (i.e. at the time we collected the seedlings from the nursery), and dried them at 65°C for three days to assess the total biomass of each individual. We log-transformed total biomass, basal diameter and vegetative height prior to modelling. The R^2 of the model was quite high ($R^2 = 0.86$, adjusted $R^2 = 0.84$), and we found a good agreement between predicted and observed values (Supporting information). This allometric relationship provided an estimation of total plant biomass based on the non-lethal measurement of plant height and stem diameter in the field (considering either only basal diameter or estimated total biomass did not alter our conclusions, Supporting information). Basal diameter was measured using a digital caliper at around 1 cm above the ground. To increase accuracy of the repeated measurements on the same plant, 1) we left a mark at the exact place where the first basal diameter measurement was taken and 2) measurements were done on the same side of the stem. Maximum height was measured using a measuring tape as the vertical distance between the soil and the top leafed stem. During the experiment, we measured the performance of individual beneficiary plants by recording 1) their survival and 2) their total biomass (using the above allometric relationship) from January to October 2016 (10 months).

To better understand the underlying mechanism through which nurse plants affect the beneficiary communities, we analysed how leaf functional traits responded to experimental treatments among beneficiaries. We focused on two leaf traits known to reflect different resource acquisition strategies: leaf dry matter content (LDMC) and specific leaf area (SLA, Pérez-Harguindeguy et al. 2013). The leaves of beneficiary plants were collected and processed in March 2016 (four months after plantation) following guidelines from Pérez-Harguindeguy et al. (2013). We only collected leaves without traces of disease, grazing or senescence, that were mature and most exposed to sunlight (i.e. close to the top of the main stem). We collected a few numbers of leaves, and only from the most healthy individuals, as to minimise the effect of leaf sampling on their response to experimental conditions. We collected three leaves per plant for *P. lentiscus*, five leaves for *A. citisoides* and ten leaves for *D. pentaphyllum*, so that the overall dry leaf biomass of each sample was sufficient for weighing. Leaves from each individual were stored in a plastic tube with a humid tissue to limit desiccation and stored in thermally-isolated cooler for transportation. Leaves were then first rehydrated with deionised water for several minutes, weighed, scanned, and then dried at least 48 h at 72°C. Once dry, we weighed individual leaves to compute LDMC and SLA. We a priori selected a random subset of microsites to be sampled, and then we effectively sampled only the subset that met the above conditions to reach a minimal sampling size per treatment combination of 7 samples for SLA (max 36) and 13 samples for LDMC (max 75, Supporting information).

Data analysis

Data analyses comprised two steps. We first modelled the survival, the biomass, and the leaf functional traits of the beneficiary communities to assess the effects of experimental treatments. We then used the predicted values of survival and biomass to compute the net effects of the nurse on beneficiary communities, and used the predicted values of biomass to compute complementarity and selection effects.

Modelling survival and biomass of beneficiary communities

We used mixed-effect generalised linear models to test whether the presence of the nurse affected the performance of beneficiary communities, i.e. their total biomass and their survival, for different levels of species richness (monoculture or mix of three species) and water stress. The presence of the nurse, the species richness of the beneficiary communities and the watering treatment were set as fixed effects. Because we hypothesised that the nurse effect on beneficiary communities was modulated by the water stress level and the richness of the beneficiary communities, we included the two-way and three-way interactions.

We further accounted for the following sources of variation via additional fixed effects: species identity in the beneficiary communities, time in months since the start of the experiment, and terrace identity. We added an extra quadratic effect of time as a fixed effect in the biomass model as it was found to decrease after summer. We further accounted for pseudoreplication linked to repeated measurements of the same beneficiary community across time by considering microsite level variation (i.e. hole containing the beneficiary communities nested within the terrace level) by specifying a random effect with these terms (Supporting information).

All models were fit using a Bayesian framework. We fit the biomass response variable with a gaussian error structure and the survival response variable with a binomial one with a logit link function. We used the integrated nested Laplacian approximation (INLA) to fit models (Rue et al. 2009, 2017) based on the 'INLA' R package (Rue et al. 2009), with default uninformative priors. The prior distribution of fixed coefficients followed a flat, zero centred, normal distribution ($N(\mu, \sigma^2) = N(0, 1000)$). The prior distribution of the random effects and the gaussian error followed a log gamma distribution with shape (s) and inverse scale (τ) parameters ($G(s, \tau) = G(1, 5.10^{-5})$). We then back-transformed the estimated coefficients to the standard deviation attributed to the random effects and the gaussian error $\left(\sigma = 1/\sqrt{\tau}\right)$. We computed the credible intervals for each model parameters at 80%, 90% and 95% using the highest posterior density method (Hyndman 1996), which can respectively be interpreted as weak, moderate and strong evidence of an effect when the interval does not include 0 (Mastrandrea et al. 2010, Klink et al. 2020).

We checked the overall quality of the model fit to the data visually by plotting the fitted versus the observed values (Supporting information) and visually inspected the agreement between predicted and observed differences between treatments (Supporting information). The conditional R^2 of the models were of 0.37, 0.09, 0.66 for biomass, LDMC and SLA respectively (Supporting information).

Estimates of nurse net effects on survival and biomass of beneficiary communities

We used the statistical models above to obtain a prediction of plant biomass and survival probability through time for all treatments, which we used to compute summary indices of interactions. The net effect of the nurse-beneficiary interactions was estimated with the additive neighbor-effect intensity index (NIntA, Díaz-Sierra et al. 2017). Positive values indicate positive net effects of the nurse on beneficiary communities (i.e. facilitation), while negative values indicate net negative effects of the nurse (i.e. competition). We used this index instead of the more-commonly used RII because the NIntA displays additive symmetry, i.e. positive and negative effects of the same magnitude are captured by opposite values (e.g. +10/−10), which avoids the underestimation of facilitation compared to competition (Díaz-Sierra et al. 2017). The NIntA is computed as follows:

$$\mathrm{NInt}_A = 2\frac{\Delta P}{P_{-N} + \Delta P} \tag{1}$$

with (P_{-N}) the performance of the beneficiary species in open microsites and (ΔP) the difference between the performance of beneficiary species in nurse patches and in open microsites (i.e. $P_{+N} - P_{-N}$). We used the sampled distribution of predicted values of survival and biomass (N = 1000 sampling) to compute the mean and the credible intervals at 80% of the NintA index.

Nurse effects on the functional traits of beneficiary species

Using the same statistical models as above (i.e. fixed effect of water treatment, presence/absence of nurse and species richness of beneficiary communities, along with their interactions), we assessed the effects of experimental treatments on both LDMC and SLA. These models did not include time as a fixed effect as functional traits were measured only once.

