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RESEARCH ARTICLE

Biodiversity stabilizes primary productivity through compensatory effects under warming conditions

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Abstract

Aim: Diversity may increase the resistance of ecosystem productivity to environmental stress, such as warming, via compensatory processes associated with adjustments of species interactions. However, experimental evidence of compensatory processes that buffer productivity declines in relation to environmental stress is limited, especially in below-ground settings. We asked whether species richness could stabilize productivity under warming via compensatory responses in root biomass and root functional traits.

Methods: Using three herbaceous species, we created plant communities composed of four individuals in either monocultures or two- and three-species assemblages. We grew them at three temperatures, simulating current climate conditions, moderate warming and severe warming, respectively. We built mixed-linear mixed models to model plant productivity by species richness and warming and we also analyzed the interactive roles of species richness and warming in species interaction and root functional traits.

Results: We found that warming reduced both above- and below-ground productivity and shifted the biodiversity–productivity relationship from negative to positive. Productivity reductions were weaker in richer species combinations. Warming ameliorated the strength of interspecific competition below-ground in mixed-species communities by reducing the root biomass of strong competitors, which benefitted root growth of weaker competitors.

Conclusions: Our results suggest warming can facilitate compensatory responses in herbaceous root productivity across species competition hierarchies. These compensatory processes by which species richness stabilizes plant community functioning emphasize the importance that plant functional diversity has in maintaining ecosystem functioning with climate change.

KEYWORDS
biodiversity–productivity relationship, compensatory effects, herbaceous plant productivity, root functional traits, species competition, species richness, subtropical grassland, warming

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Chenlan Li and Yuan Jiang contributed equally to the work.

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1 | INTRODUCTION

Anthropogenic climate change and global biodiversity loss continue to drive the need for understanding the effects of biodiversity on ecosystem functioning and stability (Dănescu et al., 2016; Hector, 1999; Ouyang et al., 2020; Tilman, 2001). Previous studies have proposed that biodiversity stabilizes productivity in fluctuating environments through compensatory effects, which occur when the reduction in biomass of one species is compensated by the increases in biomass of other species (Naeem & Li, 1997). These effects are likely more prominent in highly diverse communities than in less diverse communities, suggesting that plant richness plays a major role in stabilizing ecosystem functioning (Bai et al., 2004; Gross et al., 2014; Hautier et al., 2015; Nagel et al., 2009; Pan et al., 2016; Tilman et al., 2006). However, there is still a lack of comprehension of the actual mechanisms of compensation contributing to this outcome, which is rarely rigorously tested in empirical experiments.

Climate change-induced environmental stressors like warming and drought are affecting plant growth and survival and threatening the maintenance of ecosystem functioning (Cavin et al., 2013). Plant communities with high diversity have been reported to be more resistant to warming and drought stress than less diverse assemblages (Isbell et al., 2015; Lloret et al., 2012), which could potentially arise from adjustments in the strength and direction of species interactions under climate change stressors (Gonzalez & Loreau, 2009; Loreau & de Mazancourt, 2013). The consequent compensatory response could occur because of two processes. One is through decreasing dominance of certain species or functional groups. On the Tibetan Plateau, for example, increased temperatures associated with climate change have led to shifts in plant community composition. These changes have not affected above-ground primary productivity because increases in the abundance of grasses have compensated for the reduced abundance of sedges and forbs (Liu et al., 2018). Accumulating evidence indicates that reduced interspecific competition caused by climate extremes is correlated with sudden declines in the biomass and density of dominant species (Cavin et al., 2013; Lloret et al., 2012a; Thibault & Brown, 2008). The second mechanism is through species-specific adaptive changes in root functional traits that determine the ability of plants to compete for water and soil resources (Luo et al., 2020; Parts et al., 2019). For instance, the average root diameter of shrubs (*Mimosa sepiaria* Benth.) was reduced under high temperature, while that of its neighboring herbaceous species (*Corchorus capsularis* L.) showed no significant change. This differential response to elevated temperature eventually resulted in novel species interactions below-ground (Luo et al., 2020). It is therefore critical to understand the actual mechanism that links to species interactions, which operates in the stabilizing effects of biodiversity on ecosystem functioning under climate change stressors.

Compensatory processes caused by the changed species interaction can potentially shift the biodiversity–productivity relationship (Callaway et al., 2002; Mulder et al., 2001). Theoretically, the effect of biodiversity on productivity is a linear combination of complementarity effects and selection effects. Complementarity effects arise because of trade-offs in species' resource use efficiencies, variability in their colonization and competitive abilities, and in their differential fitness in specific environmental conditions (Loreau, 2000; Loreau & Hector, 2001), while selection effects arise from the relative abundance of high vs low biomass-producing species (Loreau & Hector, 2001; van Ruijven & Berendse, 2005). Complementarity effects are generally positive but can be negative with strong chemical or physical interference (e.g., allelopathic effects or intense competition for resources or space) (Grace et al., 2016). Selection effects over biomass productivity vary from negative to positive depending on the strength of interspecific competition and whether competitively superior species yield greater biomass than competitively inferior species (Loreau & Hector, 2001). Overall, reduced interspecific competition potentially contributes to a positive relationship between biodiversity and ecosystem productivity (e.g., by alleviating negative complementarity effects). Such a pattern has been widely observed in nature; for example, plant diversity negatively affects productivity under favorable environmental conditions (e.g., high availability of water, light, and nutrients) where competitive interactions dominate, while when under stressful environments, the competitive interactions become weaker, shifting the diversity–productivity relationship from negative to positive (Buttler et al., 2019; Callaway et al., 2002; He et al., 2013; Maestre et al., 2009, 2012; Mariotte et al., 2013; Paquette & Messier, 2011; Wang et al., 2019). However, direct experimental evidence of whether reduced species competition changes the relationship between biodiversity and productivity is still lacking. Therefore, the complementarity or selection processes underlying changes in biodiversity–productivity relationships are unclear.

