

Competitive effects are significantly affected by soil water condition in the first year and by neighbor richness in the second year: A two-year simulated experiment

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Abstract

Background and aims

Understanding how plant-plant interactions vary with biotic and abiotic factors is vital to protect degraded grassland communities, especially under global climate changes. However, how soil water condition and species diversity interactively affect competition between the dominant species and its neighbors over time remains unclear.

Method

Using a dominant species in semi-arid Inner Mongolia Steppe, *Leymus chinensis*, as the target species and ten other species as neighbors, we carried out a two-year microcosm experiment to evaluate how soil water condition (SWC) and neighbor richness (NR) affected the competitive effect of neighbors (CRCI) on *L. chinensis* directly or indirectly.

Results

(1) In the first experiment year, SWC affected CRCI directly and indirectly via regulating community-weighted mean (CWM) of height absolute distance, supporting competition-trait similarity hypothesis. (2) In the second experimental year, NR showed significant effect on CRCI. Moreover, functional dispersion (FDIs) of neighbors mediated the response of CRCI to the changes in neighbor richness, supporting vacant niche hypothesis. In addition, there was a negative association between CWM of height hierarchical distance and CRCI, and a positive association between CWM of specific leaf area hierarchical distance and CRCI in the second year, supporting competition-trait hierarchy hypothesis. In general, the relative importance of NR on CRCI increased over time.

Conclusions

These findings provide strong empirical evidence of how plant-plant interactions respond to changes of biotic and abiotic factors in semi-arid Inner Mongolia Steppe over time, and novel insights for mechanisms by which biodiversity and climate changes affect plant-plant interactions.

Introduction

Biodiversity loss is happening in various terrestrial communities due to the global climate changes, human disturbances and the expansion of dominant species, especially in semi-arid regions (Dong et al. 2020; Wang et al. 2019; Xu et al. 2021). Plant-plant interactions are related to species abundance, coexistence, exclusion and community composition, and is a determinant driver of community assembly and ecological processes (Saiz et al. 2016; Siebenkäs et al. 2015). In order to predict plant community dynamics and succession in semi-arid regions, a growing number of studies have focused on how plant-plant interactions vary with the changes of biodiversity or abiotic conditions such as drought (Dong et al. 2020; Pan et al. 2021). As the research progressed, the researchers also found that the response of plant-plant interactions to environmental conditions will change over time. According to prediction of community assembly theory rooted in ideas of species coexistence (Cornwell et al. 2006; Hao et al. 2021), the effect of abiotic factors (e.g. drought) on plant-plant interactions gradually weakened, while the effect of biotic factors (e.g. species diversity) gradually increased with time. To the best of our knowledge, however, few studies have focused on the interaction between abiotic and biotic factors on plant-plant interactions to explore the relative importance of each factor in one study, still less on the effects of each factor and their potential mechanisms over time, which limits our ability to understand the dynamics and succession of communities, especially in the degraded regions.

Plant functional traits can reflect plant resource utilization ability, and affect the competitive ability and fitness of plants (Pérez-Harguindeguy et al. 2013). Additionally, the variation of these traits can reflect how species respond to the changes in environmental conditions. Therefore, plant functional trait-based theory has been proposed in explaining ecological processes in the condition of environmental changes (Díaz et al. 2004; Siebenkäs et al. 2015). Three mechanisms of plant functional trait-based theory are proved useful to explain the response of plant-plant interactions to the changes of environmental changes, termed as competition-trait similarity hypothesis, competition-trait hierarchy hypothesis and vacant niche hypothesis (Dong et al. 2020; Kunstler et al. 2012; Pan et al. 2021). These mechanisms depend on two assumptions. One is that the niche differences are negatively associated with the similarity of functional trait values; and the other is that the relative fitness of species relates to its plant functional trait value (Funk et al. 2016). Competition-trait similarity hypothesis posits that the neighbor effect intensity on the target species would increase with the decrease of trait similarity distance between neighbors and target species. Competition-trait hierarchy hypothesis posits that the neighbor effect intensity relates to the trait hierarchical distance between neighbors and target species. Vacant niche hypothesis posits that neighbors with higher functional dispersion (FDIs) would have less vacant niche and lead to more competition intensity on the target species. Meanwhile, three functional profile indices of plant communities, including community-weighted mean (CWM) of absolute or hierarchical distance ($CWM_{\text{trait absolute/ hierarchical distance}}$) of individual functional trait between neighbors and target species, and functional dispersion (FDIs) of neighbors, can be used to explain each mechanism accordingly (Dong et al. 2020; Fort et al. 2014). However, few studies have explored which mechanism of plant functional trait-based theory dominates the responses of plant-plant interactions to the changes of both neighbor species and soil water condition over time; therefore, any effort on this topic would promote the core theory of community assembly and take effective management measures for community restoration (Dong et al. 2020; Hao et al. 2021).

The semi-arid Inner Mongolia Steppe, one of the most diverse grasslands in the Eurasian steppes, is highly vulnerable to drought (Li et al. 2019), with a decline in species diversity and the dramatic changes of species relative abundance (Bai et al. 2007). However, the population sizes of *Leymus chinensis* (Trin.) Tzvel.

one of the dominant species in this region, have increased gradually in the degraded communities (Yang 2008). Previous pairwise competition studies have demonstrated that the competition between *L. chinensis* and a neighbor species varied with abiotic factors, such as water or nitrogen availability (Niu et al. 2008), soil fertility (Zhao et al. 2021) and combinations of abiotic factors (Jiang et al. 2014). However, no research has focused on how neighbor richness and drought affect the competitive effects and the potential mechanisms.

