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The importance of facilitation on community assembly disappears under severe drought stress

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Abstract

1. Despite the recognition of positive interactions as an important driver of species coexistence and community structure, the underlying mechanism of how facilitation affects assembly processes along stress gradients is poorly explored. Understanding the responses of functional diversity to benefactor species at the extreme end of the stress gradient could provide valuable insight about facilitation-involved assembly mechanisms and contribute to the predictions of species coexistence under climate change.

2. In the drought-stressed community in the Badain-Jaran Desert, the responses of the local community to the nurse shrub species *Calligonum mongolicum* Turcz. were evaluated using hierarchical Bayesian models. For the 3-year experiment, summer rainfall in each year formed a natural gradient of drought stress. To evaluate the shrub's effects on the assembly process along that gradient, individual samples were collected in pairwise under-shrub and open habitats, and four traits related to stress tolerance and resource acquisition were measured simultaneously.

3. Under moderate drought stress, we observed shifting community-weighted means, broadening ranges and reducing overlaps of functional traits under shrubs. These effects were partly driven by a distinct microenvironment created by shrub plants, in particular the improvement and heterogeneity of soil moisture conditions. However, this influence on trait distributions was strongly dependent on the environmental context, and generally disappeared as drought stress shifted towards its driest end, almost in line with the decreased positive interaction assessed by plant density and species diversity.

4. This study focused on water-limited community that lies at the driest end of drought gradient and confirmed that facilitation can drive the assembly process through both environmental filtering and niche differentiation. More importantly, these assembly mechanisms are proven to become less efficient under extreme drought stress, which may suggest the occasionally disappearing role of benefactor plants on community assembly and an increasing risk of biodiversity loss in the context of climate change.

1 | INTRODUCTION

The importance of positive interactions for natural communities has been well established over the past two decades (Bertness & Callaway, 1994; Brooker et al., 2015; McIntire & Fajardo, 2014; Michalet, 2007; Soliveres et al., 2015). The stress-gradient hypothesis (SGH), the most influential model for positive interaction, predicts the dominance of facilitation over negative interactions in severe environments (Bertness & Callaway, 1994). Consistent with the hypothesis, monotonic changes in facilitative–competitive outcomes along environmental gradients have been demonstrated in different ecosystems (reviewed in He et al., 2013). However, its generality has been actively debated (Maestre & Cortina, 2004; Michalet, 2006, 2007; Soliveres et al., 2015). For example, the reduction, collapse or even switching back to competition under harsh environments has been reported in many studies (Chaieb et al., 2021; Filazzola et al., 2020; Guignabert et al., 2020; Le Bagousse-Pinguet et al., 2014; Liancourt et al., 2017; but see Pugnaire et al., 2015). To seek ecological explanations, the original SGH theory has been refined (Holmgren & Scheffer, 2010; Michalet et al., 2006, 2014), and researchers have proposed several non-monotonic formalisms, such as symmetric and asymmetric unimodal models (Michalet et al., 2021).

The processes that determine community assembly under the influence of benefactor species may differ from those in open areas (Kikvidze et al., 2015). Typically, species richness in communities can be increased by the presence of foundation or nurse plants, such as cushions in alpine communities and shrubs in drylands (Abdallah et al., 2016; Cavieres et al., 2014; Duarte et al., 2020; Liancourt et al., 2017; Michalet, 2006; Noumi et al., 2016). Likewise, functional traits driven by a range of environmental factors may also respond to favourable habitats created by the benefactor species (Chacón-Labella et al., 2016; Le Bagousse-Pinguet et al., 2017; Siefert et al., 2015). Thus, a shift towards more conservative or acquisitive functions among interacting species can be expected (Wang et al., 2017). For instance, alleviating drought stress due to nurse plants in arid ecosystems affects functional traits and leaf economics (e.g. specific leaf area, lamina–petiole length ratio and intrinsic water use efficiency), leading to relative changes in the community assembly process (García-Cervigón et al., 2015). Nevertheless, some researchers also reported that intraspecific trait variation of beneficiary individuals could not be well explained by the plant–plant interaction (van der Merwe et al., 2021). Evidence from alpine communities suggested that cushion-forming plants can support more species with larger leaves and greater heights than those from the surroundings (Ballantyne & Pickering, 2015; Dolezal et al., 2019). As a result, the realized niche of associated species can be expanded in response to the distinct microhabitats created by facilitators,

consequently improving species performance and leading to a positive interaction.

Facilitation affects species coexistence and assembly processes through several mechanisms (Bulleri et al., 2016; McIntire & Fajardo, 2014; Schöb et al., 2012). First, the filtering process can be changed in the local community adjacent to benefactor species, causing community-level shifts in functional traits. This trait-shifting mechanism, driven by facilitation, may create niche space for neighbours and lead to a distinct species composition compared with open areas (Butterfield & Callaway, 2013; Chacón-Labella et al., 2016). Second, facilitation can expand the range of traits by relaxing environmental filtering, which has often been reported in studies of cushions and shrubs (Bruno et al., 2003; Schöb et al., 2012; Wang et al., 2021). Spatial and temporal complexity, resulting from canopy structures, resource use and competition release of foundation plants, creates considerable heterogeneity at different arrays of stresses and then provides more available niche spaces for neighbouring plants (Le Bagousse-Pinguet et al., 2017). Third, facilitation can induce a decrease in trait overlaps among interacting species through the creation of microscale resources or sheltering heterogeneity (Doudová & Douda, 2020; but see Bulleri et al., 2016). The intracommunity trait divergence has been predicted to increase the probability of competition intransitivity among beneficiary plants and thus reduce the chance of competitive exclusion (McIntire & Fajardo, 2014; Soliveres et al., 2011). Overall, disentangling the responses of trait distribution to benefactor species under different conditions can enhance our understanding of the underlying assembly mechanism and predictions of species coexistence in changing environments (Liancourt & Dolezal, 2021).

Precipitation is considered the primary limiting factor for the growth of plant species in arid and semiarid ecosystems. Some previous studies projected that dry lands would become warmer with frequent uneven rainfall and prolonged droughts (IPCC, 2019). This climate change-driven extreme heat and drought can alter the survival thresholds of some species (Bachelet et al., 2016) and negatively affect community stability and ecosystem functioning. In water-limited communities, the modulation of available water by shrub species usually determines plant interactions and affects species coexistence (Butterfield et al., 2016; Michalet et al., 2014). Since benefactor plants can enhance richness more in systems with inherently lower numbers of species, Cavieres et al. (2016) suggested that facilitation could serve as an insurance mechanism for sustaining regional diversity under climate change. However, mounting evidence has indicated that the facilitative effects observed in drought-stressed ecosystems could be weakened by the higher level of environmental severity (Butterfield et al., 2016; Chaieb et al., 2021; Filazzola et al., 2020; Guignabert et al., 2020). This implies that the importance of facilitation on water-limited communities in response

to extreme climates might be overestimated. Therefore, this study intends to evaluate the effect of plant interaction on the local community from the perspective of functional diversity. The overall aim is to understand how facilitation affects assembly processes under harsh environments in the context of climate change.