Despite the widely-recognized role that warming can play in biodiversity and ecosystem function (Duffy et al., 2017; Grace et al., 2016), the interactive effect of how individual species responses and species interactions modulate primary productivity with warming is not well understood. Thus, exploring the interaction of warming and biodiversity and the associated underlying processes is vital to protect biodiversity and sustain ecosystem function in the Anthropocene. Based on previous studies (García-Palacios et al., 2018; Maestre et al., 2012; Mulder et al., 2001; Nagel et al., 2009), we assumed that temperature and diversity would synergistically interact to determine productivity. Specifically, we hypothesized that: (1) greater species richness would weaken the negative effect of warming on productivity through species compensatory responses; (2) warming would reduce interspecific competition through species-specific changes in root functional traits; and thus (3) warming would change the biodiversity–productivity relationship from negative to positive. We tested these hypotheses mechanistically by manipulating species assemblages in mesocosm plant communities consisting of three herbaceous species at three temperature levels, simulating current climate conditions, moderate warming and severe warming, respectively.

2 | MATERIALS AND METHODS

2.1 | Species selection

Three annual herbaceous species were selected. They were *Xanthium sibiricum* Patrin ex Widder (Asteraceae), *Sesbania cannabina* (Retz.) Poir (Fabaceae) and *Celosia argentea* L. (Amaranthaceae). The selection criteria were that: (1) species had high germination rates under sterile environments; (2) species grew well in solid growth mediums; (3) species did not have strong allelopathic effects; and (4) species showed differences in root architecture and competitive ability. Our pre-experiment suggested that *Xanthium sibiricum* was aggressively rooted with lateral roots evenly distributed in the solid growth medium (Appendix S1). When grown alone at the normal temperature, *Sesbania cannabina* had abundant shallow roots in the solid growth medium (Appendix S1) and *Celosia argentea* had deep and wide roots with most lateral roots distributed at shallow depth (Appendix S1). *Xanthium sibiricum* grew better in mixed assemblages as the proportion of heterospecific neighbors increased, while *Celosia argentea* exhibited worse growth and *Sesbania cannabina* was hardly affected (Appendix S1). These findings suggested that *Xanthium sibiricum* was the most competitive species, followed by *Sesbania cannabina* and then *Celosia argentea*, which was the least competitive species.

2.2 | Seeds collection and generation

We collected seeds from grasslands throughout Heishiding Natural Reserve (23.27° N, 11.15° E, Guangdong Province, China). Seeds of similar size and shape for each species were selected to minimize variation in seed quality. To promote seed germination and sterilize the seed surface for each species, we tried different concentrations of hydrogen peroxide and treatment times to soak seeds in our pre-experiment and finally determined the optimal methods. *Xanthium sibiricum* and *Celosia argentea* seeds were soaked using a 10% hydrogen peroxide solution for 20 min and 1 h, respectively, while *Sesbania cannabina* seeds were sterilized using a 15% hydrogen peroxide solution for 20 min. Seeds were then rinsed 3–5 times with sterile water and immediately soaked in sterile water for approximately 1 h. All seeds were finally sown in Petri dishes (1/2 Hoagland medium with 0.05% Plant Preservative Mixture [PPM™]) in a dark incubator (IGS100, Thermo, CN, 30°C) to germinate.

2.3 | Experimental design

Seedlings of similar performance (with straight roots of similar length and no infection) for each species were selected and then transplanted into cylindrical cultivation containers (12 cm in diameter and 27 cm in height), filled with 1.7 L of sterilized solid growth medium containing 1/2 Hoagland solution. Four seedlings were grown together in a single container as a plant community. Fifteen combinations were grown, including three monocultures,

nine mixtures of two species and three mixtures of three species. A 2 cm × 2 cm square was drawn at the center of the cultivation container, and four seedlings were planted at the corners of the square. Meanwhile, individual plant growth experiments (one plant per cylinder) were performed. One seedling was planted in the center of each container. All seedlings were grown at three experimental temperature levels based on the mean temperature of the warmest quarter (MTWQ, from a range of 23.5°C to 27.5°C) over the last 10 years in the Heishiding grasslands. The three temperature treatments (daytime/nighttime temperatures) were: 26/21°C, 30/25°C, and 34/29°C, corresponding to the temperatures of current conditions, moderate warming and severe warming, respectively. The latter two treatments may be caused by future global warming in subtropical grasslands (IPCC, 2014; Pau et al., 2018). A total of 54 experimental treatments (15 species assemblages and three single individual plantings at three temperature treatments) were set, and each treatment was replicated 3–9 times. Multiple replicates of treatments were considered because we preferred more replicates for species assemblages that contained species of low survival rate to make sure we could harvest enough replicates for each treatment in the end. All growth containers under the same temperature treatment were randomly arranged in an artificial growth chamber that was set to a 12-h light/12-h dark photoperiod and to the respective temperature. Seedlings were grown for four weeks.