To explore how neighbor richness and drought conditions affected competitive effects of neighbors on *L. chinensis* directly and indirectly via regulating functional profiles of plant communities, we performed a two-year soil water condition × neighbor richness microcosm experiment, with *L. chinensis* as a target species and ten other species as neighbors in degraded *L. chinensis* communities as neighbors. We specifically addressed three hypotheses. First, the relative importance of soil water condition and neighbor richness on competitive effects would change over time (Milbau et al. 2005; Funk et al. 2016), and soil water condition would play more important roles in the first year and less in the second year compared with neighbor richness. Second, soil water condition and neighbor richness would affect competitive effects of neighbors on *L. chinensis* directly or indirectly via regulating functional profiles of plant communities (Conti et al. 2018; Dong et al. 2020). Third, the trait-based mechanism by which dominates the responses of competitive effects of neighbors to environmental changes would be changed with time.

Material And Methods

Study materials

Leymus chinensis and ten common species, including five perennial grasses (*Achnatherum sibiricum*, *Agropyron cristatum*, *Cleistogenes squarrosa*, *Koeleria cristata*, *Stipa grandis*), three perennial forbs (*Allium ramosum*, *Anemarrhena asphodeloides*, *Potentilla acaulis*), one sedge (*Carex korshinskyi*) and one semi-shrub (*Artemisia frigida*), were collected in a *L. chinensis* community in China (116°42' E, 43°38' N), and then acclimated for at least two months at Nankai University (China). At the same site, soil in 0-10 cm layer was collected. In addition, *L. chinensis* was used as the target species, and ten common species were used as neighbor species.

Experimental design

This experiment employed a two-factor design, including soil water condition (10-15% soil water content for non-drought treatment and 5-8% soil water content for drought treatment) and neighbor richness (1-, 3- and 6-neighbor species).

On July 2, 2018, 104 plastic pots (20 cm in diameter, 21 cm in depth) were filled with the homogenized soil (4.0 kg per pot). According the species density and their relative abundances in the sampled community, six individuals of *L. chinensis* and six individuals of neighbors were transplanted into each pot. For 1-neighbor species treatment, six individuals from one common species were transplanted, using 10 common species as replicates for each soil water condition. For 3-neighbor species treatment, two individuals from each of three different common species were transplanted. For 6-neighbor species treatment, one individual from each of six different common species was transplanted. The treatment of 3-/6-neighbor species had 12 replicates per soil water condition, and there were the same plant assemblages under both soil water treatments. All species used except *L. chinensis* had the same probability in any pot within each neighbor richness treatment (supplementary data Table S1). To test the competitive effects of neighbors on *L. chinensis*, the monoculture of *L. chinensis* (18 replicates) per soil water condition was set up, with 12 individuals per pot. All individuals of the same species used in this experiment were roughly the same size.

Non-drought and drought treatments were carried out from July 15, 2018 to the end of experiment, and soil water condition per pot was monitored by an ECH₂O Check except for the winter when the plants wilted. The experimental pots were randomly placed under the large-scale rain-proof shelter at Nankai University and changed the position every other week.

Data collection

Considering that the main limiting factors in the semi-arid grasslands are light and nutrients as well as water, three functional traits related to light and nutrients acquisition were measured every year following the standard protocols (Pérez-Harguindeguy et al. 2013), including plant height (hereafter Height), specific leaf area (SLA) and leaf dry matter content (LDMC). Height is the vertical distance from the upper boundary of plant photosynthetic tissue to ground level. SLA is the ratio of the leaf area and leaf dry mass, and LDMC is the ratio of the leaf dry mass and water-saturated fresh mass. For each species, these traits were measured with at least 3 replicates under each soil water condition, and mean values of each trait were used to calculate functional profiles of plant communities.

The aboveground shoot that was 2.54 cm higher than ground level were harvested on October 15, 2018, and June 25, 2019, respectively. The tiller number and aboveground shoot dry biomass per species were recorded for each pot every year. The tiller number of each species was used as species abundance to calculate functional profiles of plant communities; and the biomass of target species and neighbor species were used for the assessment of competitive effects.

Data analyses

Competitive effect index

To quantify the competitive effect of neighbors on target species *L. chinensis*, the corrected index of relative competition intensity (CRCI) was calculated (Oksanen et al. 2006), within each soil water condition (2), neighbor richness (3) and year (2).

$$\text{CRCI} = \arcsin (B_{\text{monoculture}} - 2B_{\text{mixture}}) / \max(B_{\text{monoculture}}, 2B_{\text{mixture}})$$

where $B_{\text{monoculture}}$ is the mean biomass of *L. chinensis* in monoculture, and $B_{\text{neighbors}}$ is the biomass of *L. chinensis* in mixture with neighbors. We doubled $B_{\text{neighbors}}$ because the initial density of *L. chinensis* in monoculture was twice of that in mixture. The positive CRCI value indicates competition, while the negative value indicates facilitation. CRCI shows a linear relationship in wide ranges of competition and facilitation intensities, so that it can detect the linear trend of competition intensity among plants, and derive an unbiased interval estimate of plant interaction intensities (Oksanen et al. 2006).