Here, we study the effect of facilitation on assembly process along an interannual drought gradient in the Badain-Jaran Desert. In this region, precipitation during the plant-growing season is typically <100 mm. In the context of climate change, the uneven distribution of summer rainfall has increased in recent decades. *Calligonum mongolicum*, a foundation plant in the southern Badain-Jaran, has been found to play an important role in maintaining species coexistence and community structure at local scales. Benefiting from the novel habitats created by *C. mongolicum* shrubs, the associated local community can hold more biomass and higher species richness than open areas (Zhang et al., 2016). Nonetheless, in line with the refinement of the SGH theory, positive interactions between *C. mongolicum* and their associated plants might decrease along the drought gradient at our study site (Zhang et al., 2018). Based on previous empirical studies and theoretical predictions, we hypothesize that (1) *C. mongolicum* shrubs can affect the assembly process through environmental filtering or niche differentiation in the water-limited community; and (2) these effects on community assembly can be weakened by the collapse of facilitation under severe drought stress.

## 2 | MATERIALS AND METHODS

2.1 | Study area and species

This study was conducted in a typical desert grassland at the southern edge of the Badain Jaran Desert (between 39°22' and 39°26' N and between 100°06' and 100°09' E at 1,380 m a.s.l.) in the province of Gansu, China, with permissions granted by Linze Inland River Basin Research Station (TZ0060/O5SS011F01). The study region has a typical temperate desert climate, characterized by dry and hot summer, cold winter, strong solar radiation and very little precipitation. The zonal soil is classified as grey–brown desert soil, derived from diluvial–alluvial materials of the denuded monadnock. Over the past 20 years, the mean daily temperature in the study area was

approximately 9.8°C, with the highest temperature (38.2°C) in July. The average annual precipitation was 112.2 mm, where about half of it concentrated in summer. The summer precipitation ranged 25.6–87.6 mm, with a mean of 60.3 mm. During the study period (2017–2019), summer rainfall declined from 71.4 mm in 2019 to 48.6 mm in 2017 and 25.6 mm in 2018 (Figure 1). The lowest summer precipitation during this period reached the two-decade record low, which can represent the extreme condition of drought stresses in this region. The evaporation (measured by AM3 evaporation pan) was relatively stable (ranged 720.7–750.4 mm) in different growing seasons. Within plant-growing season, summer rainfall was distributed more evenly in 2019; but in 2017 and 2018, rainfall mainly occurred in the mid- and late-growing seasons (Figure 1a). All of these form a natural gradient of drought stress across years. For simplicity, the sampling years are marked as D, D+ and D++ according to decreased summer rainfall.

At the study site, the above-ground vegetation is discontinuous, covered with scattered shrub patches and sparse herbaceous plants. Affected by climatic conditions and soil properties, plant communities are commonly comprised of several drought- and salt-tolerant species. *Calligonum mongolicum* Turcz. (Polygonaceae) is a common perennial shrub species in the arid desert of the north-western China. It is widely distributed on flat desert or sand dunes and is important for the formation of plant communities. In this region, the canopy size of adult individual typically ranges 1.2–2.5 m. As a nurse plant, *C. mongolicum* can improve the moisture regime and soil fertility beneath its canopy, and consequently create a locally stable and distinct microenvironment relative to the surrounding open lands (Zhang et al., 2018). Due to harsh environments, the vegetation cover of herbaceous layer ranges 5%–15% (Zhang et al., 2018). The main species of subcanopy communities are forbs (e.g. *Bassia dasyphylla*, *Salsola ruthenica*, *Halogeton arachnoideus*, *Agriophyllum squarrosum* and *Corispermum mongolicum*) and grasses (e.g. *Chloris virgata and Eragrostis Pilosa*), all of which can grow in both open and under-canopy habitats.

2.2 | Sampling design

We investigate the effect of *C. mongolicum* shrubs on community assembly along the interannual drought gradient from 2017 to 2019 in
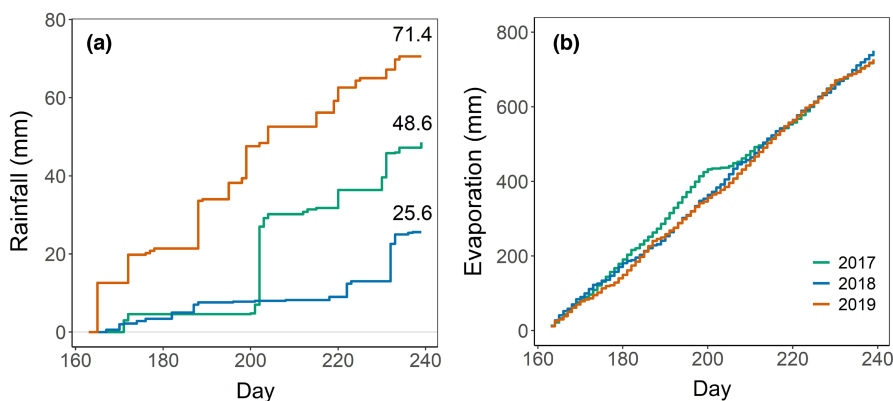
FIGURE 1 Rainfall and evaporation during plant-growing season at our study site. The accumulated values of (a) rainfall and (b) evaporation from mid-June to late-August are displayed

two fenced plots (200 m × 400 m). The two plots were about 1.5 km apart, with similar habitat type and species composition. Because of enclosure protections, the disturbances due to grazing and other human activities can be negligible. In each year, we selected stand-alone *C. mongolicum* shrubs with the crown width of 1.6–2.1 m and height of 1.5–1.8 m. In early September, a single 2 m × 2 m quadrat was established beneath the canopy of each selected shrub, while another quadrat of the same size was placed in an open area. To avoid any shrub effect while account for the spatial heterogeneity among different habitats, the open quadrat was placed over 10–20 m away from the selected shrub. There were 40, 45 and 39 pairwise quadrats at each open and under-canopy habitat in 2017, 2018 and 2019 respectively. We identified and recorded plant species in these quadrats ($n = 248$), and counted individual numbers of each species.

