

ARTICLE

Darwin's naturalization conundrum reconciled by changes of species interactions

Jiang Wang¹  | Shao-Peng Li²  | Yuan Ge³  | Xiao-Yan Wang¹ |
 Song Gao¹ | Tong Chen¹ | Fei-Hai Yu¹ 

¹School of Life Science/Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, Zhejiang, China

²Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China

³State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China

Correspondence

Fei-Hai Yu
 Email: feihaiyu@126.com

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Abstract

Although phylogenetic distance between native and exotic species has a close link with their interactions, it is still unclear how environmental stresses and species interactions influence the relationship between phylogenetic distance and biological invasions. Here we assessed the effect of invader–native phylogenetic distance on the growth of the invader (*Symphyotrichum subulatum*) under three levels of drought (no, moderate, or intense drought). Under no drought, interspecific competition between close relatives was the dominant process and native communities more closely related to the invader showed higher resistance to invasion, supporting Darwin's naturalization hypothesis. In contrast, under intense drought, facilitation between close relatives by mutualism with arbuscular mycorrhizal fungi (AMF) became more important, and the invader became more successful in their more closely related native communities, supporting the preadaptation hypothesis. The colonization rate of AMF of the invader was higher in more closely related native communities regardless of the drought treatment, but it was only positively related to invader biomass under intense drought. Therefore, the shift of species interactions from competition to facilitation may be ascribed to the promotion of AMF to invasion occurring under intense drought, which leads to the effect of closely related natives on the invader shifting from negative to positive. Our results provide a new angle to resolve Darwin's naturalization conundrum from the change of species interactions along a stress gradient, and provide important clues for invasion management when species interactions change in response to global climatic change.

KEYWORDS

arbuscular mycorrhizal fungi, drought, invasion, light, phylogenetic distance, species interaction, species richness

INTRODUCTION

Biological invasions have become a worldwide problem due to their major ecological, social and economic consequences (Crowley et al., 2017; de la Riva et al., 2019;

Diagne et al., 2021). Understanding which exotic species are likely to establish in the wild and subsequently become invasive is therefore critical (Cadotte et al., 2018; Li et al., 2015). Charles Darwin provided two opposite hypotheses incorporating phylogenetic distance to explain biological invasions (Darwin, 1859), named Darwin's naturalization hypothesis (DNH) and the

Jiang Wang and Shao-Peng Li contributed equally to this study.

preadaptation hypothesis (PAH), which has received a large amount of attention recently (Cadotte et al., 2018; Gallien & Carboni, 2017; Ma et al., 2016). On the one hand, DNH suggests that exotic species that are more distantly related to native communities should be more successful, as they share fewer natural enemies and compete less intensively with the native species (Daehler, 2001). On the other hand, PAH indicates that exotic species closely related to native communities should be favored because close relatives share similar traits and therefore are well suited to the same habitats (Ricciardi & Mottiar, 2006). These two opposite hypotheses have been encapsulated under the term “Darwin’s naturalization conundrum” (DNC; Diez et al., 2008; Thuiller et al., 2010), which has been tested in many studies. Previous studies have shown positive (Parker et al., 2012; Peay et al., 2012; Tan et al., 2015), negative (Li et al., 2015; Marx et al., 2016; Ricotta et al., 2010) or no (Dawson et al., 2009; Lim et al., 2014; Skóra et al., 2015) relationship between phylogenetic distance and invasion success. This inconsistency raises the question of the feasibility of using exotic–native phylogenetic relationships to predict biological invasions.

Many studies have tried to reconcile these inconsistent results and have suggested that Darwin’s two opposing hypotheses need not be mutually exclusive (Gallien & Carboni, 2017; Kusumoto et al., 2019). Studies indicated that the validity of the two hypotheses may change with, for instance, spatial scales, invasion stages, and temporal scales (Cadotte et al., 2018; Ma et al., 2016). For spatial scales, it has been suggested that DNH should be more applicable to local scales at which interspecific competition determines invasion success, whereas PAH may be more likely to emerge at regional scales in which adapting to environments determines invasion success (Park et al., 2020). Different invasion stages, such as transport, naturalization/establishment, spread, and impact, may also influence the validity of the two hypotheses (Dawson et al., 2009; Theoharides & Dukes, 2007). PAH may be more applicable to the early stages when environmental filtering was the dominant factor, whereas DNH may be more applicable to later stages, when competition becomes increasingly important (Ma et al., 2016). However, spatial scales and invasion stages could not completely reconcile the inconsistent results of DNC (Cadotte et al., 2018). These studies take it for granted that competition and environmental filtering are the principal factors that determine the validity of DNH and PAH. However, facilitation is also an important interaction between native and invasive species (Altieri et al., 2010; Bulleri & Benedetti-Cecchi, 2008; Smith et al., 2004; Von Holle, 2013; Zabin & Altieri, 2007), and has often been ignored when framing and testing DNC.