Functional profiles of plant communities

Three functional profile indices, including $CWM_{\text{trait absolute distance}}$, $CWM_{\text{trait hierarchical distance}}$ and $FDis$, were calculated with the package 'FD' in R (R Core team 2020), within each soil water condition (2), neighbor richness (3) and year (2). $CWM_{\text{trait hierarchical distance}}$ reflects fitness differences and $CWM_{\text{trait absolute distance}}$ reflects niche differences between neighbors and the target species for each trait (Height, SLA and LDMC), and $FDis$ which is a multi-trait index reveals the occupancy of niche space of neighbors (vacant niche in resource use).

$$CWM_{\text{trait absolute distance}} = \sum_{i=1}^S NSRA_i \cdot |T_i - T_{\text{target}}|$$

$$CWM_{\text{trait hierarchical distance}} = \sum_{i=1}^S NSRA_i \cdot (T_i - T_{\text{target}})$$

S : neighbor richness; $NSRA_i$: the relative abundance of neighbor species i in a certain pot; $|T_i - T_{\text{target}}|$ and $(T_i - T_{\text{target}})$: the absolute and relative value of the trait difference between neighbor species i and the target species *L. chinensis*, respectively.

$$FDis = \frac{\sum_{i=1}^S (a_i z_i)}{\sum_{i=1}^S a_i}$$

$$c = \frac{\sum_{i=1}^S (a_i T_{ij})}{\sum_{i=1}^S a_i}$$

S : neighbor richness; a_i : the abundance of neighbor i ; z_i : distance of neighbor i to c in a certain pot; T_{ij} : the mean value of trait j of neighbor species i .

Statistical analyses

The data of CRCI and functional profile indices were log-transformed prior to analyses to meet the normality distribution and homogeneity of variances.

To assess the difference between CRCI and zero in each pot, one-sample t-test was performed. CRCI value higher than zero indicates competition, and lower than zero indicates facilitation.

To explore the effects of soil water condition, neighbor richness and their interactions on functional profile indices ($CWM_{\text{trait absolute/hierarchical distance}}$ of each trait, $FDis$ of neighbors) and CRCI, linear mixed models (LMMs) were used for data collected in each year, with soil water condition and neighbor richness as fixed factors, and plant assemblage as the random factor. Then, the significance of differences was assessed among treatments by Tukey post hoc analysis. These analyses were conducted using the packages "nlme" and "emmeans" in R, respectively.

To quantify the relative importance of predictors (soil water condition, neighbor richness, plant assemblage, each functional profile indices) for CRCI, a variance partitioning analysis was performed for data collected in each year. Before the analysis, collinearity between variables was tested with the variance inflation factor (VIF) and correlation coefficients of pairwise predictors in both year (Menard 1995; Xu et al. 2021), and no collinearity was found because of no VIF value being higher than 5 and no correlation coefficient being higher than 0.7 (supplementary data Fig. S1). Four models were assessed. Model 1: soil water condition and neighbor richness; model 2: predictors in Model 1 and $CWM_{\text{trait absolute distance}}$ of each trait; model 3: predictors in Model 2 and $CWM_{\text{trait hierarchical distance}}$ of each trait; model 4: predictors in Model 3 and $FDis$ of neighbors. Then, these four models were fitted by stepwise procedures, and the predictors which did not improve the model-fitting were removed based on the Akaike information criterion (AIC). These analyses were constructed in R, with package 'variancePartition' for variance partitioning analysis and 'MuMIn' for model selection.

To disentangle the direct and indirect causal relationships between predictors (soil water condition, neighbor richness, plant assemblage, functional profile indices) and CRCI, Shipley's d -sep approach (Shipley 2013) was used to construct models for data collected in each year using the 'piecewiseSEM' package in R, with plant assemblage as a random factor. For the case that several models were accepted, the one with the smallest AIC was selected as the final model. The direct or indirect relationships between predictors and CRCI were expressed by standardized path coefficients (Grace and Bollen 2005).

Results

Effects of soil water condition and neighbor richness on functional profiles of plant communities

The interaction between soil water condition and neighbor richness had no significant effects on functional profile indices in both experimental years (Table 1). Soil water condition significantly decreased $CWM_{\text{Height absolute distance}}$, $CWM_{\text{Height hierarchical distance}}$, $CWM_{\text{SLA hierarchical distance}}$, and increased $CWM_{\text{LDMC hierarchical distance}}$ in the first year (Table 1; Fig. 1a, e, f, g). Neighbor richness affected FDis of neighbors significantly and positively in both experimental years (Table 1; Fig. 1d, k).

Table 1

Results of the effects of soil water condition (SWC), neighbor richness (RN) and their interactions on functional profiles of plant communities and CRCI on *chinensis* by linear mixed models (LMM) in the first and second year, respectively. df: degree of freedom; R²: R-squared for LMM; R²_m: variance explained by fixed factors; R²_c: variance explained by fixed and random factors