Nurse effects on complementarity and competitive hierarchy in beneficiary communities

We estimated how experimental treatments affected net diversity effects on beneficiary biomass and its partition into complementarity and selection effects. We used the same statistical model as for biomass, in which we added an interaction term between species effects and experimental treatments in order to estimate the differential responses of species to treatments, which is necessary to estimate selection effects. We used the model predictions for biomass to estimate how nurses alter complementarity and competitive hierarchy (i.e. selection effects) in beneficiary communities (Loreau and Hector 2001). The complementarity effect measures whether species in diverse communities have higher or lower biomass than expected from monoculture. A negative complementarity effect reflects a prevalence of competitive interference in beneficiary communities, while positive values indicate the prevalence of resource use partitioning or facilitation among beneficiary species. Complementarity effects were computed as the species richness times the average species relative biomass change from monoculture to mixture times the average species biomass in monoculture. Selection effects assess changes in species dominance in the beneficiary communities. Positive selection effects indicate that species that have the highest performance (here, measured as biomass) in monoculture are the ones that have the highest relative gain in biomass in mixture and reversely, meaning that the species that produce the most biomass in monoculture are the competitively dominant. Negative selection effects indicate that species that have the highest biomass in monoculture also have the lowest biomass gain in diverse communities, meaning that the species that are the most productive in monoculture are poor competitors (Fargione et al. 2007). Finally, neutral selection effects reflect an absence of relationship between species performance in monoculture and in mixture, indicating an absence of competitive dominance. Selection effects were computed as the species richness (i.e. 3) times the covariance between the species relative biomass change from monoculture to mixture and the species biomass in monoculture. As for NIntA computation, we used the biomass predicted from the statistical model to compute the diversity net effects, complementarity and selection effects, along with their 80% credible intervals.

Results

Effects of the nurse on the survival and biomass of beneficiary communities

We found no effect of the presence of the nurse alone on the survival and biomass of monospecific beneficiary communities (survival odd-ratio = CI80%: −0.15 [−0.38, 0.16], Fig. 2a; biomass: β = CI80%: −0.01 [−0.05, 0.02], Fig. 2b; CI: credible interval), resulting in an overall neutral net effect of the nurse on monospecific beneficiary communities (Fig. 2c–d, red and blue points).

We further found that, in open microsites, the species in diverse beneficiary communities had the same survival (OR = CI80%: −0.14 [−0.45, 0.34], Fig. 2a) but lower biomass (β = CI95%: −0.08 [−0.15, −0.01], Fig. 2b) than in monospecific communities. Watering increased the survival and biomass of beneficiary communities in open microsites (survival OR = CI95%: 1.11 [0.29, 2.44], biomass: β = CI80%: 0.0343 [0.0012, 0.0673]), and this effect was enhanced in diverse beneficiary communities (survival: OR = CI80%: 0.97 [0.03, 2.74], biomass: β = CI90%: 0.10 [0.01, 0.18]). This translated into a watering effect that was of +80% ((1.11 + 0.97)/1.11 − 1) in diverse communities than in monoculture. The positive watering effect on survival and biomass in monospecific beneficiary communities was similar regardless of the presence or absence of the nurse (survival OR = CI80%: 0.28 [−0.18, 1.01]; biomass: β = CI80%: 0.00 [−0.05, 0.05]), resulting in near-neutral net effects of the nurse on monospecific beneficiary communities in watered and non-watered treatments (Fig. 2c–d, blue and red points).