While investigating plants in different years, we also collected soil samples from these selected quadrats to measure soil moisture content (SWC) and soil organic matter (SOM) of the pairwise habitats. To determine SWC, we randomly chose 20 pairwise quadrats at the under-canopy and open habitats each year, collected four soil cores (5 cm diameter, 10–20 cm in depth) along the diagonal of each quadrat and measured them gravimetrically after oven-drying for 48 hr at 110°C. In the same way, we randomly chose 10 pairwise quadrats each year, collected four soil cores within each quadrat and applied the dichromate oxidation method (Kalembasa & Jenkinson, 1973) to determine SOM.

To measure functional traits at different years and habitats, we randomly selected two to five adult individuals for every observed understorey species according to their abundance in each selected quadrat at both habitats. During the study period, a total of 12 species were recorded. However, five species (three shrubs and two herbs) were omitted from the analyses because they were too rare to accurately estimate trait values (Appendix S1). To get robust estimation, at least 30 individuals of each species were sampled in different years and habitats. When the suitable samples of a species did not reach this amount, we randomly collected additional individuals from the same habitats (i.e. similar-sized shrubs or open area) in the fenced plots. From 2017 to 2019, respectively, we collected 328, 316 and 299 individuals under shrubs and 325, 320 and 296 individuals at open area for trait estimation. Sample size for each species was balanced. Then, we measured functional traits of each individual and estimated the community-level trait distribution of both open and under-canopy habitats in each year.

2.3 | Functional traits

We used specific leaf area (SLA), leaf dry matter content (LDMC), lateral spread (LS) and height (H) of understorey species to evaluate the effect of foundation species on trait-based community assembly under drought stress. Specific leaf area indicates a trade-off between an investment in leaf surface area to capture light for photosynthesis and an investment in constructing more protected tissues to avoid dehydration (Long et al., 2011). There

is a high phenotype variation in SLA among species, which decreases with increasing canopy openness at the community level (Carlucci et al., 2015). Leaf dry matter content characterizes plant resource acquisition strategies and is negatively correlated with the maximum relative growth rate (Westoby et al., 2002). It generally decreases with increasing water availability and is positively correlated with species susceptibility to herbivory (Cornelissen et al., 2003). Both lateral spread and height can be influenced by resource situation and competition intensity of microhabitats (Danet et al., 2018; Reich et al., 1998). Variations in lateral spread and height of understorey plants can indicate the interactions between benefactors and their associated species, or among beneficiary plants (Schöb et al., 2012; Wang et al., 2021).

Specific leaf area (m/g) was determined as the ratio of fresh leaf area to leaf dry mass. LDMC (mg/g) was determined as the ratio of leaf dry mass to fully rehydrated fresh mass. Lateral spread (cm) was measured as the maximum crown width of individuals in the understorey community. Height (cm) was measured as the distance between the extended upper boundary of the crown and the ground level. To calculate SLA and LDMC, three to five healthy leaves per individual were collected. In the laboratory, we rehydrated the samples for 12 hr in the dark and measured the fresh weight using an electronic balance and calculated the leaf area using ImageJ software (Cornelissen et al., 2003). Then, the dry weight was quantified using an electronic balance after oven-drying at 80°C for 48 hr.

2.4 | Hierarchical Bayesian framework

Dealing with data collected from sparse vegetation or species-poor communities is a major challenge. This is because rare species are usually missing during finite sampling, which increases the difficulty in data processing and causes vast noise in statistical inferences. To address this problem, we employ a hierarchical Bayesian (HB) framework that simultaneously evaluates multiple relationships and explicitly accounts for uncertainty in both ecology and sampling processes (Hooten & Hobbs, 2015). The Bayesian approach treats all unobserved quantities as random variables to capture the uncertainty. By setting reasonable priors and building ecological models, the distributions of posterior parameters that contain statistical information of the unobserved variables can be estimated from the given data. As an advantage of HB frameworks, ecological indices can be calculated from the posterior parameters (Golicher et al., 2006), which allow underrepresented species or individuals to borrow strength from well-observed ones and transmit the stochastic information of the assembly process to target indices (Marion et al., 2018).

2.4.1 | Quantifying effect size of facilitation by Poisson-lognormal model

The effect size of shrubs on the understorey community is quantified using the Poisson-lognormal model conditional on individual

abundance (i.e. density or sample size). First, we assume that the total abundance in the k-th quadrat (N_k) follows a Poisson distribution, which can describe the sampling process,

$$N_k \sim \text{Poisson}\left(\lambda_\kappa\right), \tag{1}$$

where λ_k is the 'true' abundance that denotes the mean and variance of the sample size in the k-th quadrat. Then, we assume that λ_k follows a lognormal distribution to incorporate the uncertainty of ecological process, such as

$$\log\left(\lambda_k\right) \sim \text{normal}\left(\beta_0 + \beta_1 y_i + \delta_i x_j + \varepsilon_i, \sigma_{ij}\right), \tag{2}$$

where y_i is the rainfall during the plant-growing season in the i-th year, and x_j is the indicator variable that describes the type of habitats. In the deterministic model $f\left(y_i, x_j\right) = \beta_0 + \beta_1 y_i + \delta_i x_j + \varepsilon_i$, the macroclimate and microhabitat effects are separated. Specifically, the product $\beta_1 y_i$ gives the effect of summer rainfall, while the product $\delta_i x_j$ gives the effect of nurse shrubs. In addition, the impacts of summer rainfall and nurse shrubs on soil moisture content and organic matter are also modelled using a lognormal likelihood, with the deterministic model $g\left(y_i, x_j\right) = \beta_0 + \beta_1 y_i + \delta_i x_j + \varepsilon_i + \omega_h$. Here, the random-effect term ω_h for different soil core locations follows a normal distribution as $\omega_h \sim \text{normal}\left(0, \sigma_{ij}^\omega\right)$, where the scale parameter σ_{ij}^ω represents the spatial variation in microenvironments inside each quadrat.

In the HB model, the posterior distribution of δ_i can quantify the strength and direction of shrub effect on either total abundance or microenvironments. For example, a positive δ indicates the net facilitative effect; a negative δ indicates the net competitive effect; a small δ (close to zero) indicates the weak influence of shrubs and vice versa. Another important parameter is σ^ω, which can be used to assess the fine-scale heterogeneity of SWC or SOM in microenvironments among different years and habitats.

2.4.2 | Incorporating community–assembly uncertainty into relative abundance

We assume that the vector of species abundance ($\vec{z}$) in the k-th quadrat follows a multinomial distribution:

$$\vec{z}_k \sim \text{multinomial}\left(\overline{\theta}_k, N_k\right), \tag{3}$$

where $\overline{\theta}$ is the probability of species occurrences and N is the total abundance of individuals. In the k-th quadrat, $\overline{\theta}_k$ can be transformed to softmax normal priors by the function:

$$\overline{\theta}_k = \text{softmax}\left(\overline{\alpha}_k\right) = \frac{\exp\left(\overline{\alpha}_k\right)}{\sum \exp\left(\overline{\alpha}_k\right)}. \tag{4}$$

In the softmax, the sum of $\overline{\alpha}_k$ in every k-th quadrat should equal one. We define that the former K-1 components of $\overline{\alpha}_k$ follow a normal distribution with means $[\eta_1, \ldots, \eta_{k-1}]$ and standard deviation ε.