Individuals were harvested and three parts were measured: leaves, stems, and roots. Fresh and dry biomass weights were measured to the nearest milligram. WinRHIZO (Pro 2013a, Regent Instrument Inc., CA) was used to measure the following nine root functional traits: tap root length (TRL, cm), root area (RA, cm^2), root length (RL, cm), root volume (RV, cm^3), average root diameter (AD, mm), specific root area (SRA, cm^2 mg^{-1}, a ratio of root area to root dry mass), specific root length (SRL, cm mg^{-1}, a ratio of root length to root dry mass), root tissue density (RTD, mg cm^{-3}, root dry mass divided by root volume) and root dry matter content (RDMC, %, a ratio of root dry mass to fresh mass).

2.4 | Statistical analysis

To evaluate the interactive effects of species diversity and warming on productivity, we built linear mixed-effects models for total, below-ground and above-ground productivity (log-transformed) at both the community and individual levels. Community productivity was estimated as the sum of the biomass of the four individuals in each container. It was modeled as a function of species richness, temperature and their interaction as fixed effects. Considering the same species richness recorded for different communities, for example, when the species richness was two, there were nine kinds of community composition: three individuals of *Xanthium sibiricum* and one individual of *Sesbania cannabina*, three individuals of *Xanthium sibiricum* and one individual of *Celosia argentea*, two individuals of *Xanthium sibiricum* and two individuals of *Sesbania cannabina*, etc., we included the community composition in the model as a random

intercept to account for the effects of different assemblages on community productivity. Individual productivity (individual biomass) was modeled using the same fixed effects as the community-level model, and three random effects were considered, namely community combinations, species identities and growth containers.

The net biodiversity effect (ΔB) on productivity for each assemblage was calculated as the difference between the biomass observed in mixtures (B_O) and the expected biomass measured from the biomass of monocultures (B_E). The net biodiversity effect was further partitioned into a complementarity effect and a selection effect using additive partitions based on the following equation:

$$\Delta B = B_O - B_E = \sum_i RB_{Oi}M_i - \sum_i RB_{Ei}M_i = \sum_i \Delta RB_i M_i = N\overline{\Delta RBM} + Ncov(\Delta RB, M)$$

(1)

where M_i refers to the biomass of species i in monocultures; $RB_{Oi} = \frac{B_O}{M_i}$ is the observed relative biomass of species i in mixed assemblages; RB_{Ei} is the expected relative biomass for species i, which is simply its planting proportion; $\Delta RB_i = RB_{Oi} - RB_{Ei}$ is the deviation from the expected relative biomass of species i in mixed assemblages; N is the number of species in the assemblage; $N\overline{\Delta RBM}$ quantifies the complementarity effect; and $Ncov(\Delta RB, M)$ quantifies the selection effect (Loreau & Hector, 2001). To test whether warming affected the biodiversity–productivity relationship, we built linear mixed-effects models to separately predict effects of net biodiversity, complementarity and selection on community productivity using species richness, temperature and their interaction as fixed effects. Community combinations were included in the model as a random effect.

The intensity of competition inhibition for a plant individual was calculated as:

$$C = \frac{S_i - B_i}{S_i}$$

(2)

where S_i and B_i are the biomass of species i when grown alone and the observed biomass of individual i when grown with other individuals, respectively (Schwinning & Weiner, 1998). Hence, we measured this relative difference using the respective biomass of the total, below-ground and above-ground portions of the plant individual to reflect the respective intensities of competition inhibition ($C_{overall}$, $C_{belowground}$, and $C_{aboveground}$). We then averaged the competitive strength among plants in each community to create community-level competition inhibition indexes ($\overline{C}_{overall}$, $\overline{C}_{belowground}$, and $\overline{C}_{aboveground}$), which included both inter- and intraspecific competition. For each individual, we also calculated the deviance of productivity in mixtures from monocultures to represent the strength of interspecific competition. Negative deviance indicates that the individual is subject to strong interspecific inhibition, while positive deviance means the individual is competitively superior to the rest of the individuals. To evaluate whether warming could interact with competition to affect individual and community productivity, we used linear mixed-effects models, where the competition inhibition indexes interacted with temperature to predict productivity.

For all root functional traits, we used principal component analysis (PCA) to visualize the functional trait space. The PCA showed that the first three axes captured 86% of the variation in these nine traits (Appendix S2). One dimension showed that individuals with higher RA had more RL and RV (Appendix S2). The orthogonal dimension captured a trade-off between individuals with "conservative" roots (high RTD and RDMC, low SRL and SRA) and individuals with "acquisitive" roots (low RTD and RDMC, high SRL and SRA) (Appendix S2). This dimension represents the carbon-construction cost of the root economics spectrum (Freschet et al., 2010; Kong et al., 2019; Reich, 2014). The third dimension illustrated a common dichotomy in below-ground root distribution among individuals with low AD and longer TRL and individuals with high AD and shorter TRL (Appendix S2). We selected RA, RTD and AD in the following analyses because they were orthogonal and correlated with the first three principal component axes, respectively. First, we computed the community weighted mean (CWM) trait values and functional dispersion (F_{dis}) using the function "dbFD" in the *FD* package (Laliberté et al., 2015). We then separately predicted the total, below-ground and above-ground productivity using these trait values at both the community and individual levels. To determine whether warming affected the relationship between root functional traits and productivity, plant community productivity was predicted in a linear mixed-effects model using CWM trait values, temperature and their interaction. We fitted the same models using individual-level data to see how patterns varied among individuals across experimental community combinations. All linear mixed-effects models were fit using the "lmer" function in the *lme4* package (Bates et al., 2014). Marginal R^2 (variance explained by all the fixed effects) and conditional R^2 (variance explained by both fixed and random effects) values were computed using the "r.squaredGLMM" function in the *MuMIn* package (Zuur et al., 2009). All analyses were conducted in R v. 3.6.2 (R Core Team, 2019).