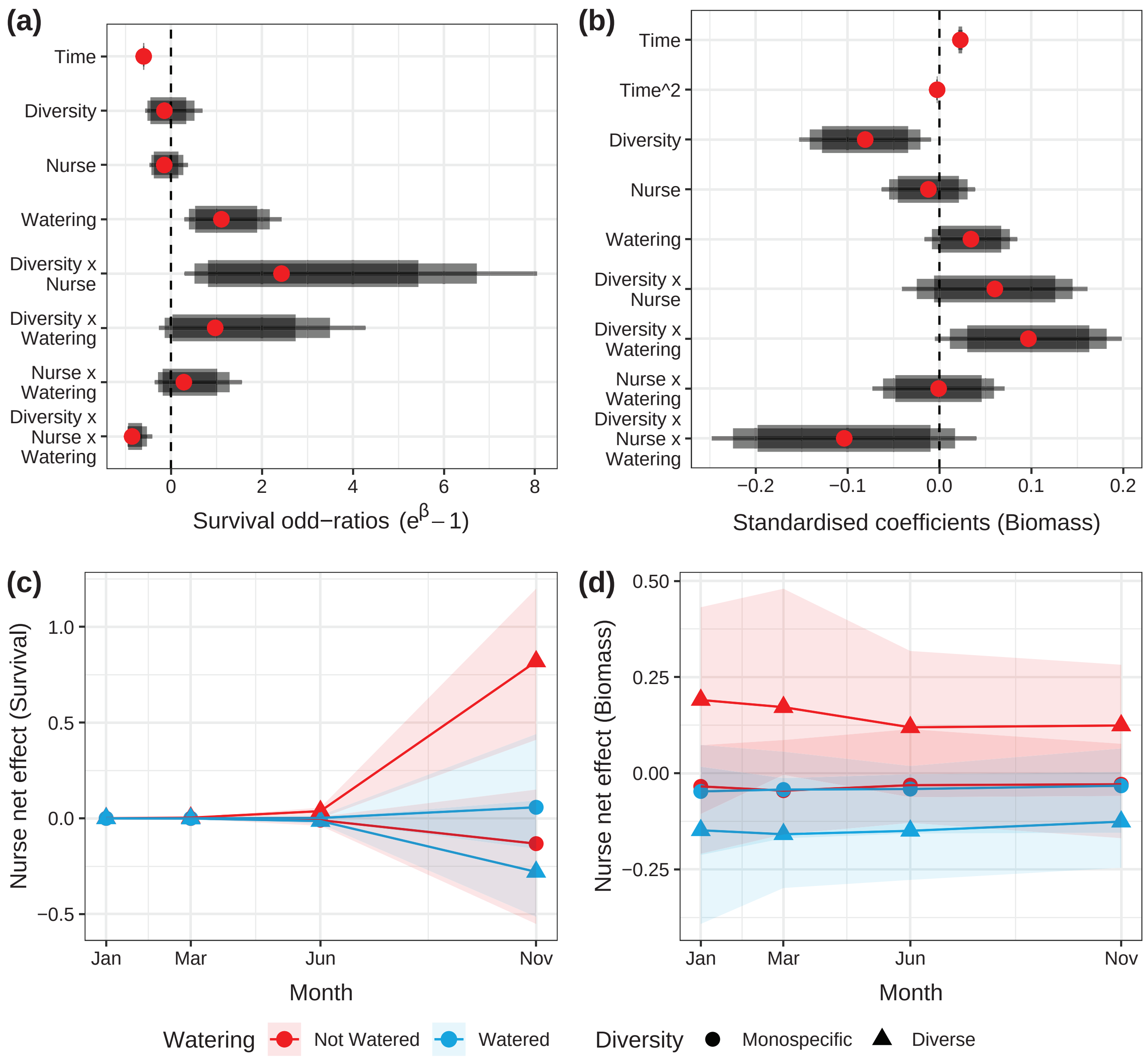

Figure 2. Model coefficients of the statistical models on survival probability (a), and biomass (b). Points represent the mean of the posterior distribution of coefficients; thin, medium and large bars represent the credible interval at 95%, 90% and 80%. Survival coefficients are the exponential of odd-ratios, values below and above 0 display respectively negative and positive effects on survival probability. The predictions of the model and the effects of control variables are displayed in the Supporting information. Nurse net effects on beneficiary communities estimated from model predictions using NIntA index on survival probability (c), and biomass (d). Nurse net effects below and above 0 represent respectively the prevalence of competitive and facilitative effects. Ribbons delimitate the 80% credible intervals.

Diverse beneficiary communities under nurses had higher survival and biomass than monospecific beneficiary communities in the same conditions (strong support for survival, OR = CI95%: 2.43 [0.30, 8.05], Fig. 2a, and weaker support for biomass β = CI80%: 0.060 [−0.006, 0.126], Fig. 2b), resulting in a strong positive net effect of the nurse in diverse and non watered assemblages (Fig. 2c–d, red triangle). However, the positive effects of nurses on the survival and the biomass of diverse beneficiary communities were reduced by watering (survival: OR = CI95%: −0.85 [−0.96, −0.41], Fig. 2a; biomass: β = CI95%: −0.10 [−0.25, 0.04], Fig. 2b), resulting in a negative net effect of the nurse in diverse and watered beneficiary communities (Fig. 2c–d, blue triangle).

Effects of the nurse on complementarity and competitive hierarchy

Partitioning the effects of species richness on the biomass of beneficiary communities, we found that the presence of the nurse interacted with water stress level to determine complementarity and selection effects (Fig. 3). We always found positive net effects of species diversity on beneficiary biomass, driven by positive complementarity effects, while selection effects were ten times lower in magnitude. Without watering, complementarity increased under nurses compared to open microsites (Fig. 3, red lines), indicating that the nurse promoted the positive effects of species richness. Conversely, with watering, increase in complementarity was higher in open microsites than under nurse patches. In open microsites, the increase in complementarity effects was much larger for watered beneficiary communities than for non-watered ones (Fig. 3, points), while watering hardly increased complementarity in nurse patches (Fig. 3, triangles). We further found that watering increased selection effects from slightly negative to slightly positive in open microsites (−0.25 versus 0.5, Fig. 3, points), while watering had no effect on selection in nurse patches (triangles). In nurse patches, selection effects were negative regardless of the water stress conditions (around −0.1, Fig. 3), indicating that nurse plants altered competitive dominance in beneficiary communities.

Effect of the nurse on trait plasticity

We found that functional traits of the beneficiary communities responded similarly to the nurses and watering treatments (effects of nurse and water alone on LDMC, Fig. 4). The leaf dry matter content (LDMC) and specific leaf area (SLA) of the beneficiary communities were found to respond to nurse patch and watering treatments. We found that beneficiary communities located under nurses had a higher SLA and lower LDMC than in open areas (standardised coefficients: β=CI90%: −0.131 [−0.265, 0.002] and CI90%: 0.37 [0.03, 0.70] respectively, Fig. 4). We further found strong evidence for lower LDMC in watered treatment (β=CI95%: −0.3 [−0.5, −0.2]) but not SLA (β=CI80%: −0.1 [−0.4, 0.2]). We did not find evidence that community diversity affected leaf traits (Fig. 4).

We found that soil moisture was quite low, 6.9% on average in March and that watering increased soil moisture by 4.1% 16 hours after watering (i.e. +59% in March, Supporting information). However, nurse patches were not found to result in higher soil moisture overall (average 95%CI: 4.0% [3.1%, 4.9%] in nurse patch versus 4.0% [3.1%, 4.8%] in open non-watered microsites in June, Supporting information). We found that nurse patches had a temperature 3°C lower than in the open at noon (28.9 [27.6, 30.1] versus 32.3 [31.2,33.5] in June, i.e. −11%, Supporting information), and a photosynthetic active radiation 100 quantum m^{-2} s^{-1} lower than in the open (255 [229, 280] versus 358 [333, 383] in June, i.e. −29%, Supporting information).

Discussion

One of the key questions about the role of facilitation in mitigating the impacts of drought and climate change in dryland communities is how the species diversity of beneficiary communities mediates facilitation and by which mechanisms. We examined the roles of nurse plants and beneficiary communities' species richness at two levels of drought stress with a manipulative field experiment that allowed us to ask four questions: 1) how does species richness of beneficiary communities affect nurse net effects on the survival and biomass of those beneficiary communities? 2) How do nurse plants and water stress interact in driving the response of the beneficiary communities? 3) How do nurse plants affect complementarity and competitive hierarchy in beneficiary communities? 4) How do nurse plants alter the functional traits of beneficiary communities? Overall, we found that nurse facilitation only occurred in case of species-diverse beneficiary communities and in the absence of watering. Nurse and watering treatments had similar effects on complementarity (gain in biomass in diverse beneficiary communities compared to monoculture)