Variable	The first year								The second year							
	Soil water condition (SWC, df = 1)		Neighbor richness (RN, df = 2)		SWC×RN (df = 2)		Model R ²		Soil water condition (SWC, df = 1)		Neighbor richness (RN, df = 2)		SWC×RN (df = 2)		Model R ²	
	F	P	F	P	F	P	R ² _m	R ² _c	F	P	F	P	F	P	R ² _m	R ² _c
$CWM_{\text{Height absolute distance}}$	7.79	0.009	1.25	0.300	0.02	0.983	0.028	0.878	1.34	0.255	0.33	0.718	0.20	0.82	0.022	0
$CWM_{\text{SLA absolute distance}}$	2.78	0.110	0.53	0.590	0.82	0.449	0.020	0.736	0.03	0.870	0.78	0.470	0.20	0.82	0.033	0
$CWM_{\text{LDMC absolute distance}}$	2.56	0.120	1.55	0.229	1.48	0.244	0.003	0.769	1.59	0.217	0.41	0.665	0.58	0.566	0.034	0
$CWM_{\text{Height hierarchical distance}}$	10.25	0.003	0.02	0.980	0.17	0.844	0.035	0.823	0.36	0.550	0.69	0.509	0.35	0.709	0.039	0
$CWM_{\text{SLA hierarchical distance}}$	13.28	0.001	0.40	0.671	0.13	0.879	0.098	0.551	1.46	0.236	0.58	0.565	1.94	0.160	0.056	0
$CWM_{\text{LDMC hierarchical distance}}$	13.97	0.001	0.64	0.535	0.63	0.538	0.058	0.761	0.21	0.654	0.06	0.945	0.81	0.454	0.011	0
FDis	1.69	0.203	164.29	<0.001	1.34	0.277	0.812	0.912	1.62	0.213	37.06	<0.001	0.46	0.637	0.617	0
CRCI on <i>L. chinensis</i>	17.27	<0.001	1.62	0.213	1.74	0.193	0.222	0.467	2.18	0.150	6.85	0.003	0.85	0.436	0.233	0

Effects Of Soil Water Condition And Neighbor Richness On Competitive Effect

The interaction between soil water condition and neighbor richness did not show significant affects CRCI in both experimental years (Table 1). Drought significantly decreased CRCI in the first experimental year, while neighbor richness significantly increased CRCI in the second experimental year (Table 1, Fig. 2). Significant negative CRCI values were found under drought treatment in the first experimental year and under 1-neighbor richness treatment in the second experimental year (Fig. 2).

Direct and indirect effects of soil water condition, neighbor richness and functional profiles of plant communities on CRCI on *L. chinensis*

By variance component analysis, the factor of plant assemblage showed the greatest effect on CRCI in both experimental years (Fig. 3). The factor which showed the second greatest effect on CRCI was soil water condition in the first experimental year and $CWM_{\text{SLA hierarchical distance}}$ in the second experimental year (Fig. 3).

By stepwise procedures, the best mode (model 4) included soil water condition, $CWM_{\text{SLA hierarchical distance}}$ and $CWM_{\text{Height absolute distance}}$ in the first experimental year, and included $CWM_{\text{SLA hierarchical distance}}$, $CWM_{\text{Height absolute distance}}$, FDis of neighbors, $CWM_{\text{Height absolute distance}}$ and soil water condition in the second experimental year (Table 2).

Table 2

Results of the stepwise procedure evaluating the effects of soil water condition, neighbor richness, community-weighted mean of absolute or hierarchical distances of individual trait ($CWM_{\text{trait absolute or hierarchical distance}}$), and multivariate trait distance (FDIs of neighbors) on CRCI on *L. chinensis* in the first and second year. We tested the responses of CRCI on *L. chinensis* to the following models: 1) soil water condition and neighbor richness, 2) individual absolute trait distance ($CWM_{\text{trait absolute distance}}$), 3) individual hierarchical trait distance ($CWM_{\text{trait hierarchical distance}}$), and 4) multivariate trait distance (FDIs) of neighbors. Df: degree of freedom; Est: direction of relationship. The mark of minus (-) indicates that the variable was not included in this model

	df	model 1			model 2			model 3			model 4		
		Est	F	P									
The first year													
Soil water condition	1		12.43	< 0.001		12.77	< 0.001		13.25	< 0.001		13.25	< 0.001
Neighbor richness	2		2.12	0.128		-	-		-	-		-	-
$CWM_{\text{Height absolute distance}}$	1				0.046	6.12	0.016	0.050	6.34	0.014	0.050	6.34	0.014
$CWM_{\text{SLA absolute distance}}$	1							-	-		-	-	
$CWM_{\text{LDMC absolute distance}}$	1							-	-		-	-	
$CWM_{\text{Height hierarchical distance}}$	1							-	-		-	-	
$CWM_{\text{SLA hierarchical distance}}$	1							0.088	2.39	0.130	0.088	2.39	0.130
$CWM_{\text{LDMC hierarchical distance}}$	1							-	-		-	-	
FDIs of neighbors	1											-	-
AIC		-288.0			-291.9			-292.4			-292.4		
Adjusted R ²		0.170			0.204			0.221			0.221		
The second year													
Soil water condition	1					1.98	0.165		2.30	0.135		2.33	0.132
Neighbor richness	2		8.64	< 0.001		9.53	< 0.001		11.04	< 0.001		-	-
$CWM_{\text{Height absolute distance}}$	1				0.073	2.49	0.120	0.051	2.88	0.095	0.047	5.25	0.025
$CWM_{\text{SLA absolute distance}}$	1				0.057	5.25	0.025						
$CWM_{\text{LDMC absolute distance}}$	1							-	-		-	-	
$CWM_{\text{Height hierarchical distance}}$	1							-0.500	10.68	0.002	-0.436	16.13	< 0.001
$CWM_{\text{SLA hierarchical distance}}$	1							0.168	6.27	0.015	0.162	8.01	0.006
$CWM_{\text{LDMC hierarchical distance}}$	1										-	-	
FDIs of neighbors	1										0.200	13.19	< 0.001
AIC		-230.3			-234.2			-234.3			-245.3		
Adjusted R ²		0.190			0.262			0.363			0.37		

In the first experimental year, the model accepted in d -sep explained 36% of the total variation in CRCI and did not include neighbor richness. Soil water condition affected CRCI directly and indirectly via regulating $CWM_{\text{Height absolute distance}}$. $CWM_{\text{Height absolute distance}}$ was positively associated with CRCI (Fig. 4a). In the second experimental year, the model accepted in d -sep explained 52% of the total variation in CRCI and did not include soil water condition. Neighbor richness had significant indirect effects on CRCI via mediating FDIs of neighbors, and higher $CWM_{\text{Height hierarchical distance}}$ values had a negative effect on FDIs of neighbors. FDIs of neighbors and $CWM_{\text{SLA hierarchical distance}}$ were positively associated and $CWM_{\text{Height hierarchical distance}}$ was negatively associated with CRCI (Fig. 4b).