3 | RESULTS

3.1 | Effects of warming and species richness on productivity

Warming reduced community-level total productivity in all combinations (Estimate = −0.075, $p < 0.001$; Table 1, Figure 1). The strength of this negative effect decreased as community species richness increased (interaction term between temperature and richness: Estimate = 0.019, $p < 0.001$; Table 1, Figure 1). These results were consistent for both above- and below-ground productivity (Table 1, Figure 1). Most of the variation in the below-ground productivity was predicted by temperature, richness and their interaction ($R^2_{marginal}$ = 0.595; Table 1). At the individual level, the results were similar to those described above for the community level (Table 1).

TABLE 1 Linear mixed-effects model coefficients and associated probabilities for fixed terms in six models where the total, above-ground and below-ground productivity were separately fitted at both the community and individual levels

Term	Total		Below-ground		Above-ground	
	Estimate	p	Estimate	p	Estimate	p
Community level						
Intercept	7.464	<0.001	8.015	<0.001	6.508	<0.001
Temperature	−0.075	<0.001	−0.145	<0.001	−0.052	<0.001
Richness	−0.512	0.012	−0.588	0.010	−0.428	0.044
Temperature:richness	0.019	<0.001	0.021	0.003	0.017	0.002
Model fit statistics						
$R^2_{marginal}$	0.141		0.595		0.057	
$R^2_{conditional}$	0.840		0.821		0.846	
Individual level						
Intercept	6.317	0.001	6.751	<0.001	5.425	0.003
Temperature	−0.077	<0.001	−0.144	<0.001	−0.056	<0.001
Richness	−0.794	0.016	−0.827	0.042	−0.745	0.021
Temperature:richness	0.020	0.008	0.020	0.038	0.019	0.014
Model fit statistics						
$R^2_{marginal}$	0.012		0.042		0.007	
$R^2_{conditional}$	0.955		0.939		0.951	

For example, a temperature increase of 8°C (daytime/nighttime temperature from 26/21°C to 34/29°C) reduced biomass by 31%–37% in monocultures, and individual plant biomass reductions tended to be weaker in mixed assemblages relative to monocultures for all species (interaction term of temperature and richness: Estimate = 0.020, $p = 0.008$; Table 1, Appendix S3).

Species richness negatively affected community-level productivity overall (Estimate = −0.512, $p = 0.012$; Table 1), but this effect tended to be positive at the highest temperature (estimate of the slope of the linear regression between richness and productivity = 0.170, $p = 0.010$). Consistently, the net biodiversity effect (ΔB) changed from negative at the lowest temperature level (26°C) to positive for the higher temperature treatments. The mean and 95% confidence intervals of ΔB in the three-species communities were −24.7 [−40.5, −8.9] at 26°C and 35.7 [20.3, 51.1] at 34°C (Figure 2b). After partitioning the biodiversity effect index into the portions of complementarity and selection effect, we found that both ΔB and the complementarity effect were affected by species richness and the interaction term between temperature and species richness, but the selection effect was not influenced (Table 2, Figure 2).

## 3.2 | Effects of warming and species richness on competition relationships

Warming decreased the average intensity of competition inhibition ($\overline{C}_{overall}$) within the three-species assemblages mainly through influencing below-ground, but not above-ground competition. Warming did not affect $\overline{C}_{overall}$ in monocultures and two-species assemblages (Figure 3). Community-level total plant productivity decreased with increasing intensity of $\overline{C}_{belowground}$ but was not affected by above-ground competition. The interaction effect of $\overline{C}_{belowground}$ and temperature on community-level total plant productivity was positive, suggesting that warming weakened the negative effect of below-ground competition (Appendix S4). At the individual level, *Xanthium sibiricum* produced greater biomass in the mixed assemblages than in monocultures; however, *Sesbania cannabina* and *Celosia argentea* produced less biomass (Appendix S5). The deviance of biomass in mixtures relative to monocultures was positive for *Xanthium sibiricum* but negative for the other two species. Warming increased the biomass deviance for *Sesbania cannabina* and *Celosia argentea*, which approached zero at the highest temperature, but did not affect the biomass deviance of *Xanthium sibiricum* (Appendix S5).