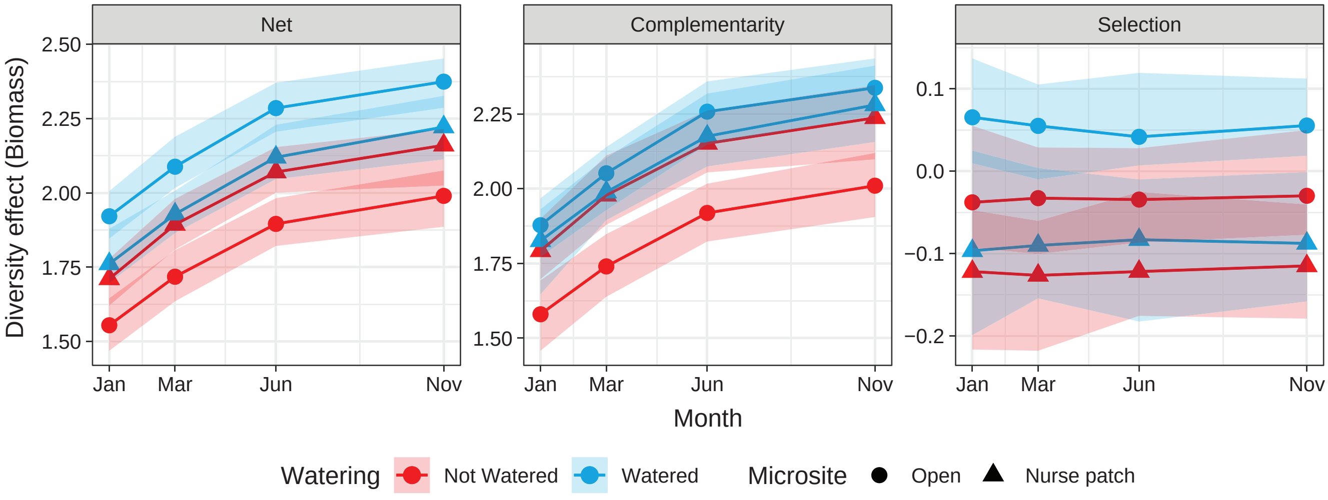

Figure 3. Effects of the nurse, watering and beneficiary community species richness on diversity effects. Species richness effects on biomass of beneficiary communities (Net effects), partionned in complementarity and selection effects. Estimations of species richness effects computed with raw values of biomass are displayed in the Supporting information. Ribbons delimitate the 80% credible intervals.

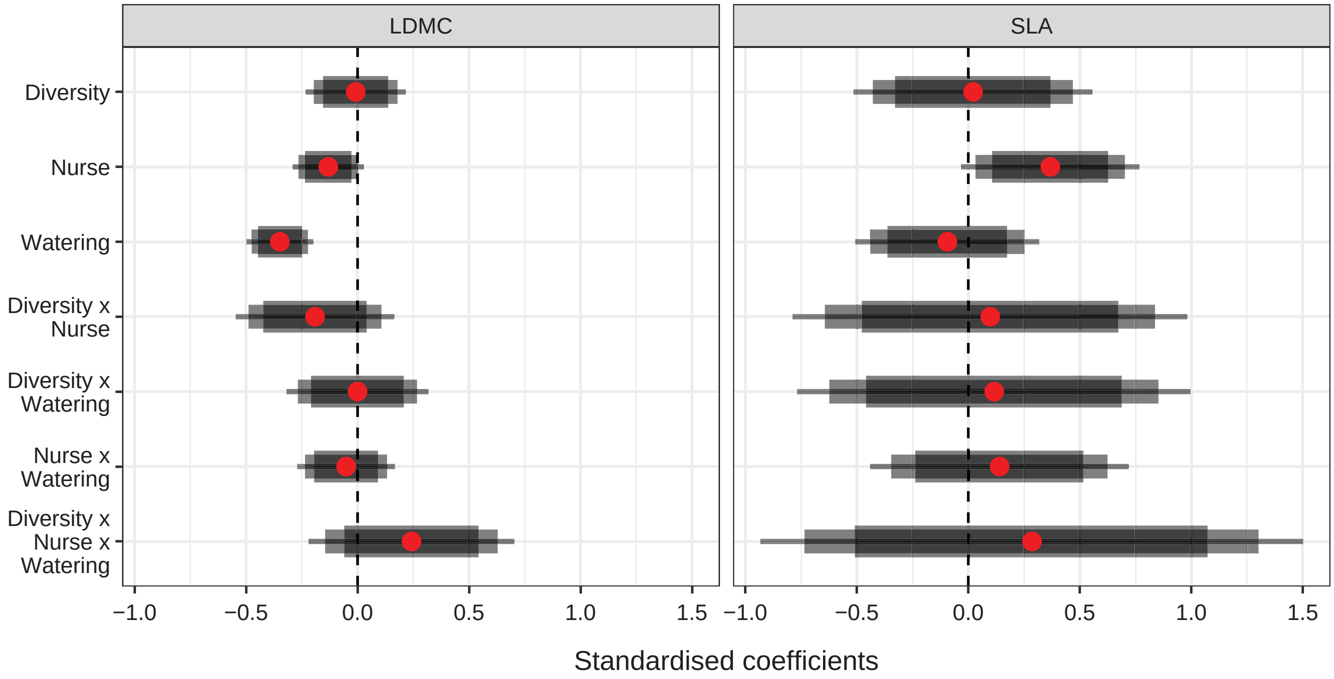

Figure 4. Effects of the nurse, watering and beneficiary community species richness on the trait plasticity of beneficiary plants. Model coefficients of the statistical models on leaf dry matter content (LDMC) and specific leaf area (SLA). Points represent the mean of the posterior distribution of coefficients; Thin, medium and large bars represent the credible intervals at 95%, 90% and 80%. The effects of control variables and the predictions of the model are displayed in the Supporting information.

and on trait plasticity. However, the nurse treatment differed from the watering one in its effect on competitive hierarchy, as nurses facilitated more the most maladapted species (i.e. slightly negative selection effects) regardless of the water stress. In what follows, we discuss our results based on the wider context of global change research in drylands, on previous work on facilitation, and on ecological theory.

Species richness and water stress determine nurse effects on survival and biomass of beneficiary communities

We found that nurses had weak and quasi-neutral net effects on the survival and biomass of monospecific beneficiary communities, regardless of the level of water stress. This result could be explained by a strong intraspecific competition among the three beneficiary individuals in monoculture that swamps the positive effects of the presence of the nurse. Those results are in line with a recent meta-analysis, reporting that intraspecific competition is several orders of magnitude higher than interspecific competition (Adler et al. 2018). This is also in agreement with coexistence theory that predicts strong competition among conspecific plants due to the absence of niche differences (Chesson 2000, Kraft et al. 2015), and this effect appeared to supersede the effect of nursing, regardless of the water treatment. Our results suggest that accounting for competition among beneficiary species is an important factor to understand the effects of nursing on beneficiary communities (Schöb et al. 2013, Michalet et al. 2015), and highlights the importance of considering assemblages of multiple individuals when evaluating and testing nurse effects.