Discussion

In this study, we did not find that the interaction of soil water condition and neighbor richness showed significant effect on the competitive effects. The relative importance of soil water condition and neighbor richness varied with the observation time, with the more important role of soil water condition in the first experiment year, and the more important role of neighbor richness in the second experiment year. Soil water condition and neighbor richness affected competitive effects of neighbors on *L. chinensis* directly or indirectly via regulating functional profiles of plant communities.

Effect of soil water condition on competitive effects of neighbors

The first experimental year

The finding that soil water condition had a significant effect on CRCI are consistent with the previous research (Conti et al. 2018; Copeland and Harrison 2017; Dong et al. 2020) For example, Dong et al. (2020) have found that drought treatment decreased the inhibitory effect of neighbors on the target species *Caragana microphylla* in a simulated experiment. The CRCI were significantly negative under drought treatment and non-significant difference with zero under non-drought treatment, which supports the stress gradient hypothesis (SGH): competitive interaction will be weaker and facilitation will occur in more stressful habitats (Bertness and Callaway 1994).

$CWM_{\text{Height absolute distance}}$ mediated the responses of CRCI to the changes of soil water condition, indicating that competition-trait similarity hypothesis dominated the community processes in the context of aridity, which supports the second hypothesis. A large number of empirical studies have suggested that intensification of drought will promote resource-conservative strategies and smaller plant stature/size (Dong et al. 2020; Xu et al. 2021), as predicted by environmental filtering theory (Cornwell et al. 2006), because smaller sizes confer plants a better adaptation to arid environments (Valencia et al. 2018; Westoby et al. 2002). Meanwhile, resource-conservative species usually show relative lower ability of growth and resource acquisition, resulting in lower competitiveness for nutrients and water (Dong et al. 2020), and the biomass of neighbors significantly decreased under drought conditions in this study (supplementary data Fig. S2). Therefore, the finding that soil water condition positively affected $CWM_{\text{Height absolute distance}}$ suggests the increasing competition in light resources between neighbors and *L. chinensis* under drought treatments (Westoby et al. 2002). In addition, Maire et al. (2009) have found that species with similar size can limit their negative plant-plant interaction with regard to acquiring underground resources when the competition for light is strong. In an experiment of non-native invading native community, the researchers also have found that ornamentals with less functionally similar to their neighbors are unable to tolerate the native community's competitive effect and show worse in the growth performance than those more similar to native community (Conti et al. 2018). These results provide empirical evidence for that competition-trait similarity hypothesis caused by niche differences may play more important roles in affecting community processes under more resource-limited conditions (Sheppard 2019). However, the significant associations between competition outcomes (or individual performance) and the CWM of trait absolute distance are hardly found in pairwise competition experiments (Ferenc and Sheppard 2020; Fort et al. 2014; Funk and Wolf 2016).

The second experimental year

As the experimental time prolongs, the effect of soil water condition were not significant (Table 1), which supported the first hypothesis. This result may be the result of rapid adaptation of species to the drought environment (Goldberg et al. 2017; Wang et al. 2019; Zuo et al. 2021), which can be confirmed by the lack of significant response of the community functional profiles to drought (Table 1). Maestre et al. (2009) have predicted that abiotic factors would not affect the main species interaction under extreme stress environments based on the stress gradient theory. In this experiment, the biomass of the first year was removed and no nutrition was added: therefore, the resource limitation would limit the facilitation effect of drought (Li et al. 2018).

Effect of neighbor richness on competitive effects of neighbors

The first experimental year

The result that neighbor richness didn't affect CRCI was out of expectation. For example, in a one-year experiment, the effects of neighbors on a shrub species are significantly affected by neighbor richness and all treatments shows competition but not facilitation interaction (Dong et al. 2020), and six neighbor individuals and one shrub individual were transplanted into a pot of 10 cm in diameter and 21 cm in depth. The pot used in this study is four times as big as above, with six neighbor individuals and six target individuals; therefore, the resource limitation is weaker than above. As a result, outcomes of CRCI were facilitation or neutrality within neighbor richness treatments.

The second experimental year

The finding that neighbor richness significantly affected CRCI was consistent with the previous research (Dong et al. 2020). We found neighbor richness affected CRCI mainly through mediating the responses of FDis of neighbors (Fig. 4b), which supports that the niche vacant hypothesis drives community processes along the biodiversity gradient and supported the second hypothesis. Higher FDis of neighbors means higher utilization efficiency of available space and resources in communities of higher diversity, thus competition among species for limited space and resources intensifies (Dong et al. 2020; Feng et al. 2018).

The finding that FDis of neighbors showed a greater effect on CRCI than neighbor richness (Fig. 3, 4b) is consistent with the previous findings (Valencia et al. 2018; Xu et al. 2021). Greater functional diversity rather than greater species richness can better capture niche occupancy and decrease vacant niche (Feng et al. 2019), which would lead to stronger competitive effects on target species. These findings were consistent with community assembly processes along succession in the semi-arid regions: abiotic factors (such as environmental filtering) play crucial roles in the initial stage of a community and biotic interactions (limiting similarity) becomes more and more obvious with time (Cornwell et al. 2006; Hao et al. 2021; Bello et al. 2013). Meanwhile, the mechanisms that dominate competitive effects also change with time, supporting the third hypothesis.