Then, the last component of $\overline{\alpha}_k$ can be calculated as $1 - \sum \overline{\alpha}_k$, which follows a normal distribution with the priors η_k and ε. From the hierarchical prior vector $\overline{\eta}$, the community-average relative abundance can be easily estimated using the softmax function: $\overline{\Theta} = \text{softmax}\left(\overline{\eta}\right)$ (Marion et al., 2018).

In the HB model, $\overline{\Theta}$ is the relative abundance of understorey species in the pooled community (assembling samples within the same habitat), whose posterior distribution can mirror the 'true' community structure at the regional scale. For each quadrat, however, the posterior distribution of species relative abundance ($\overline{\theta}_k$) can show the stochasticity of assembly process at the local scale. Therefore, the estimated values of $\overline{\Theta}$ and $\overline{\theta}_k$, that incorporate the uncertainty of community assembly, are used to calculate the community-weighted mean (CWM) of target trait in the following and estimate species diversity (see Appendix S1) as well.

2.4.3 | Estimating trait distribution by multivariate normal likelihood

For n-th individual of each observed species within a community, we employ a multivariate normal likelihood to estimate the population-average trait μ and intrapopulation variance σ:

$$\begin{bmatrix} \log(SLA) \\ \log(LDMA) \\ \log(LS) \\ \log(H) \end{bmatrix}_n \sim \text{normal}\left(\begin{bmatrix} \mu_{SLA} \\ \mu_{LDMC} \\ \mu_{LS} \\ \mu_H \end{bmatrix}, \Sigma\right). \tag{5}$$

In the multivariate normal, the vectors $[\log(SLA), \ldots, \log(H)]_n$ are the log-transformed trait values of the n-th individual; the vector $[\mu_{SLA}, \ldots, \mu_H]$ is their expected values at the population level for the given habitat and year; and Σ is a 4×4 covariance matrix composed of intrapopulation variances $(\sigma_{SLA}, \sigma_{LDMC}, \sigma_{LS}, \sigma_H)$ and between-trait correlations. For the given trait, we employ the distribution $\mu_s \sim \text{normal}(\varphi, \tau)$ as the prior of the population-average trait of the s-th species within a community, where φ and τ can represent the expected value and standard variance of the target trait at the community scale, respectively.

From the multivariate normal, we obtain the posterior estimates of intraspecies trait distribution (i.e. μ and σ) and intracommunity trait distribution (i.e. φ and τ), both of which contain information about the stochasticity in ecological process and can be directly used for calculating functional diversity among different habitats and stress levels.

2.4.4 | Calculating functional diversity from posterior parameters

Community-weighted Mean

To assess the effect of shrubs on community-level traits of the understorey species, the expected values of population-average traits
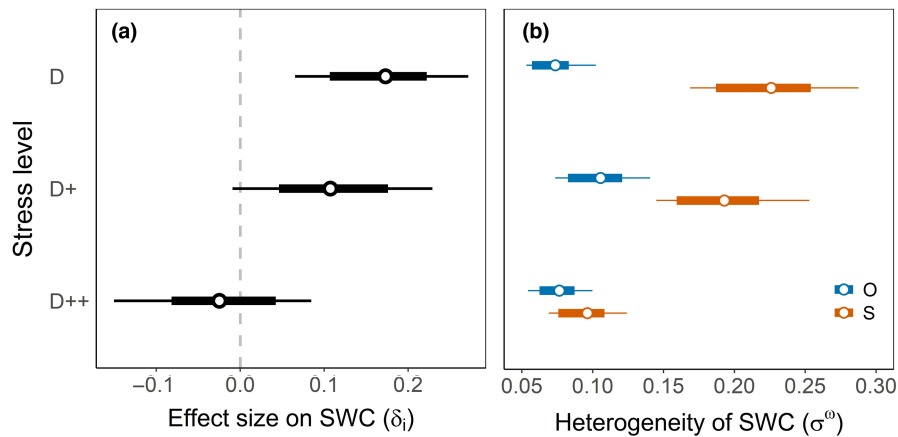
FIGURE 2 The effect of *Calligonum mongolicum* shrubs on soil water content (SWC) in microenvironments among different drought stress levels. (a) The posterior distributions of δ's that represent the effect size of *C. mongolicum* shrubs on SWC and (b) the posterior distributions of σ^ω that represent the variation of SWC within quadrat at under-shrub [S] and open [O] habitats are displayed. The values of effect size are dimensionless. The open circles represent the means; the horizontal lines are the 95% Bayesian credible intervals; and the rectangles are the 80% credible intervals

for the s-th species (μ_s) can be employed. However, considering distinct probabilities of occurrences for different species, the estimated trait values should be weighted by the relative abundance of the corresponding species (Lavorel et al., 2008). Here, we employ the posterior estimates of community-average relative abundance ($\overline{\Theta}$), which can sufficiently represent the 'true' structure of understorey communities and also include the uncertainty of assembly process. Then, community-weighted means (CWMs) of functional traits among years and habitats can be secondly derived from the posterior parameters, as follows:

$$CWM_{posterior} = \sum_{s=1}^{S} \Theta_s \exp(\mu_s). \quad (6)$$

Trait range

To quantify the intracommunity range of functional traits, we use the variance of population-average trait among different species (μ_s). To eliminate the influence of value size from different habitats and make the range measurement dimensionless, we divide the standard variance by the intracommunity average (φ). In general, the larger range indicates less environmental filtering, while the smaller range indicates more filtering limitations. Then, the trait range at the community level within a given year and habitat can be calculated as

$$R_{posterior} = \frac{\sqrt{\sum (\mu_s - E(\mu_s))^2}}{\varphi}. \quad (7)$$

Trait spacing

To evaluate changes in trait spacing among different years and habitats, the degrees of separation between interspecies trait distributions are quantified. Here, we employ $T_{IP/IC}$ (Violle et al., 2012) to assess trait spacing, which is the average intraspecies variance relative to intracommunity variance. To incorporate the uncertainty of ecological process into trait distribution, we use the posterior σ_s to

quantify the niche range of a specific species and the posterior τ to quantify the whole range of all species within a community. Then, the posterior distribution of $T_{IP/IC}$ in different years and habitats can be secondly derived from

$$T_{posterior} = \frac{\frac{1}{S} \sum_{s=1}^{S} \sigma_s^2}{\tau^2}, \quad (8)$$

When the interspecies trait distributions are perfectly separated inside the community, $T_{posterior}$ approaches zero. In contrast, as the trait distributions of different species intensively overlap with each other, $T_{posterior}$ tends to move towards positive infinity.