3.3 | Effects of warming and species richness on root traits

Community-weighted mean values of all three selected root traits explained 53% of the variance in total productivity, 91% of the variance in below-ground productivity and 36% of the variance in above-ground productivity. F_{dis}, however, only explained 12% of the variance in total productivity, 9% of the variance in below-ground productivity and 11% of the variance in above-ground productivity. At the individual level, root traits accounted for 92%, 99% and 87% of the variation in total, below-ground and above-ground productivity, respectively. Warming influenced the relationship between root traits and productivity at both community and individual levels (Appendix S6). For example, warming increased the slope of the positive relationship between productivity and the root traits of RA,
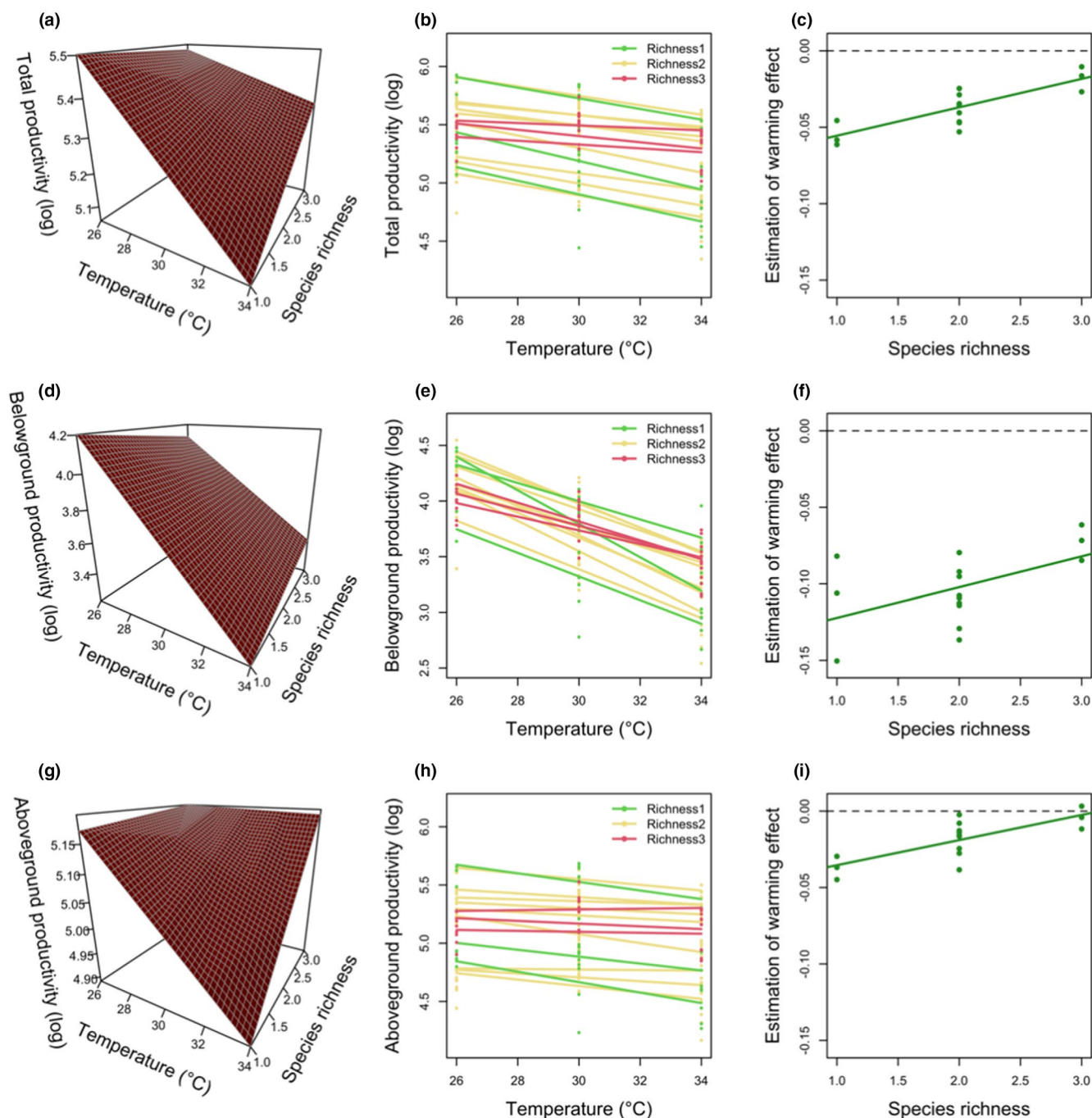
FIGURE 1 The interactive effect of temperature and species richness on total (a-c), below-ground (d-f) and above-ground (g-i) productivity at the community level. Left panels (a, d and g) show productivity as a function of temperature and species richness and their interaction as fixed effects in the mixed-effects model. Middle panels (b, e and h) show linear relationships between productivity and temperature for communities of differing species richness. Right panels (c, f and i) show the strength of species richness effects on the slope of temperature-productivity relationships

RTD and AD (Figure 4, Appendixes S6, S7, S8). Warming also affected root trait values directly and interacted with species richness to differentially affect root traits among species in mixed assemblages (Figure 4, Appendixes S7, S8). The RA and AD of strong competitors, such as *Xanthium sibiricum* and *Sesbania cannabina*, were also significantly decreased by warming, whereas root functional traits of the competitively inferior species *Celosia argentea* were unaffected in mixed assemblages (Figure 4c,d, Appendix S8).

4 | DISCUSSION

Ecosystem functioning, including plant biomass productivity, may be threatened by ongoing anthropogenic global climate change and biodiversity loss (Isbell et al., 2013; Worm & Duffy, 2003). Although the roles of both warming and biodiversity have been thoroughly investigated, we nonetheless have a limited understanding of the synergistic effects of warming and species richness on ecosystem

TABLE 2 Linear mixed-effects model coefficients and associated probabilities for fixed terms in models predicting the net biodiversity effect (ΔB) and the complementarity and selection effects on community productivity

| Term	ΔB Estimate	p	Complementarity effect Estimate	p	Selection effect Estimate	p
Intercept	158.308	0.138	113.887	0.233	44.185	0.399
Richness	−119.048	0.012	−119.161	0.005	0.275	0.990
Temperature	−4.978	0.142	−3.574	0.231	−1.394	0.296
Richness:temperature	4.048	0.008	3.644	0.006	0.399	0.498
Model fit statistics						
$R^2_{marginal}$	0.176		0.229		0.053	
$R^2_{conditional}$	0.463		0.566		0.844	