Effect of functional profiles of plant community on competitive effects of neighbors

The variance explained by predictor factors was higher in the second than in the first experimental year, with the greater effects of functional profile indices in the second experimental year (Fig. 3). According to resource competition theory, resource availabilities decreased due to increased species richness and plantation time (Chase and Leibold 2003). Thus, neighbor richness presumably aggravated competition interactions of neighbors on *L. chinensis* with time (Purschke et al. 2013; Teixeira et al. 2020). Moreover, three CWMs of trait hierarchical distance showed the first three greatest effects in the second year, consistent with that competitive hierarchy plays a more important role in the competition for limited resources (Feng et al. 2018; Funck et al. 2016).

The finding that $CWM_{SLA \text{ hierarchical distance}}$ was positively associated with CRCI agreed with that higher SLA usually associates with a fast growth rate and represents competitive advantage (Kraft et al. 2015; Sheppard 2019). The negative correlation between $CWM_{Height \text{ hierarchical distance}}$ and CRCI (Fig. 4) was out of our expectation because plant height has a positive correlation with competitive ability for light interception as assumed (Kraft et al. 2015). However, such results have been found in previous studies (Carmona et al. 2019; Goldberg et al. 2017). For example, using a community ecosystem model, the researchers have found a unimodal relationship between competitive ability and maximum potential size, and plants with different height are disproportionately suppressed by competitors (Goldberg et al. 2017). These results might be caused by the joint influence of species resource acquisition strategies and environmental factors (Goldberg et al. 2017; Siebenkäs et al. 2015). In addition, several studies have demonstrated that species with higher height might not have competitive advantage because they have to transport water over a larger distance with greater investment, especially under more drought conditions (Carmona et al. 2019; Westoby et al. 2002). Besides, $CWM_{Height \text{ hierarchical distance}}$ was negatively associated with FDis of neighbors (Fig. 4b), which demonstrates that fitness differences could limit the occupation of niche space because species with particular trait values will dominate communities (Funk et al. 2016; Kunstler et al. 2016).

Conclusion

Our findings demonstrate that the effects of soil water condition and neighbor richness on the competitive effect of neighbors on *L. chinensis* are independent of each other. Soil water condition plays more important roles than neighbor richness in the first experimental year, and is mainly mediated by niche difference, supporting competition-trait similarity hypothesis. Neighbor richness rather than soil water condition significantly affected competitive effects in the second experiment year, which is mediated by fitness difference (competition-trait hierarchy hypothesis) and functional dispersion (vacant niche hypothesis). Therefore, from a long-term perspective, biodiversity effects on species interactions and coexistence should not be ignored in semi-arid grasslands in the context of aridity. This study provides a novel experimental perspective for mechanisms by which biodiversity and climate change affect species interactions as well as ecological processes.

Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Guang Hao, Nan Yang, Yulin Liu, Jinlong Wang, Nianxi Zhao, Hongyuan Li, Anzhi Ren and Yubao Gao. The first draft of the manuscript was written by Guang Hao, Nan Yang and Nianxi Zhao and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability statement

The datasets generated during the current study are available from the corresponding author on reasonable request.

Code availability

The R code is available upon request to the corresponding author.

Ethics approval

Not applicable

Consent to participate

Not applicable

Consent for publication

Not applicable

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Figures

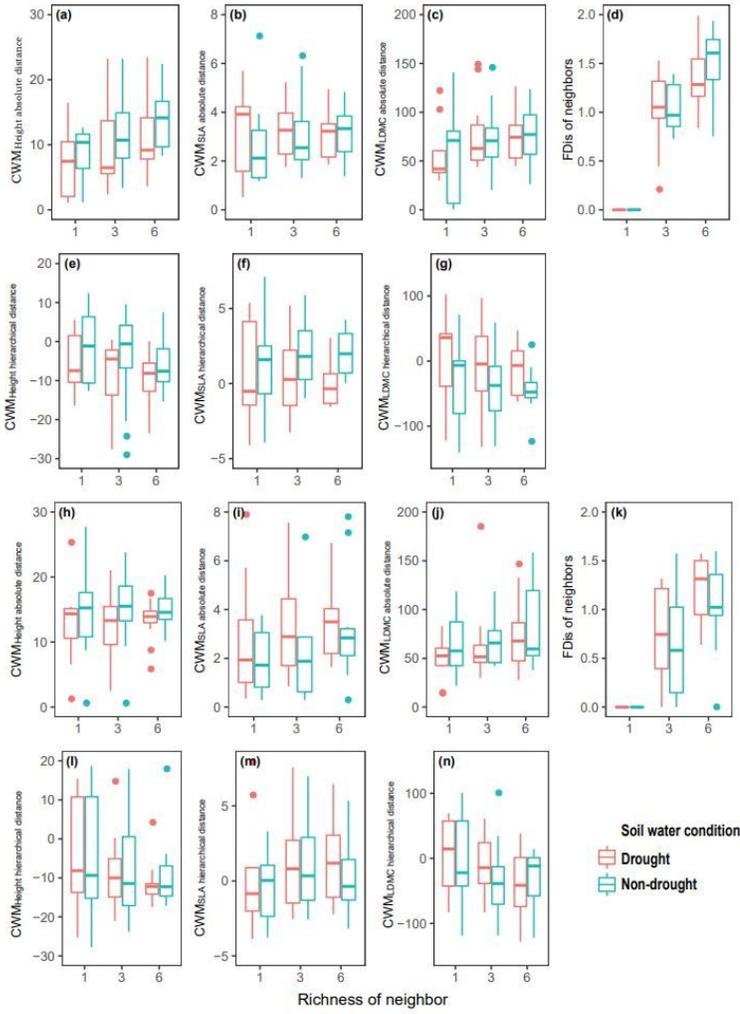


Figure 1

Effects of soil water condition (drought and non-drought), neighbor richness (1- 3- and 6-neighbor species) on functional profiles of plant communities in the first year (a-g) and second year (h-n)