2.5 | Statistical inference

Statistical analyses are performed using R software (R Development Core Team, 2021). All models are fitted using Stan statistical algorithms (Stan Development Team, 2021), which employ the Hamiltonian Monte Carlo sampling methods to characterize the posterior distributions of the parameters from a given dataset and Bayesian model. Four separate sampling chains are simulated from the posterior distributions with 8,000 total iterations for each chain (4,000 warm-up iterations). To diagnose whether the chains converge to an equilibrium distribution, the potential scale reduction statistic $\hat{R}$ and the effective sample size N_{eff} are evaluated, and the mixing of these sampling chains is also visually inspected via trace plots (Gelman et al., 2014). To minimize the influence of priors on posterior distribution, we follow Gelman et al. (2014) and select the prior values of unknown parameters that are weakly informative. Specifically, the priors of location parameters are defined as *normal* (0, 10), while the scale parameters are given flat-tail priors as *cauchy*⁺ (0, 5). In addition, we define the Bayesian credible intervals (CIs), which are calculated by the two-tailed highest posterior

density, to measure uncertainty in the point estimate and compare differences in the parameters or second-derived indices among different years and habitats.

3 | RESULTS

Soil moisture and organic matter can be influenced by *C. mongolicum* shrubs. On the one hand, the significantly positive microhabitat effect (positive δ's) on both SWC and SOM appeared in the moist year (Figure 2a; Figure S1a). However, this positive effect on SWC dropped with the decline in summer rainfall. On the other hand, the random effects of the spatial distribution (σ^ω) of SWC and SOM in undershrub habitats were larger than those in open areas (Figure 2b; Figure S1b), indicating a higher heterogeneity in microenvironments under shrubs. However, the higher spatial variations of SWC due to shrub's effect declined with the decrease in summer rainfall (Figure 2b).

During the study period, 12 species appeared in the understorey communities (Table S1). The total abundance of these species declined from 44.4 to 28.5 and 18.9 m^{-2} on average along the drought gradient. In the moist year, *C. mongolicum* shrubs supported 55% more individuals and 28% more species than open area. However, this facilitative effect on shrub-associated communities decreased along the drought gradient and disappeared in the driest year (Table S1). In this study area, *B. dasyphylla* was the most abundant species, whose relative abundance ranged between 38% and 76% during the study period. Under the influence of shrubs, *B. dasyphylla* was 36% more abundant in the moist year, while only 1% more abundant in the driest year. Other species (e.g. *S. ruthenica* and *H. arachnoideus*) also experienced similar variations.

The influence of *C. mongolicum* shrubs on species composition fluctuated in the study period. The posterior distribution of δ_i did not overlap zero (95% CI) in the moist year, reflecting a high confidence

in the positive shrub effect on neighbouring plants (Figure 3a). By contrast, there was a strong overlap between posterior δ_i and zero in the driest year. Similarly, alpha and gamma diversity increased due to the presence of *C. mongolicum* shrubs. Nevertheless, the positive shrub effect on species diversity disappeared in the driest growing season (Figure 3b; Figure S2).

With the influence of shrub plants, significant shifts occurred in various functional traits. In plant-growing seasons with more summer rainfall, CWMs calculated from posterior SLA, LS and H increased (but decreased for LDMC) with the presence of shrubs at the 95% CI level (Figure 4). However, these positive effects on CWMs dropped (i.e. LDMC, SLA and LS; Figure 4a–c) or even reversed (i.e. H; Figure 4d) in the driest season (95% CI), indicating a declining shrub effect on the trait distribution at the community level as summer rainfall decreased.

Trait ranges expanded in habitats under the influence of *C. mongolicum*. In the moist-growing season, trait ranges of LS and H under shrubs were significantly larger than ranges in open areas at the 95% CI level (Figure 5c, d). Likewise, the presence of shrubs significantly expanded the trait ranges of SLA and LDMC at the 80% CI level (Figure 5a, b). We found that the expansion of trait ranges due to shrub effects can be affected by macroclimate conditions. In the driest growing season, there were no significant differences (95% CI) between undershrub and open habitats for SLA, LDMC and LS (Figure 5).

There were less trait overlaps among interacting species under shrubs than in open areas. The SLA, LS and H of species in the undershrub habitat diverged significantly (95% CI for SLA and LS; 80% CI for H) during the moist-growing season (Figure 6), indicating that the species-specific traits are more strongly separated within communities under the influence of *C. mongolicum* shrubs. However, these effects of shrub plants on trait spacing are dependent on the environmental context. For instance, no significant differences in intracommunity trait overlaps occurred between pairwise habitats under the most drought
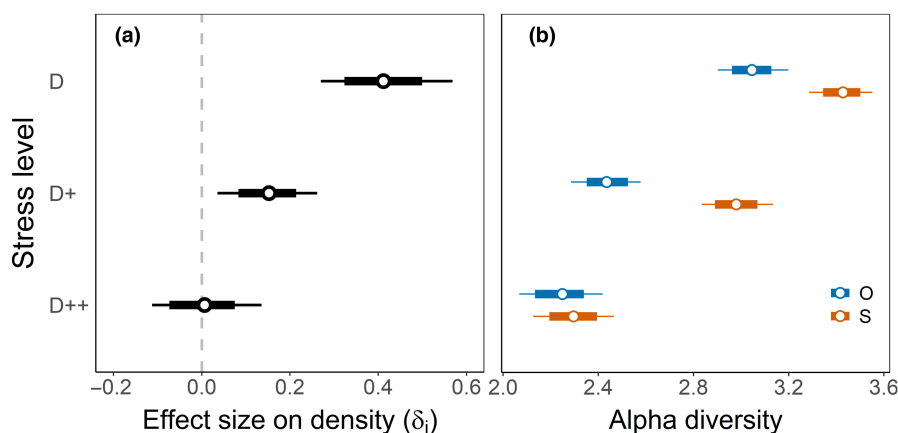
FIGURE 3 The effect of *Calligonum mongolicum* shrubs on their associated communities among different drought stress levels. (a) The posterior distributions of δ's that represent the effect size of *C. mongolicum* shrubs on plant density and (b) the distributions of alpha diversity (Hill numbers, see Appendix S2) that calculated from the estimates of the relative abundance θ's at under-shrub [S] and open [O] habitats are displayed. The values of effect size are dimensionless. The open circles represent the means, the horizontal lines are the 95% Bayesian credible intervals and the rectangles are the 80% credible intervals