FIGURE 2 Net biodiversity (ΔB) (a, b), complementarity (c, d) and selection (e, f) effects along the experimental temperature gradient. Left panels (a, c and e) show the net effect (±95% confidence interval) for two-species communities, while right panels (b, d and f) show the net effects of three-species communities. p-Values correspond to ANOVA statistics for each effect across the three temperatures
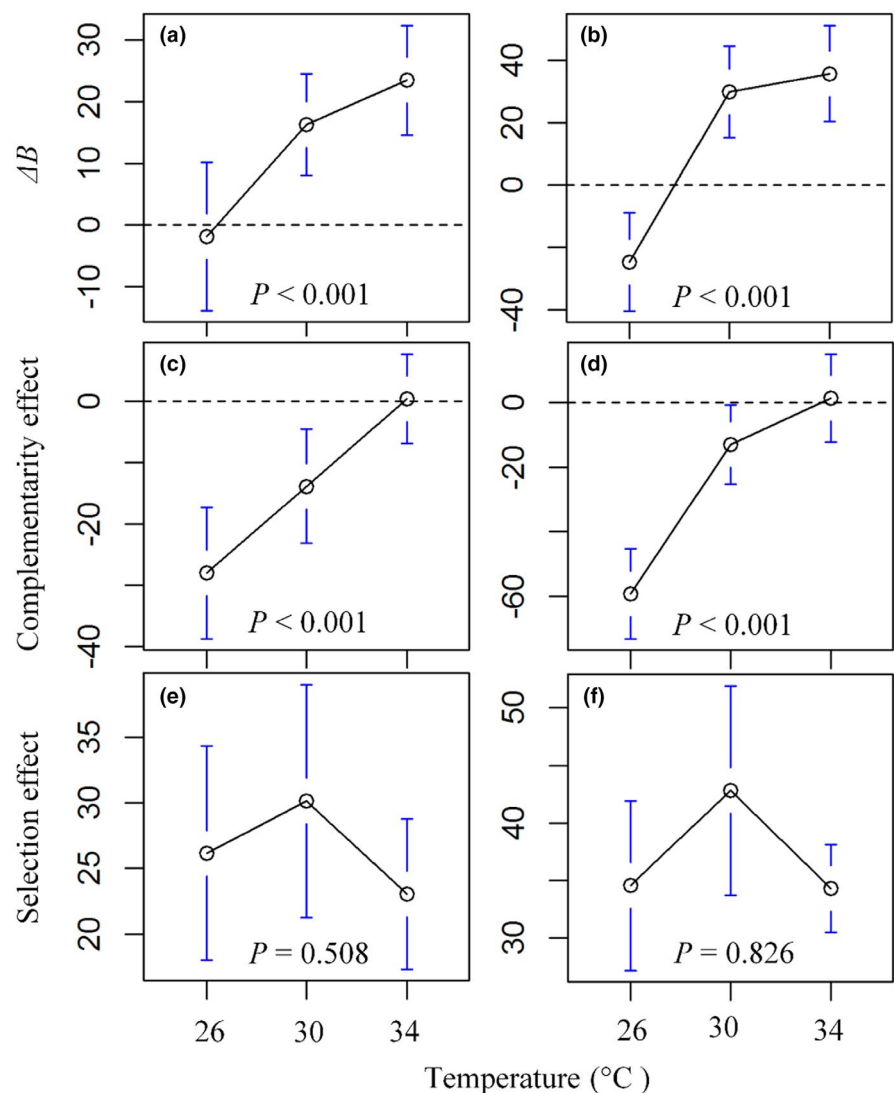
function. We grew three herbaceous species and observed the response of productivity and root functional traits to warming and assemblage richness, thus investigating the integrated effects of temperature and species richness on subtropical rangeland productivity. Our results show that greater species richness buffers the negative effect of warming on productivity (Table 1, Figure 1, Appendix S3), and that warming alters the biodiversity–productivity relationship from negative to positive (Table 2, Figure 2). We also provide evidence that warming reduces below-ground interspecific competition by reducing functional differences in root architecture
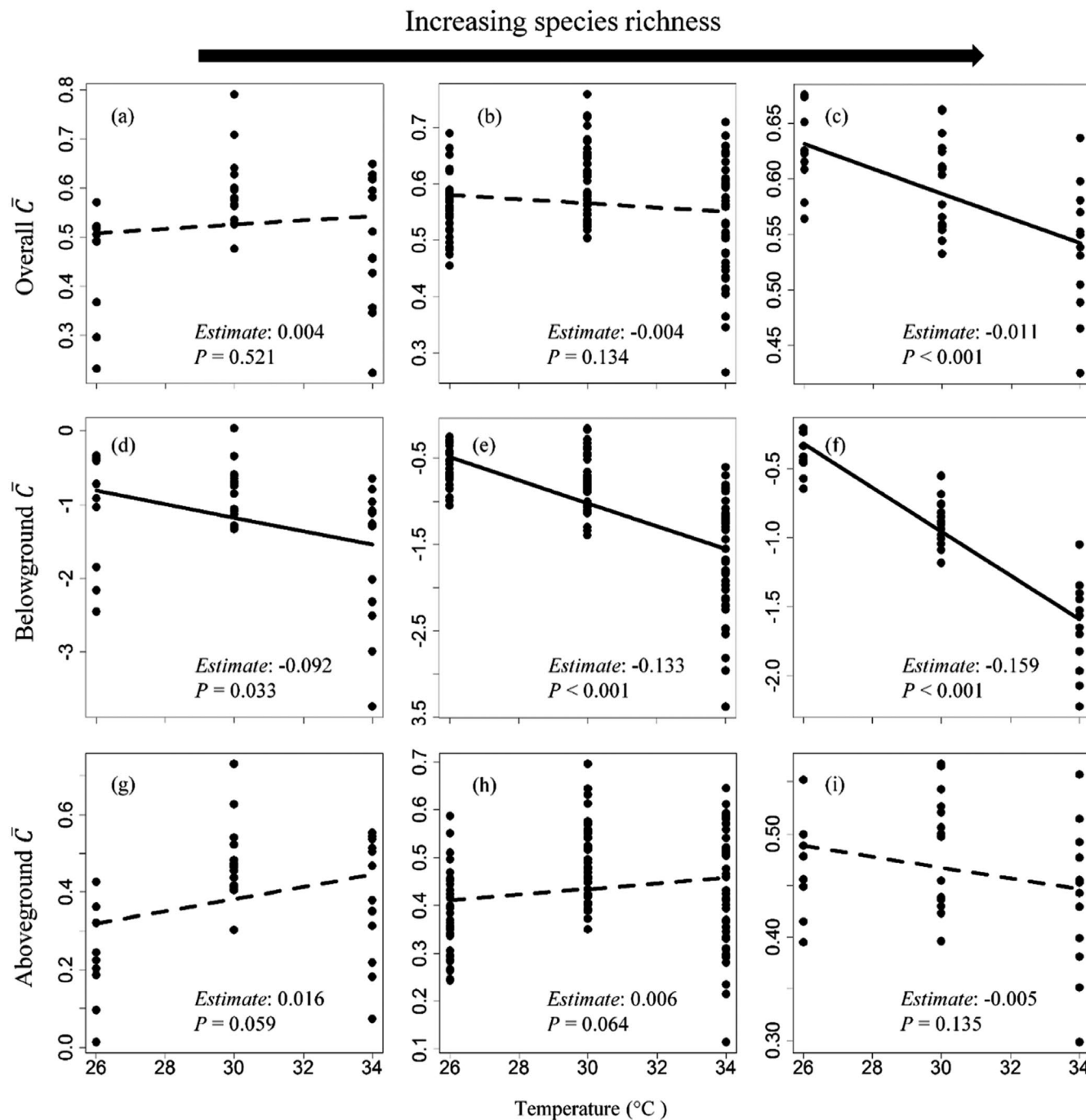
FIGURE 3 Linear regressions between the average intensity of competition inhibition ($\overline{C}$) from the community overall (a-c), below-ground (d-f), and above-ground (g-i) in relation to temperature. The arrow at the top of the figure indicates increasing species richness. Left panels (a, d and g) are monocultures, middle panels (b, e and h) are two-species communities and right panels (c, f and i) are three-species communities. Dashed lines represent non-significant relationships while solid lines show statistically significant relationships. Slope estimates and probabilities are shown for each regression