In contrast to monospecific beneficiary communities, we found that nurses had strong positive effects on plant survival and biomass in unwatered, species-diverse beneficiary communities. This could be explained by the lower competition experienced by the beneficiary species in species-diverse communities, which makes the facilitation provided by the nurse exceed the competition among beneficiary species. This is in line with coexistence theory which states that niche differentiation is key to achieve stable coexistence (Chesson 2000). However, we also found that the positive effect of the nurse in mixture shifted to a negative effect in watered conditions, in accordance with numerous studies showing that nurse-beneficiary net interactions shift from positive in stressful environments to negative in more benign environments (Bertness and Callaway 1994, Callaway 2007, Graff and Aguiar 2017). This shift toward a negative effect of the nurse could be due to two processes: watering improved the performance of beneficiaries in open microsites, or nurses were more efficient than beneficiary plants in consuming the added water in patch microsites through a more developed root system (Aguiar and Sala 1994, Maestre et al. 2003). Many dryland species respond quickly to water pulses, yet the differences in size and associated capacity for water uptake between an adult nurse plant and its neighbour saplings could explain that watering primarily benefited the nurse plant (Morcillo and Bautista 2022), thus resulting, as in our study, in negative net effects between the nurse and beneficiary communities.

Nurse increases complementarity effects in beneficiary communities

We found consistent net positive effects of species richness on beneficiary community biomass, driven solely by positive complementarity effects. We report total net effects of biodiversity that are five times lower than previously reported in species-rich, temperate grasslands (Loreau and Hector 2001), and we suggest that it could be due to three factors: 1) the combination of dryness and drought conditions in the study, 2) the use of shrub species which have slower growth than grass species, and 3) the small number of species in our beneficiary communities. Overall, diversity net effects associated with competitive hierarchy (measured by selection effects) were very low compared to complementarity effects, a result that matches previous findings in grasslands (Loreau and Hector 2001, Fargione et al. 2007). The dominance of complementary effects rather than competitive hierarchy suggests that the processes linked to niche differentiation and facilitation play a more important role than the ones linked to competitive dominance. Watering increased complementarity effects in open sites and nursing increased complementarity effects in non-watered sites. This highlights, similar to functional traits, the commonality in the effects of watering and nursing.

Although ten times lower than complementarity effects in magnitude, we found that the effects of nurse plants on competitive hierarchy differed from the ones of watering, such that watering enhanced competitive hierarchy in open sites (positive selection effects) while nurse plants facilitated more the most drought-sensitive species (negative selection effects) in water stress conditions. The effect of watering on selection indicates that the direct alleviation of water stress by watering results in the competitive dominance of species that already perform best in monoculture while drier, more stressful conditions suppress this competitive dominance. This result is in line with previous findings showing that even small changes in environmental conditions can result in a shift in the competitive hierarchy among species (Alexander et al. 2016, Morcillo et al. 2019, Van Dyke et al. 2022). The small negative selection effects found in nurse patches regardless of the water stress indicate that species that had the lower biomass in monoculture had the higher increase in biomass in species-diverse communities, suggesting that the more maladapted species benefited the most from being in a nurse patch. This result lines up well with earlier findings showing that nurse plants can change the competitive hierarchy of beneficiary species (Schöb et al. 2013, Michalet et al. 2015) and that mal-adapted species tend to be the most facilitated species (Liancourt et al. 2005, Graff and Aguiar 2017). Hence, the use of nurse plants may be key to maintain the positive effects of biodiversity on ecosystem functioning, by buffering environmental stochasticity in ecosystems that are expected to experience increasing extreme environmental variations (Jiang et al. 2008, Wright et al. 2017).

Effects of nurse on trait plasticity

We found that beneficiary communities followed less resource-conservative strategies (or more resource-exploitative strategies) when watered or in a nurse patch than when not watered or in open sites. Specifically, we found that the LDMC of beneficiary communities decreased in watered microsites and in nurse patch microsites. At biogeographic scales, LDMC has been found to decrease with increasing annual rainfall (Borgy et al. 2017). Our results suggest that we can draw a parallel between the effects of being under a nurse and in sites with increased water resources, which are both characterised by lower water deficit. We further found an increase in the specific leaf area (SLA) of beneficiary communities in nurse patches, which might also indicate a less resource-conservative strategy in nurse patches (Galmés et al. 2005, Zhang et al. 2015). Another possible explanation could be that the decrease in LDMC and the increase in SLA in nurse patches might be due to the shading effect of the nurse. Such shading can induce a compensation for the limited amount of radiation received and is a common adaptation in understorey plants (Pons 1977, Ackerly et al. 2002, Liu et al. 2016, Yang et al. 2019 Májeková et al. (2021)). We, however, did not find that watering affected the SLA of beneficiary communities in open sites, but did lead to lower LDMC. This result suggests that the response of leaf traits to the decrease in water stress in open sites did not imply changes in leaf area, possibly because of the higher evapotranspiration in open sites, which might constrain leaf area to small sizes despite lower water stress. Overall, our results are consistent with previous results showing that a decrease in water stress results in plant plastic responses toward higher SLA and lower LDMC (Galmés et al. 2005, Jung et al. 2014, Zhang et al. 2015, but see Májeková et al. 2021). This change fixes Query number 9 about Jung et al. 2014). However, a direct measurement of plant physiological activity would be needed to draw a stronger conclusion on the links among nurse presence, water stress and plant strategy. We did not find an effect of species richness of beneficiary communities on average LDMC and SLA. This may be because functional traits are expected to respond to variations in species richness in terms of trait variance and overlap (Violle et al. 2012, Danet et al. 2018) rather than in average values, which are expected to respond to environmental changes as we found in the present study (Enquist et al. 2015, Danet et al. 2017).

Facilitation potential to mitigate climate change effects on biodiversity

Our results show that the facilitation provided by nurse plants can improve the performance of species diverse beneficiary communities in water stress conditions by increasing biomass and survival, lead to trait plasticity toward a reduced water stress syndrome, increase the complementarity effects (i.e. niche differentiation and facilitation) in beneficiary communities while facilitating more the most maladapted species (i.e. negative selection effects) of species regardless of the water stress. Furthermore, our results show that the nurse effect is similar to the effect of adding water to open sites (on functional traits and complementarity effects). Altogether, the results suggest that facilitation by nurse shrubs can promote the diversity of beneficiary communities under high water deficit by increasing survival, which points to its importance for maintaining biodiversity in a climate change context. Secondly, our study also suggests that nurse shrubs can promote the species richness effects on biomass production.