FIGURE 4 The effect of *Calligonum mongolicum* shrubs on community-weighted mean trait values among different drought stress levels. The posterior distributions of community-weighted means (CWM) for (a) specific leaf area (SLA), (b) leaf dry matter content (LDMC), c. lateral spread (LS) and d. height (H) at under-shrub [S] and open [O] habitats are displayed. The community-weighted mean values are log-transformed. The open circles represent the means, the horizontal lines are the 95% Bayesian credible intervals and the rectangles are the 80% credible intervals
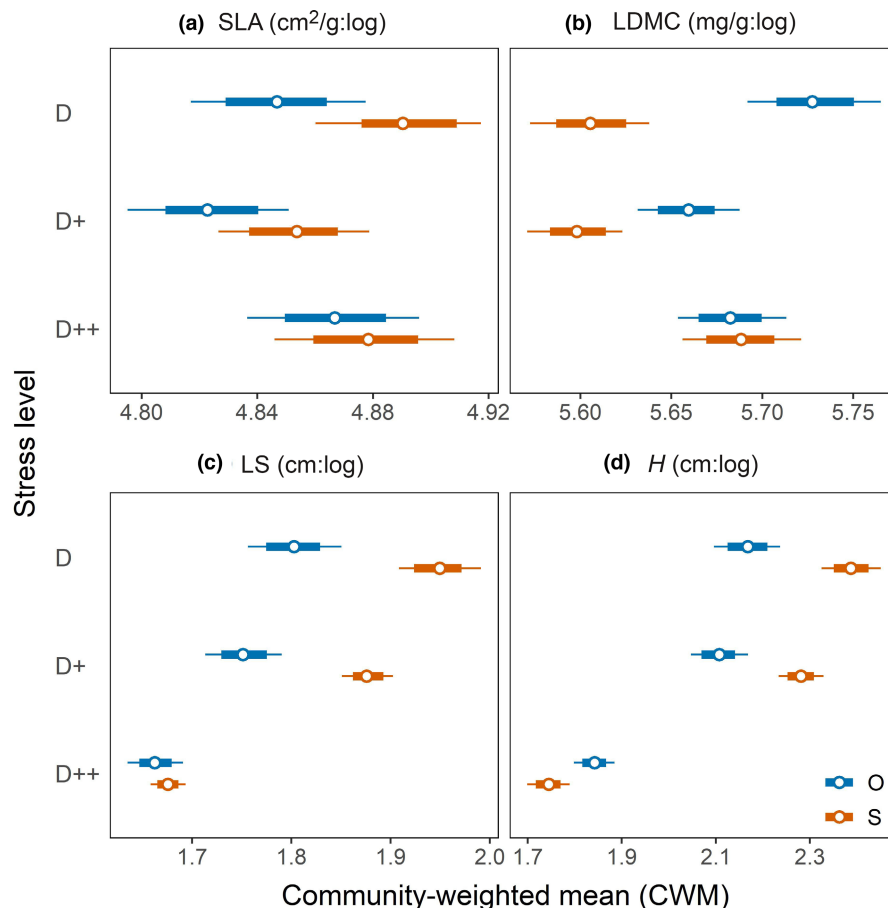
stress (Figure 6). Furthermore, the largest divergence in trait overlaps for LDMC happened at the medium level of drought stresses (D+).

4 | DISCUSSION

Consistent with our expectation, we found significant changes in trait distribution in response to the distinct microenvironment created by *C. mongolicum* shrubs. With decreased summer rainfall, however, the effects of shrub plants declined or disappeared for different functional traits, in line with their collapsed positive effects on soil moisture, plant density and species diversity of associated communities. These results imply that facilitation can drive assembly processes through both environmental filtering and niche differentiation mechanisms under moderate stresses, and results in the higher density and diversity observed at under-shrub habitats. However, consistent with the prediction of refined SGH, the importance of facilitation on assembly processes declined with their stress-ameliorating effects at the stressful end of drought gradient.

4.1 | Facilitation along the drought gradient

The shrub effect on plant abundance varied along the drought gradient at our study site. More specifically, the net positive

interaction between *C. mongolicum* and their associated plants shifted to a neutral interaction as the drought stress shifted to its driest end. Likewise, the effect of shrubs on species diversity displayed a similar variation along the drought gradient. This scenario supports the refined SGH, which predicted that positive interactions might be weakened or reversed in very harsh environments (Guignabert et al., 2020; Holmgren & Scheffer, 2010; Liancourt et al., 2017; Michalet et al., 2006; O'Brien et al., 2017). Nonetheless, it should be pointed out that the drought gradient in this study might not perfectly equal to the stress gradient in SGH (Bertness & Callaway, 1994; He et al., 2013; Michalet, 2007). Constrained by regional climates, this study merely considered situations near the stressful end of environmental gradient. Thus, it is difficult to currently confirm whether a humped back facilitation exists for *C. mongolicum* along the entire drought gradient. In addition, this study did not account for the natural sequence of these consecutive years with different summer rainfall, but only regarded them as independent stress environments. As a result, species abundance or diversity might be underestimated in the community that suffered severe drought at last growth season.