between strongly competitive and less competitive species (Figures 3, 4). Such changes in species interactions, especially in highly diverse plant communities, could compensate for the negative effects of warming on productivity and mediate the impacts of warming on the biodiversity–productivity relationship.

The relationship between biodiversity and productivity has been debated extensively, and both negative and positive relationships

attributed to environmental stress have been reported for natural systems (Paquette & Messier, 2011; Wang et al., 2019). The intensity of species interactions likely changes along environmental gradients, and these changes thus mediate the relationship between biodiversity and productivity through complementarity or selection effects (Cardinale et al., 2013). Our study provides empirical evidence for herbaceous grasses that the effect of species richness on

FIGURE 4 Linear regressions relating plant productivity (mg) to root area (cm²) at the community (a) and individual (b) levels and bar plots of root area by temperature treatment for each species in monocultures (c) and mixtures (d). Error bars indicate 95% confidence intervals and asterisks indicate statistical significance in an ANOVA statistics for the trait of each species under the three temperatures (***, $p < 0.001$; **, $0.001 \leq p < 0.01$; *, $0.01 \leq p < 0.05$)
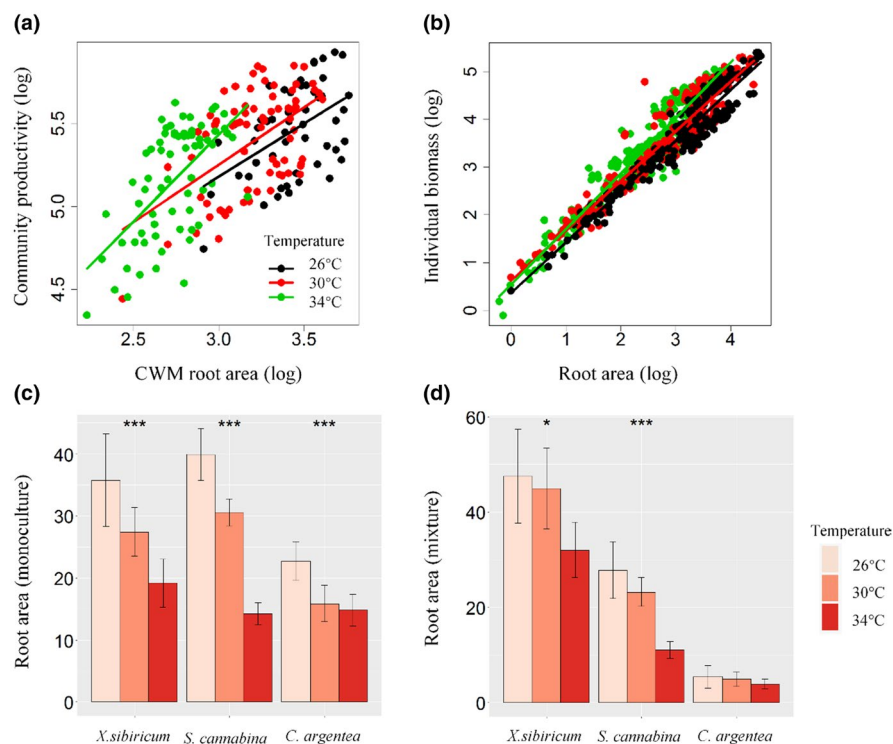
productivity depends on the degree to which warming reduces the strength of below-ground competition (Figure 3). Previous studies have shown that the reduction in below-ground interspecific competition changed the net biodiversity effect mainly by weakening negative complementarity effects, which mostly occur in more homogeneous habitats where niche partitioning is weak and competing species interference is strong (Wang et al., 2019). Thus, a reduction in the strength of below-ground interspecific competition along environmental stress gradients may be responsible for shifting the biodiversity–productivity relationship from slightly negative to increasingly positive. A similar pattern was previously reported in drylands (Maestre et al., 2012).