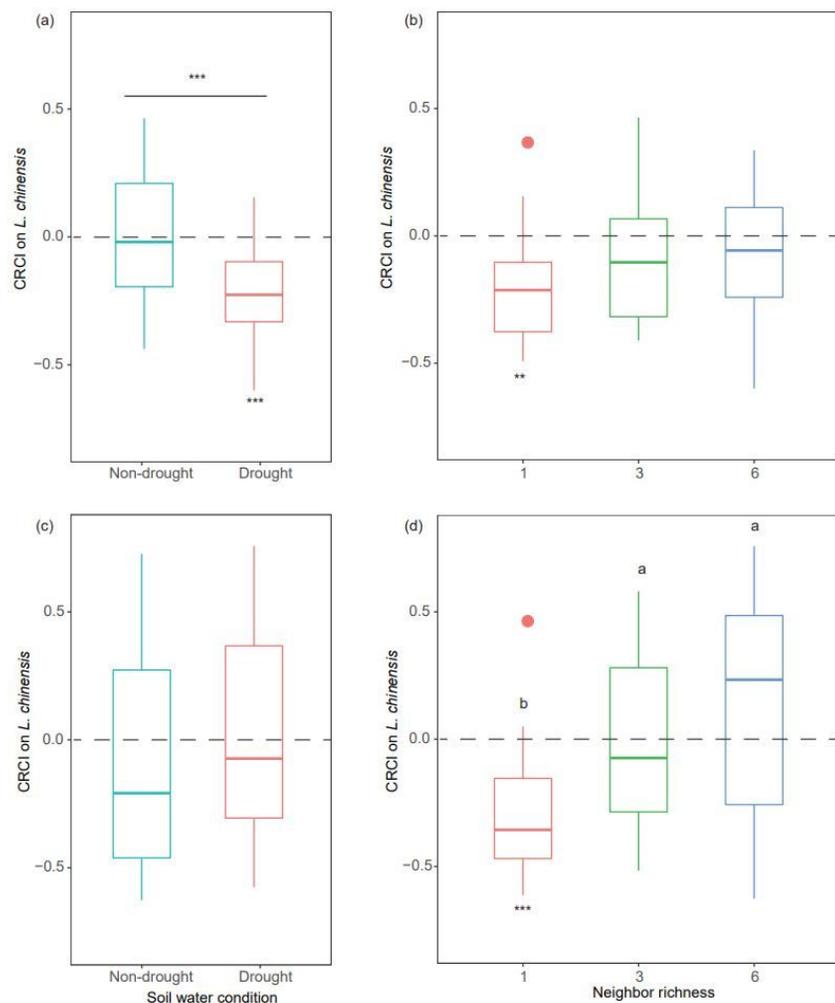


Figure 2

Effects of soil water condition (drought and non-drought), neighbor richness (1- 3- and 6-neighbor species) on CRCI on *L. chinensis* in the first year (a, b) and second year (c, d). Different lowercase letters indicate significant differences. The asterisks represent significant difference between soil water condition treatment and between variables and 0