Positive interactions are driven by the relationship between macroenvironmental factors and plant effect on microhabitat conditions. As suggested by Butterfield et al. (2016), the direct and indirect effects on local moisture can be changed along the precipitation gradient, thereby causing shifts in the balance between positive and
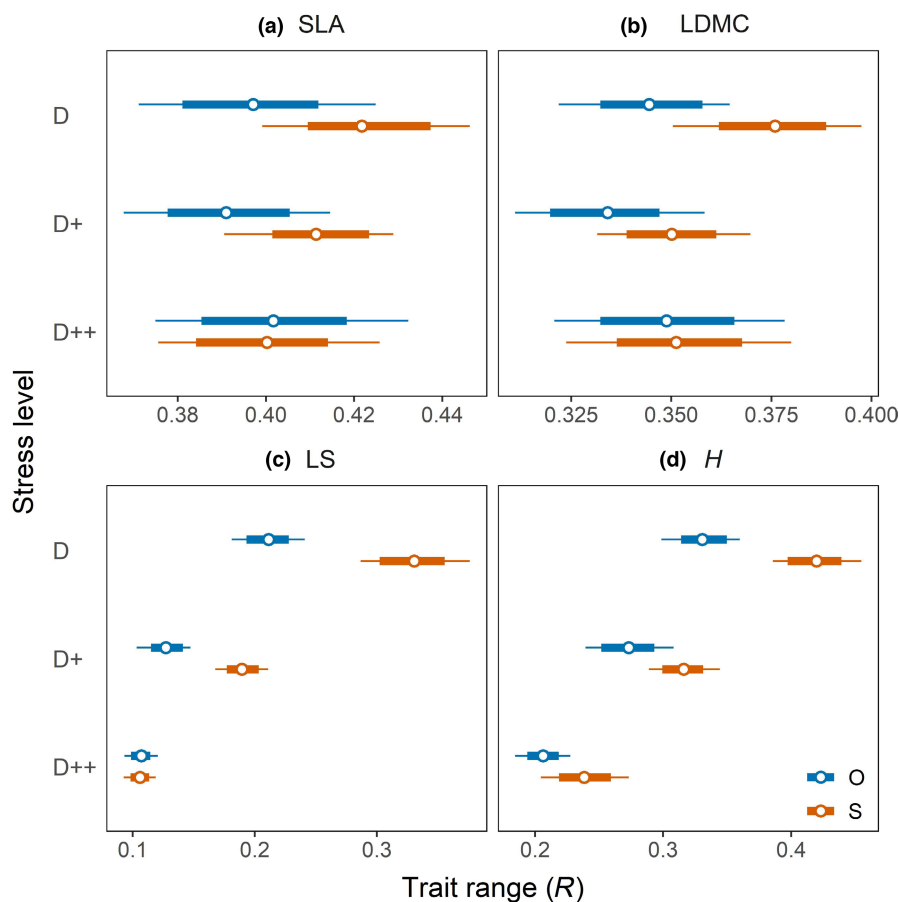
FIGURE 5 The effect of *Calligonum mongolicum* shrubs on the intracommunity trait ranges among different drought stress levels. The posterior distributions of trait ranges (R) for (a) specific leaf area (SLA), (b) leaf dry matter content (LDMC), (c) lateral spread (LS) and (d) height (H) at under-shrub [S] and open [O] habitats are displayed. The open circles represent the means, the horizontal lines are the 95% Bayesian credible intervals and the rectangles are the 80% credible intervals

negative interactions. In arid land, shrub species play an important role in ameliorating water stress and improving soil nutrients in their associated communities (Abdallah et al., 2016; Noumi et al., 2016; Zou et al., 2005). Moreover, canopy shading of desert shrubs can typically reduce evapotranspiration and heat stress at the cost of reduced available light (Filazzola et al., 2018; Muhamed et al., 2013). This can significantly improve water availability and nutrient availability, which often increase with increasing soil moisture (Abdallah et al., 2016; Liancourt et al., 2005). As a result, a relatively favourable habitat for neighbouring plants can be created in local communities, which have consequences for large-scale biodiversity patterns (Gavini et al., 2020). However, our data showed that the facilitative effect related to moisture improvement was highly dependent on the external water input (also see Zhang et al., 2018). As drought stress moved towards its driest end, the improvement of soil moisture due to canopy shading decreased and eventually disappeared. It subsequently led to the waning influence of shrub species on its understorey community.

4.2 | Facilitation and Environment filtering

C. mongolicum shrubs can affect the local environmental filtering process through shift and expansion mechanisms. On the one hand, *C. mongolicum* changes the expected value (CWM) of the functional traits of the understorey community. For instance, we recorded a higher CWM for SLA in communities under shrub canopies than in open areas, while the expected value of LDMC decreased in response to the presence of shrub plants. This shift in SLA and LDMC illustrates the creation of distinct microhabitats by *C. mongolicum*, which might provide refugia for some species but reduce the chances of survival for others. Meanwhile, these results also demonstrated shifts to resource-acquisive strategies for beneficiary plants in response to favourable microhabitats created by benefactor species (also see Doudová & Douda, 2020; but see van der Merwe et al., 2021). In contrast, a conservative resource-use strategy that produces smaller leaves with a higher content of structural carbohydrates (Lhotsky et al., 2016) can be expected for species growing beyond the influence of nurse plants. On the other hand, the broadened ranges of traits under shrubs suggested that relaxing restrictive filtering in the shrub-associated community (compared to open areas) can allow more diverse resource-use strategies to co-exist. The expanded ranges of all surveyed traits (i.e. SLA, LDMC, LS and H) were probably due to the amelioration of environmental stresses, for example, improved SWC and SOM under shrub canopies. Likewise, the study in alpine communities also showed that the relaxation of environmental filtering due to the impact of cushion plants can expand the trait ranges of lateral spread, specific leaf area and leaf dry matter content (Schöb et al., 2012). According to Wang et al. (2021), the range of functional traits is no less important than the taxonomic diversity and CWM of traits in explaining the facilitative effect of nurse shrubs on their local communities.
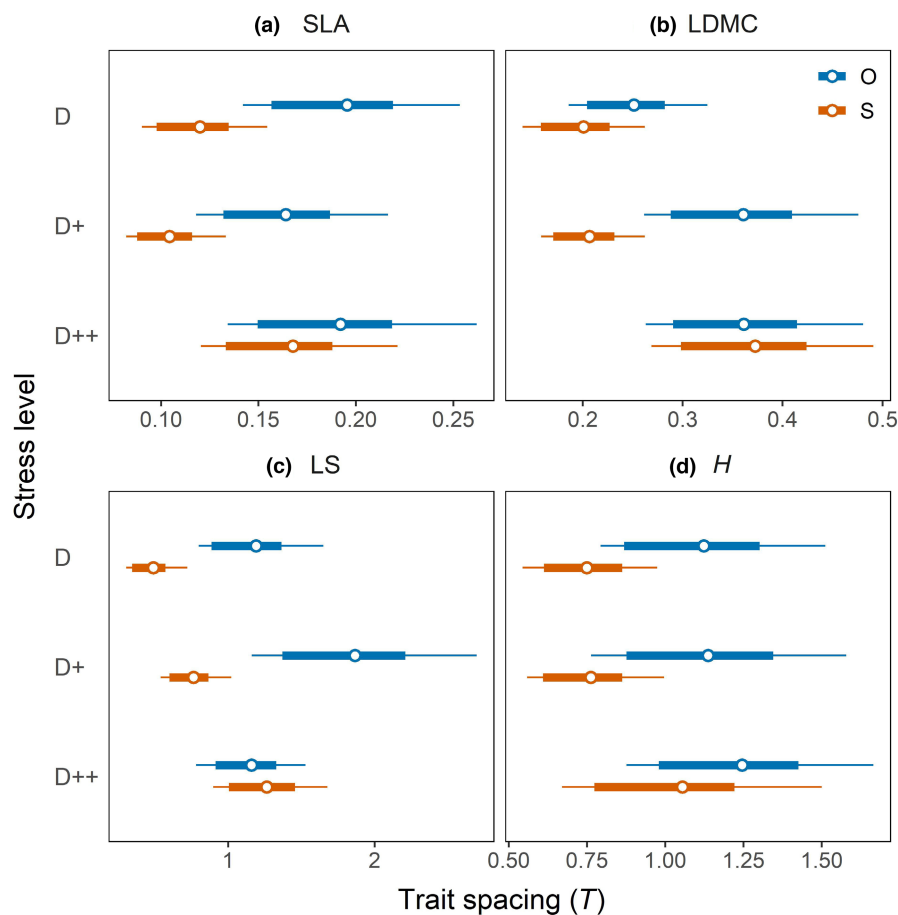
Similar to previous studies, this study indicates that there is probably no well-defined boundary between environmental filtering and plant interactions (Blonder et al., 2018; Le Bagousse-Pinguet et al., 2017; Mod et al., 2020). As predicted by Coyle et al. (2014), the strength of assembly processes changes along the stress gradient, where environmental filtering is stronger under harsher conditions (also see Lhotsky et al., 2016). These abiotic constraints can be weakened by the positive interactions at the microscale, subsequently relaxing environmental filtering and enabling the coexistence of various water and nutrient use strategies. In particular, the local modification of environmental filtering disappears at the driest end of the rainfall gradient, probably due to the waned shrub effect on the soil moisture distribution in response to scarce summer rainfall. Hence, the relatively higher similarity in trait distributions or species composition between under-shrub and open habitats can be expected.