Conclusion and perspectives

Our study shows that the species richness of beneficiary communities plays a major role in the net effects that nurses have on survival and biomass, suggesting that facilitation of beneficiary communities is more likely to occur in species-diverse communities. Furthermore, we report that facilitation can maintain high complementarity effects and alter competitive hierarchy among beneficiary species despite water stress, indicating a key role of facilitation in maintaining ecosystem functioning in stressful conditions. While our study stresses that species-diverse beneficiary communities might benefit more from facilitation provided by a nurse, our species-diverse beneficiary communities were of three species, so that the generality of our results should be confirmed with more species-diverse communities. Because most seedlings died after the first summer, our study precludes strong inference over dryland dynamics timescale. It is noteworthy, however, that the effects of species richness that we report about complementarity and competitive hierarchy are consistent with the critical findings in biodiversity–ecosystem functioning (Loreau and Hector 2001, Fargione et al. 2007) and facilitation (Liancourt et al. 2005) research. Our study opens up new perspectives on the mechanisms by which facilitation can improve the functioning of water-limited ecosystems and contributes to integrate facilitation more explicitly into biodiversity and ecosystem functioning concepts.

Our study calls attention on the importance of facilitation in maintaining biodiversity and biomass production in ecosystems that are expected to become drier, as our results show that facilitation by nurse plants not only increases the survival of plants in their species diverse understorey, but also amplifies the beneficial effects of species richness on biomass production. The potential of using facilitation as a restoration tool in drylands largely depends on the nurse and the beneficiary species (Fagundes et al. 2022). However, according to our results, facilitation by nurse shrubs could help species-rich transplanted communities to establish, by increasing the potential for niche differentiation and facilitation among beneficiary species. The drawback of relying on such keystone plants to maintain ecosystem functioning, is that if nurses come to be impacted by climate change and/or targeted by land-use change, then we could expect dramatic cascading effects in drylands communities (Losapio and Schöb 2017). This is the well-known 'double-edge sword' effect of facilitation, where facilitation increases productivity and species richness but also comes at the cost of increased fragility for the corresponding ecological communities (Kéfi et al. 2007a, 2008, 2016, Gross 2008, Danet et al. 2020).

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Author contributions

Alain Danet: Conceptualization (equal); Data curation (lead), Formal analysis (lead); Investigation (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Susana Bautista**: Conceptualization (equal); Investigation (supporting); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Alexandre Génin**: Formal analysis (supporting); Investigation (supporting); Writing – review and editing (equal). **Andrew P. Beckerman**: Writing – review and editing (equal). **Fabien Anthelme**: Conceptualization (supporting); Supervision (supporting); Writing – review and editing (equal). **Sonia Kéfi**: Conceptualization (equal); Funding acquisition (lead); Investigation-Supporting, Methodology (equal); Supervision (lead); Writing – original draft-Supporting, Writing – review and editing (equal).

Data availability statement

Data are available from the Zenodo Digital Repository: https://zenodo.org/doi/10.5281/zenodo.10171338 (Danet 2023). The manuscript and the supplementary materials are written in Rmarkdown, i.e. combining code and text, and are available on github: https://github.com/alaindanet/plant-interactions-stress-strategies. We further implemented a code pipeline using the targets R package to ensure that the code, the data, the figures, the manuscript and the results are up to date.

Supporting information

The Supporting information associated with this article is available with the online version.

References

Ackerly, D., Knight, C., Weiss, S., Barton, K. and Starmer, K. 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. – Oecologia 130: 449–457.

Adler, P. B., Smull, D., Beard, K. H., Choi, R. T., Furniss, T., Kulmatiski, A., Meiners, J. M., Tredennick, A. T. and Veblen, K. E. 2018. Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. – Ecol. Lett. 21: 1319–1329.

Aguiar, M. R. and Sala, O. E. 1994. Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. – Oikos 70: 26–34.

Alados, C. L., Gotor, P., Ballester, P., Navas, D., Escos, J. M., Navarro, T. and Cabezudo, B. 2006. Association between competition and facilitation processes and vegetation spatial patterns in alpha steppes. – Biol. J. Linn. Soc. 87: 103–113.

Alexander, J. M., Diez, J. M., Hart, S. P. and Levine, J. M. 2016. When climate reshuffles competitors: a call for experimental macroecology. – Trends Ecol. Evol. 31: 831–841

Amat, B., Cortina, J. and Zubcoff, J. J. 2015. Community attributes determine facilitation potential in a semi-arid steppe. – Perspect. Plant Ecol. Evol. Syst. 17: 24–33.

Anthelme, F., Michalet, R. and Saadou, M. 2007. Positive associations involving the tussock grass *Panicum turgidum* Forssk. in the Aïr-Ténéré Reserve, Niger. – J. Arid Environ. 68: 348–362.

Arroyo, A. I., Pueyo, Y., Pellissier, F., Ramos, J., Espinosa-Ruiz, A., Millery, A. and Alados, C. L. 2018. Phytotoxic effects of volatile and water soluble chemicals of *Artemisia herba-alba*. – J. Arid Environ. 151: 1–8.

Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. – Trends Ecol. Evol. 9: 191–193.

Borgy, B. et al. 2017. Plant community structure and nitrogen inputs modulate the climate signal on leaf traits. – Global Ecol. Biogeogr. 26: 1138–1152.

Bruno, J. F., Stachowicz, J. J. and Bertness, M. D. 2003. Inclusion of facilitation into ecological theory. – Trends Ecol. Evol. 18: 119–125.

Callaway, R. M. 2007. Positive interactions and interdependence in plant communities. – Springer.

Callaway, R. M., DeLucia, E. H., Moore, D., Nowak, R. and Schlesinger, W. H. 1996. Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs montane pines. – Ecology 77: 2130–2141.

Calvin, K. et al. 2023. IPCC, 2023: Climate change 2023: synthesis report. Contribution of working groups I, II and III to the sixth assessment report of the intergovernmental panel on climate change (Core Writing Team, Lee, H. and Romero, J., eds.) – IPCC.

Caravaca, F., del Mar Alguacil, M., Díaz, G. and Roldán, A. 2003. Use of nitrate reductase activity for assessing effectiveness of mycorrhizal symbiosis in *Dorycnium pentaphyllum* under induced water deficit. – Commun. Soil Sci. Plant Anal. 34: 2291–2302.

Cardinale, B. J., Palmer, M. A. and Collins, S. L. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. – Nature 415: 426–429.

Catchpole, W. R. and Wheeler, C. J. 1992. Estimating plant biomass: a review of techniques. – Austral Ecol. 17: 121–131.

Cavieres, L. A. et al. 2014. Facilitative plant interactions and climate simultaneously drive alpine plant diversity. – Ecol. Lett. 17: 193–202.

Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. – Theor. Popul. Biol. 58: 211–237.

Coste, H. 1937. Flore descriptive et illustrée de la France de la Corse et des contrées limitrophes. – Librarie des Sciences et des Arts.