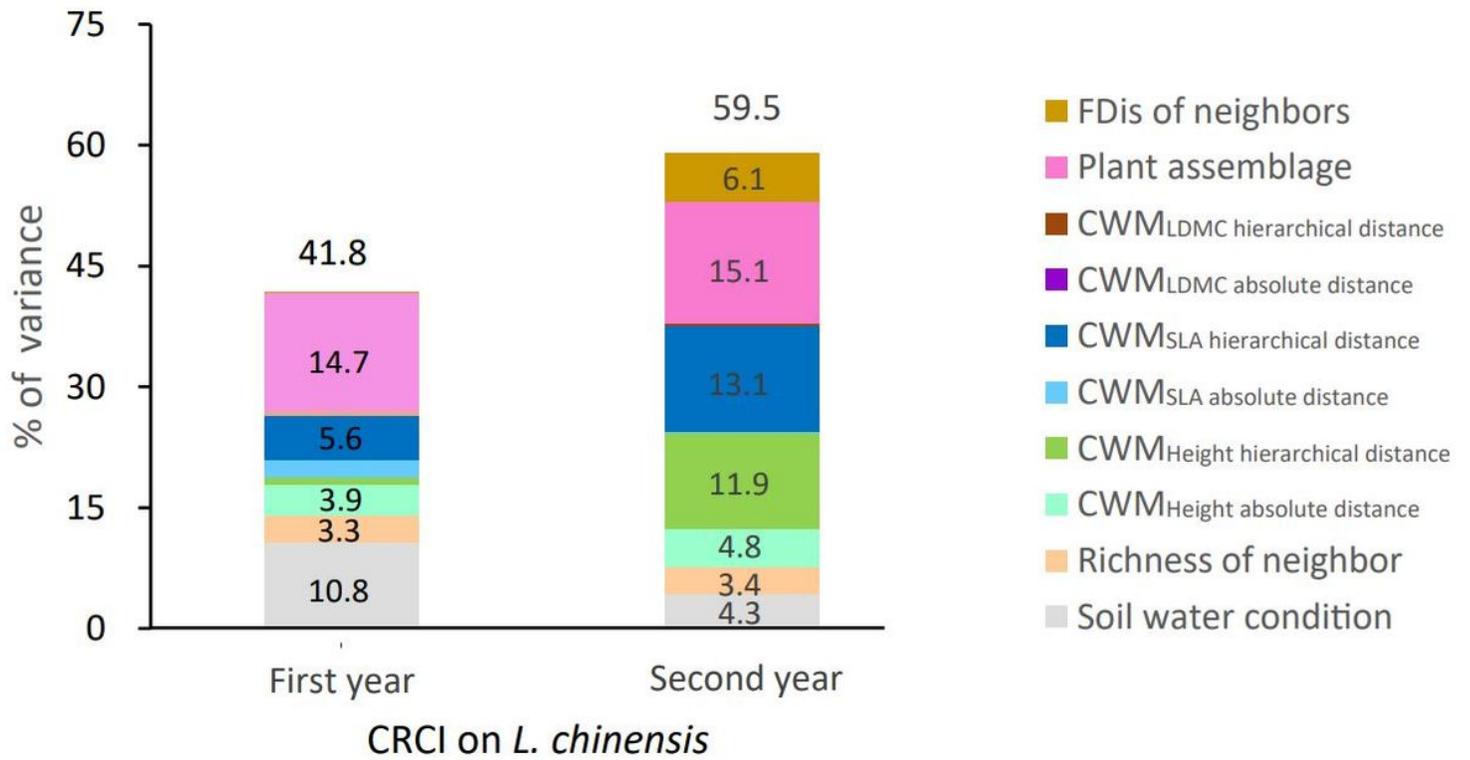
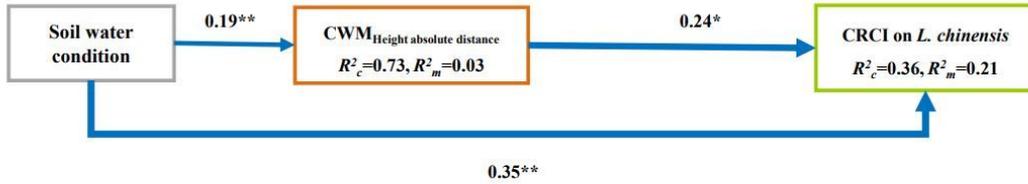


Figure 3
 Variance components showing the percentage of total R^2 explained by each predictor on CRCI on *L. chinensis* by variance partitioning analysis. The predictors used are soil water condition, neighbor richness, community-weighted mean of absolute/hierarchical distances of individual trait ($CWM_{\text{trait absolute/hierarchical distance}}$), multivariate trait distances (FDIs of neighbors) and plant assemblage

(a) AIC=18.000; Fisher's C=0.000; $p = 1.000$



(b) AIC=27.935; Fisher's C=5.935; $p = 0.204$

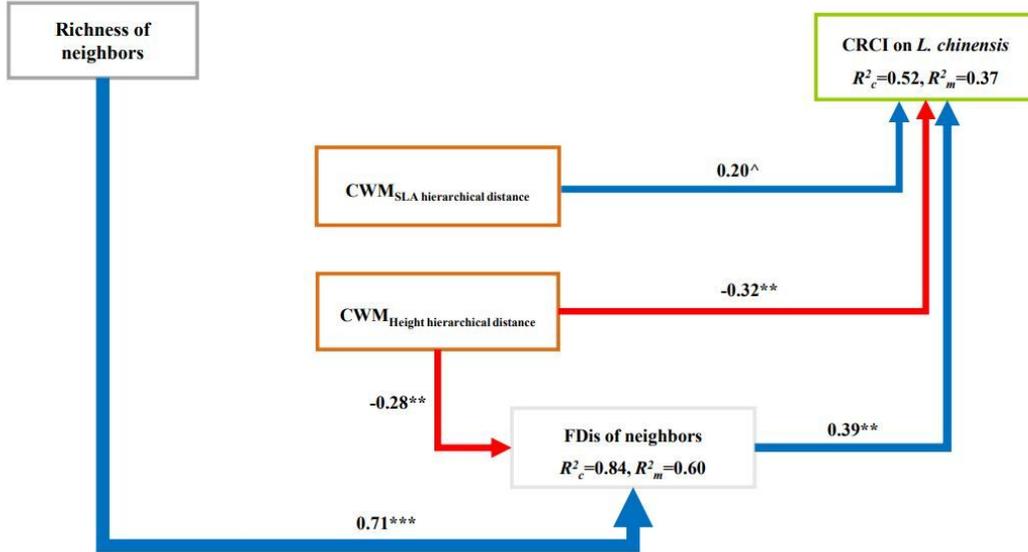


Figure 4

Relationships between soil water condition (8% and 15%), neighbor richness (one, three and six species), functional profiles of plant communities and CRCI on *L. chinensis* in the first year (a) and second year (b). The width of each arrow and numbers on each arrow indicate the standardized path coefficients. R^2_m : variance explained by fixed factors; R^2_c : variance explained by fixed and random factors. Blue and red arrows reflect positive and negative pathways respectively. ^, *, **, and *** indicate significance levels at 0.1, 0.05, 0.01 and 0.001, respectively

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