In addition, our unpublished investigation of seed trait at same study region also supports the general hypothesis that *C. mongolicum* can affect the local filtering process (Appendix S5). Under drought stress, the expected value (CWM) of seed mass at the community level showed significant responses to the influence of shrub plants (80% CI; Figure S3), indicating a shift mechanism of environmental filter. However, such trait-shifting effect decreased by the collapse of facilitation at the stressful end of drought gradient. Therefore, we deduce that the random collapse of facilitation under

extreme climate might have a long-term impact on shaping the local community.

4.3 | Facilitation and niche differentiation

Under drought stress, we found the evidence of intracommunity trait divergence in response to the microenvironments created by *C. mongolicum* shrubs. The lower overlaps in SLA, LDMC, LS and H might indicate distinct resource-acquisitive strategies among species in close proximity to shrub plants. In this case, the intracommunity trait distributions under the influence of habitat former are likely to be flatter or even multimodal (Gross et al., 2017) and thus lead to greater spatial and temporal stability among species (Danet et al., 2018). Nevertheless, the fact that there was no significant difference in the level of trait overlap between pairwise communities at the driest end of the drought gradient indicates that niche differentiation under shrubs is largely dependent on environmental severity.

Although niche differentiation is acknowledged as an important process promoting stable coexistence among species (Carrión et al., 2017; Levine et al., 2017), its facilitation-involved mechanism in community assembly is still poorly understood. The intracommunity divergence under shrubs in our study is contrary to the assumption made by Bulleri et al. (2016). By constructing a conceptual model, Bulleri et al. (2016) assumed that the generalized expansion of the

fundamental niche of beneficiary species could increase the average niche overlap, thus leading to stronger competition among beneficiary species. Nevertheless, that study also proposed that reduced niche overlap could still be expected when the amelioration of environmental severity is associated with increased heterogeneity on the fine scale. Our results clearly support the latter hypothesis, in which the divergence of trait distribution may result from the heterogeneity of soil moisture distribution created by shrubs. In addition, we have recorded the increased heterogeneity of SOM under the influence of *C. mongolicum*. Nonetheless, different from the weakened effect on the heterogeneity of SWC along drought gradient, the influence of shrub species on the heterogeneity of SOM has not changed among different stress levels (Appendix S3). Some empirical studies have also demonstrated that by modifying the distribution of access to light resources and soil nutrients, benefactor species can foster environmental heterogeneity and thus support a change in trait spacing observed in local communities (Abdallah et al., 2016; Doudová & Douda, 2020; Ehlers et al., 2016; Schöb et al., 2012; Soliveres et al., 2011). Likewise, species coexistence can be promoted as a result of magnified variations in soil moisture status due to heterogeneous microtopography (Brooker et al., 2015). Overall, the niche differentiation that results from environmental heterogeneity created by benefactor species is one of the possible facilitation-driven mechanisms of community assembly.

4.4 | Facilitation mechanism under extreme climate

Theoretical and statistical models for the relationship between stress tolerance and associated facilitative-competitive outcomes along environmental severity gradients have been established (reviewed in Butterfield & Callaway, 2013; Liancourt & Dolezal, 2021; Michalet et al., 2014; Soliveres et al., 2015). They mostly focused on drought-stressed ecosystems such as alpine regions or arid and semiarid lands. However, previous studies rarely examined the most severe spectrum within a stress gradient (Chaieb et al., 2021; Filazzola et al., 2020; Noumi et al., 2015; O'Brien et al., 2017; Zhang et al., 2018). Here, we extended the model to cover a water-limited community that lies at the driest end of drought gradients. We conclude that facilitation drives community assembly through environmental filtering and niche differentiation under moderate stress, yet both mechanisms become inefficient as the drought stress shifts towards its driest end. This variation, for the most part, may be due to the decreasing effect of benefactor species on their microenvironments at the extreme end of the stress gradient. To move one step forward, it might imply that changes in macroclimate conditions modulate the assembly process in the local community by affecting the relationship between microhabitat factors and plant interactions.

Understanding how interactions between benefactor plants and their associated species change along a stress gradient allowed us to explore the underlying mechanism affecting the assembly process, so that we could better predict community responses to ongoing climate change (Liancourt & Dolezal, 2021). As suggested by Cavierers et al. (2016), facilitations can act as an insurance mechanism to maintain biodiversity under harsh conditions by buffering the negative impact of changing climates. However, our results indicated the collapse of the influence of benefactor species on both environmental filtering and niche differentiation in the driest year. Although it does not conflict with the general findings that support the importance of facilitation in abiotically stressful environments (Ballantyne & Pickering, 2015; Carrión et al., 2017; Gavini et al., 2020; Soliveres et al., 2015), it implies a caution against the evaluation of facilitative effects on species coexistence and diversity maintenance under extreme climate. According to the predictions of future climate change scenarios, violent rainfall pulses and extremely dry weather are becoming more frequent (IPCC, 2019). In this context, decreasing available water in response to climate change would limit the role of benefactor plants as a habitat former or insurance mechanism, thus raising the risk of biodiversity loss. More broadly, exposure to extreme climate is likely to reduce the importance of facilitation in driving community assembly under harsh environments.

CONFLICT OF INTEREST

There is no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

Z.G. and Z.W. conceived the ideas and designed methodology; Z.G. and W.X. collected the data; Z.G. analysed the data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data are available via the *Dryad Digital Repository* at https://doi.org/10.5061/dryad.2547d7wsc (Zhang et al., 2022).

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SUPPORTING INFORMATION

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