Danet, A., Kéfi, S., Meneses, R. I. and Anthelme, F. 2017. Nurse species and indirect facilitation through grazing drive plant community functional traits in tropical alpine peatlands. – Ecol. Evol. 7: 11265–11276.

Danet, A., Anthelme, F., Gross, N. and Kéfi, S. 2018. Effects of indirect facilitation on functional diversity, dominance and niche differentiation in tropical alpine communities. – J. Veg. Sci. 29: 835–846.

Danet, A., Schneider, F. D., Anthelme, F. and Kéfi, S. 2020. Indirect facilitation drives species composition and stability in drylands. – Theor. Ecol. 189–203.

Danet, A.2023. Species diversity promotes facilitation under stressful conditions. [Data set].Zenodo , https://doi.org/10.5281/zenodo.10171339.

Díaz-Sierra, R., Verwijmeren, M., Rietkerk, M., de Dios, V. R. and Baudena, M. 2017. A new family of standardized and symmetric indices for measuring the intensity and importance of plant neighbour effects. – Methods Ecol. Evol. 8: 580–591.

Enquist, B. J., Norberg, J., Bonser, S. P., Violle, C., Webb, C. T., Henderson, A., Sloat, L. L. and Savage, V. M. 2015. Scaling from traits to ecosystems. – In: Advances in Ecological Research. Elsevier, pp. 249–318.

Fagundes, M. V., Oliveira, R. S., Fonseca, C. R. and Ganade, G. 2022. Nurse-target functional match explains plant facilitation strength. – Flora 292: 152061.

Fargione, J., Tilman, D., Dybzinski, R., Lambers, J. H. R., Clark, C., Harpole, W. S., Knops, J. M. H., Reich, P. B. and Loreau, M. 2007. From selection to complementarity: shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment. – Proc. R. Soc. B 274: 871–876.

Galmés, J., Cifre, J., Medrano, H. and Flexas, J. 2005. Modulation of relative growth rate and its components by water stress in Mediterranean species with different growth forms. – Oecologia 145: 21–31.

Graff, P. and Aguiar, M. R. 2017. Do species' strategies and type of stress predict net positive effects in an arid ecosystem? – Ecology 98: 794–806.

Gross, K. 2008. Positive interactions among competitors can produce species-rich communities. – Ecol. Lett. 11: 929–936.

Haase, P., Pugnaire, F. I., Clark, S. C. and Incoll, L. D. 2000. Photosynthetic rate and canopy development in the drought-deciduous shrub *Anthyllis cytisoide*s L. – J. Arid Environ. 46: 79–91.

Hyndman, R. J. 1996. Computing and graphing highest density regions. – Am. Stat. 50: 120–126.

Jiang, L., Pu, Z. and Nemergut, D. R. 2008. On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning. – Oikos 117: 488–493.

Jung, V., Albert, C. H., Violle, C., Kunstler, G., Loucougaray, G. and Spiegelberger, T. 2014. Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. – J. Ecol. 102: 45–53.

Kéfi, S., Rietkerk, M., van Baalen, M and Loreau, M. 2007a. Local facilitation, bistability and transitions in arid ecosystems. – Theor. Popul. Biol. 71: 367–379.

Kéfi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A. and Ruiter, P. C. de 2007b. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. – Nature 449: 213–217.

Kéfi, S., Baalen, M. van, Rietkerk, M. and Loreau, M. 2008. Evolution of local facilitation in arid ecosystems. – Am. Nat. 172: E1–E17.

Kéfi, S., Miele, V., Wieters, E. A., Navarrete, S. A. and Berlow, E. L. 2016. How structured is the entangled bank? The surprisingly simple organization of multiplex ecological networks leads to increased persistence and resilience. – PLoS Biol. 14: e1002527.

Kikvidze, Z. et al. 2015. The effects of foundation species on community assembly: a global study on alpine cushion plant communities. – Ecology 96: 2064–2069.

Klink, R. van, Bowler, D. E., Gongalsky, K. B., Swengel, A. B., Gentile, A. and Chase, J. M. 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. – Science 368: 417–420.

Koffel, T., Daufresne, T. and Klausmeier, C. A. 2021. From competition to facilitation and mutualism: a general theory of the niche. – Ecol. Monogr. 91: e01458.

Kraft, N. J. B., Godoy, O. and Levine, J. M. 2015. Plant functional traits and the multidimensional nature of species coexistence. – Proc. Natl Acad. Sci. USA 112: 797–802.

Kreyling, J., Arfin Khan, M. A. S., Sultana, F., Babel, W., Beierkuhnlein, C., Foken, T., Walter, J. and Jentsch, A. 2017. Drought effects in climate change manipulation experiments: quantifying the influence of ambient weather conditions and rain-out shelter artifacts. – Ecosystems 20: 301–315.

Kröel-Dulay, G. et al. 2022. Field experiments underestimate aboveground biomass response to drought. – Nat. Ecol. Evol. 6: 540–545.

Liancourt, P., Callaway, R. M. and Michalet, R. 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. – Ecology 86: 1611–1618.

Liu, Y., Dawson, W., Prati, D., Haeuser, E., Feng, Y. and van Kleunen, M. 2016. Does greater specific leaf area plasticity help plants to maintain a high performance when shaded? – Ann. Bot. 118: 1329–1336.

Loreau, M. and Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. – Nature 412: 72–76.

Losapio, G. and Schöb, C. 2017. Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. – Funct. Ecol. 31: 1145–1152.

Maestre, F. T., Bautista, S. and Cortina, J. 2003. Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. – Ecology 84: 3186–3197.

Maestre, F. T., Cortina, J. and Bautista, S. 2004. Mechanisms underlying the interaction between *Pinus halepensis* and the native late-successional shrub *Pistacia lentiscus* in a semi-arid plantation. – Ecography 27: 776–786.

Maestre, F. T., Eldridge, D. J., Soliveres, S., Kéfi, S., Delgado-Baquerizo, M., Bowker, M. A., García-Palacios, P., Gaitán, J., Gallardo, A., Lázaro, R. and Berdugo, M. 2016. Structure and functioning of dryland ecosystems in a changing world. – Annu. Rev. Ecol. Evol. Syst. 47: 215–237.

Májeková, M., Hájek, T., Albert, Á. J., Bello, F. de, Doležal, J., Götzenberger, L., Janeček, Š., Lepš, J., Liancourt, P. and Mudrák, O. 2021. Weak coordination between leaf drought tolerance and proxy traits in herbaceous plants. – Funct. Ecol. 35: 1299–1311.