Warming may reduce the strength of below-ground interactions by altering root architecture (Figure 4), which affects plant resource acquisition. Some root morphological traits such as RA, RTD, and AD are associated with the acquisition of water and nutrients and determine acquisition efficiency under high levels of environmental stress (Comas et al., 2013; Fitter, 2002; Qin et al., 2007). Our study identified CWM values as better predictors of plant productivity than the functional dispersion of root traits, suggesting that root functional trait values of species, rather than functional diversity, are more important for maximizing ecosystem functioning in homogeneous environments (Paquette & Messier, 2011). Warming strengthened the positive relationships between productivity and RA, RTD and AD (Figure 4, Appendixes S7, S8), indicating that warming might increase the resource acquisition efficiency of the entire community via intraspecific changes in root functional traits. Nonetheless, the effects of warming on root system architecture were species-specific (Luo et al., 2020). In our study, RA significantly decreased with increasing temperature for strong competitors but was seldomly affected for

weakly competitive species when compared to the RA in monocultures. Species interactions in species-rich communities were thus modified because warming restricted the root growth of strong competitors, leaving more space and resources for relatively weak competitors.

Although the importance of species interactions in determining species coexistence and community composition has been widely recognized (Levine & HilleRisLambers, 2009; Macarthur & Levins, 1967; May, 1972), the influence of species interactions (e.g., competition interactions or physical and chemical interference) on ecosystem functioning and stability remains less clear. In this study, we found that strong interspecific competition for either space or nutrients reduced community productivity, but warming alleviated this reduction. This finding is likely attributable to strong intraspecific competition in monocultures and/or asymmetric interspecific interaction in mixed assemblages, which are not beneficial for promoting community productivity compared to cases where species were grown alone (Cameron et al., 2007; Cavin et al., 2013; Cornwell & Ackerly, 2010; Freckleton & Watkinson, 2001; Thibault & Brown, 2008). However, such asymmetric interspecific interactions could be modified when warming restricts stronger competitors to a greater degree than relatively weak competitors (Cavin et al., 2013; Partzsch, 2019). This species-specific restriction contributes to the productivity gain for relatively weak competitors to offset the loss of community productivity. Under these circumstances, any process, like an environmental change, that weakens the strength of these species interactions will alter the biodiversity–productivity relationship. The intensity and direction of species interactions vary along environmental stress gradients. For example, species competition dominates under favorable

conditions, but as stress increases, competition is hypothesized to weaken and may even shift toward facilitation in harsh environments (Callaway et al., 2002; Coleman et al., 1994; Maestre et al., 2009). The results of our study suggest that warming can be viewed as an environmental stressor that reduces the growth of plants. The strength of competitive inhibition was reduced with increasing temperature, in support of our hypothesis. This inverse relationship increased as community species richness increased and primarily occurred below-ground.

Theoretical studies have emphasized the role of species interactions in both biodiversity–productivity and biodiversity–stability relationships (Tilman, 2001; Cardinale et al., 2013). However, experimental investigations of the role of wide-ranging species interactions, such as competition, facilitation and species interference, have just begun. We used a homogeneous plant growth system to examine how changes in interspecific competition for space and nutrients varied with temperature and species richness. We recognize our laboratory experiment was less complicated than similar field experiments, which may yield different results. It was, however, a reliable and convenient approach, which isolated warming effects on plant assemblages of varying composition and richness, while controlling for the effects of other factors (e.g., soil nutrients and microbiome). Our results provide strong evidence that warming reduces the strength of below-ground competition through species-specific changes in root architecture, and that the reduced below-ground competition has compensatory effects on productivity, potentially stabilizing ecosystem functioning.

AUTHOR CONTRIBUTIONS

Suqin Fang conceived the project. Chenlan Li performed the experiment. Chenlan Li and Yuan Jiang wrote the manuscript. Chenlan Li, Yuan Jiang and Zihui Wang performed the analysis. All authors discussed the results and contributed to the revision.

DATA AVAILABILITY STATEMENT

The datasets analyzed in this study are archived on Figshare https://figshare.com/s/cdc801a5622049474f36.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1 Root architectures and competition ability quantification of the three herbaceous species

Appendix S2 Principal component analysis of nine root traits measured from 744 individuals

Appendix S3 Linear regressions between the individual biomass and temperature for the three species

Appendix S4 Linear mixed-effects model coefficients and associated probabilities for fixed terms in models predicting productivity at the community and individual levels using the competition inhibition index, temperature and their interaction as predictors

Appendix S5 Linear regressions between the individual biomass and species richness for the three species, and warming effect on the biomass in mixtures relative to that in monocultures

Appendix S6 Linear mixed-effects model coefficients and associated probabilities for fixed terms in models predicting productivity at the community and individual levels using trait, temperature and their interaction as predictors

Appendix S7 Linear regressions relating productivity to root tissue density and bar plots of root tissue density by temperature treatment for each species

Appendix S8 Linear regressions relating productivity to average root diameter and bar plots of average root diameter by temperature treatment for each species