Mastrandrea, M. D., Field, C. B., Stocker, T. F., Edenhofer, O., Ebi, K. L., Frame, D. J., Held, H., Kriegler, E., Mach, K. J., Matschoss, P. R., Plattner, G.-K., Yohe, G. W. and Zwiers, F. W. 2010. Guidance note for lead authors of the IPCC fifth assessment report on consistent treatment of uncertainties. – Intergovernmental Panel on Climate Change (IPCC). http://www.ipcc.ch.

Michalet, R., Brooker, R. W., Cavieres, L. A., Kikvidze, Z., Lortie, C. J., Pugnaire, F. I., Valiente-Banuet, A. and Callaway, R. M. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? – Ecol. Lett. 9: 767–773.

Michalet, R., Brooker, R. W., Lortie, C. J., Maalouf, J.-P. and Pugnaire, F. I. 2015. Disentangling direct and indirect effects of a legume shrub on its understorey community. – Oikos 124: 1251–1262.

Michalet, R., Maalouf, J.-P. and Hayek, P. A. 2017. Direct litter interference and indirect soil competitive effects of two contrasting phenotypes of a spiny legume shrub drive the forb composition of an oromediterranean community. – Oikos. 1090–1100.

Morcillo, L. and Bautista, S. 2022. Interacting water, nutrients, and shrub age control steppe grass-on-shrub competition: implications for restoration. – Ecosphere 13: e4093.

Morcillo, L., Camacho-Garzón, A., Calderón, J. S. and Bautista, S. 2019. Functional similarity and competitive symmetry control productivity in mixtures of Mediterranean perennial grasses. – PLoS One 14: e0221667.

Müller, L. M. and Bahn, M. 2022. Drought legacies and ecosystem responses to subsequent drought. – Global Change Biol. 28: 5086–5103.

Nafus, A. M., McClaran, M. P., Archer, S. R. and Throop, H. L. 2009. Multispecies allometric models predict grass biomass in semidesert rangeland. – Rangel. Ecol. Manage. 62: 68–72.

O'Brien, M. J., Pugnaire, F. I., Armas, C., Rodríguez-Echeverría, S. and Schöb, C. 2017. The shift from plant–plant facilitation to competition under severe water deficit is spatially explicit. – Ecol. Evol. 7: 2441–2448.

Paniagua, L. L., García-Martín, A., Moral, F. J. and Rebollo, F. J. 2019. Aridity in the Iberian Peninsula (1960–2017): distribution, tendencies, and changes. – Theor. Appl. Climatol. 138: 811–830.

Pérez-Harguindeguy, N. et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. – Aust. J. Bot. 61: 167–234.

Pons, T. L. 1977. An ecophysiological study in the field layer of ash coppice Ii experiments with *Geum urbanum* and *Cirsium palustre* in different light intensities. – Acta Bot. Neerl. 26: 29–42.

Rue, H., Martino, S. and Chopin, N. 2009. Approximate bayesian inference for latent Gaussian models using integrated nested laplace approximations with discussion. – J. R. Stat. Soc. B 71: 319–392.

Rue, H., Riebler, A. I., Sørbye, S. H., Illian, J. B., Simpson, D. P. and Lindgren, F. K. 2017. Bayesian computing with INLA: a review. – Annu. Rev. Stat. Appl. 4: 395–421.

Ryel, R. J., Caldwell, M. M., Leffler, A. J. and Yoder, C. K. 2003. Rapid soil moisture recharge to depth by roots in a stand of *Artemisia tridentata*. – Ecology 84: 757–764.

Sánchez-Martín, R., Verdú, M. and Montesinos-Navarro, A. 2023. Interspecific facilitation favors rare species establishment and reduces performance disparities among adults. – J. Veg. Sci. 34: e13185.

Schöb, C., Butterfield, B. J. and Pugnaire, F. I. 2012. Foundation species influence trait-based community assembly. – New Phytol. 196: 824–834.

Schöb, C., Armas, C. and Pugnaire, F. I. 2013. Direct and indirect interactions co-determine species composition in nurse plant systems. – Oikos 122: 1371–1379.

Schöb, C., Macek, P., Pistón, N., Kikvidze, Z. and Pugnaire, F. I. 2017. A trait-based approach to understand the consequences of specific plant interactions for community structure. – J. Veg. Sci. 28: 696–704.

Slette, I. J., Post, A. K., Awad, M., Even, T., Punzalan, A., Williams, S., Smith, M. D. and Knapp, A. K. 2019. How ecologists define drought, and why we should do better. – Global Change Biol. 25: 3193–3200.

Van Dyke, M. N., Levine, J. M. and Kraft, N. J. B. 2022. Small rainfall changes drive substantial changes in plant coexistence. – Nature 611: 507–511.

Verwijmeren, M., Rietkerk, M., Bautista, S., Mayor, A. G., Wassen, M. J. and Smit, C. 2014. Drought and grazing combined: contrasting shifts in plant interactions at species pair and community level. – J. Arid Environ. 111: 53–60.

Verwijmeren, M., Smit, C., Bautista, S., Wassen, M. J. and Rietkerk, M. 2019. Combined grazing and drought stress alter the outcome of nurse: beneficiary interactions in a semi-arid ecosystem. – Ecosystems 22: 1295–1307.

Vicente-Serrano, S. M., Beguería, S. and López-Moreno, J. I. 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. – J. Clim. 23: 1696–1718.

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V. and Messier, J. 2012. The return of the variance: intraspecific variability in community ecology. – Trends Ecol. Evol. 27: 244–252.

Vogel, S. 2009. Leaves in the lowest and highest winds: temperature, force and shape. – New Phytol. 183: 13–26.

Wright, A. J., Wardle, D. A., Callaway, R. and Gaxiola, A. 2017. The overlooked role of facilitation in biodiversity experiments. – Trends Ecol. Evol. 32: 383–390.

Yang, M., Liu, M., Lu, J. and Yang, H. 2019. Effects of shading on the growth and leaf photosynthetic characteristics of three forages in an apple orchard on the Loess Plateau of eastern Gansu, China. – PeerJ 7: e7594.

Zhang, C., Zhang, J., Zhang, H., Zhao, J., Wu, Q., Zhao, Z. and Cai, T. 2015. Mechanisms for the relationships between water-use efficiency and carbon isotope composition and specific leaf area of maize (*Zea mays* L.) under water stress. – Plant Growth Regul. 77: 233–243.

Zomer, R. J., Xu, J. and Trabucco, A. 2022. Version 3 of the Global Aridity Index and Potential evapotranspiration Database. – Sci. Data. 9: 409.