The sign and strength of species interaction may depend on phylogenetic distance between species (Martorell et al., 2021). Prior studies have found that competition often occurred in closely related species (Bonanomi et al., 2010, 2011). If closely related, native and exotic species could also compete more preferably, which may support DNH. Even though competition prevails in closely related species, indirect interactions (such as sharing similar mycorrhizal fungi) can frequently lead to facilitation between closely related species (Beltrán et al., 2012; Bukowski et al., 2018). Prior studies have found that the invasion of exotic species was promoted by sharing arbuscular mycorrhizal fungi (AMF) in the soil of invaded communities (Aslani et al., 2019; Dong et al., 2021; Paudel et al., 2014). Moreover, a strong phylogenetic signal was frequently found in plant–AMF interactions, which leads to closely related plant species preferring to select similar AMF symbiosis partners (Montesinos-Navarro et al., 2012, 2015). Therefore, in addition to the mechanism of shared environmental affinity used to interpret PAH in prior studies (Hock et al., 2020; Kusumoto et al., 2019; Park et al., 2020), the facilitation between invaders and their closely related natives may be a potential mechanism that leads to PAH.

Competition and facilitation should drive community structure simultaneously and their relative roles can be affected by abiotic stresses (Bornette & Puijalon, 2011; Zhang & Wang, 2016). The stress gradient hypothesis predicts that, with increasing abiotic stress, the importance of competitive interactions will decrease, and the importance of facilitative interactions will increase (Bertness & Callaway, 1994; He et al., 2013; Silliman et al., 2015). Similarly, the benefit of sharing AMF for host plants will also increase with increasing abiotic stress (In’t Zandt et al., 2019; Porter et al., 2020), which may provide more benefits to closely related exotic species. Consequently, we postulate that interspecific interactions between closely related native and exotic species may shift from competition to facilitation with increasing abiotic stress. Under benign environments, exotic species closely related to natives should find it more difficult to invade native communities due to the dominance of interspecific competition, whereas exotic species distantly related to natives could escape strong interspecific competition and become more successful, supporting DNH. In contrast, under stressful environments, exotic species closely related to natives should invade native communities more easily due to the prevalence of interspecific facilitation, whereas exotic species distantly related to natives should find it more difficult to invade for lack of environmental adaptation, supporting PAH.

To test these hypotheses, we constructed experimental native plant communities and subjected them to no, moderate, or intense drought treatments. These communities were then invaded by an exotic plant species *Symphytotrichum subulatum* (Michx.) G.L.Nesom (Asteraceae). *S. subulatum* is native to South America, but is now widespread in warm regions of the world (Zhuge et al., 2011). In China, *S. subulatum* is listed as a malignant invasive plant species, and has invaded many areas (Zhuge et al., 2011). The effects of phylogenetic distance between the native and the exotic species on invasion success of *S. subulatum* were analyzed under each drought treatment. We aimed to test whether the effect of phylogenetic distance on invasion success changed along the drought gradient, and whether these changes were driven by a shift in species interactions (competition vs. facilitation). To test the generality of these hypotheses, we constructed communities with different levels of species richness with different species compositions.

MATERIALS AND METHODS

The experiment

We constructed experimental plant communities with five levels of species richness (1, 2, 4, 8, and 16 species) at Taizhou University (28°39' N, 121°23' E) in Taizhou, Zhejiang Province, China. This site is characterized by a subtropical monsoon climate with mean annual precipitation of 1632 mm. The average temperatures in January and August are 8.5°C and 30°C, respectively. The species pool consisted of 16 native herbaceous species (Appendix S1: Table S1). These species naturally grow in brush grassland communities of valley and hillside around Taizhou city in Zhejiang Province, China. Most species of brush grassland communities are annuals and perennials. Nine perennial species and seven annual species were selected to simulate natural communities. *Patrinia scabiosaefolia* (Valerianaceae), *Achyranthes aspera* (Amaranthaceae), *Solanum nigrum* (Solanaceae), and *Artemisia migoana* (Asteraceae) are usually dominant species. We constructed a total of 46 communities with different species compositions: one monoculture for each of the 16 species, 10 two-species mixtures, 10 four-species mixtures, nine eight-species mixtures, and one 16-species mixture. Each of the two-, four-, or eight-species mixtures had a different species composition (Appendix S1: Table S2), and the species were randomly chosen from the species pool.

All the 45 communities of the one-, two-, four-, and eight-species mixture were replicated six times, and the community of the 16-species mixture was replicated

30 times, resulting in a total of 300 communities. The six replicates of the 45 communities were assigned randomly to the six combinations of three drought intensity treatments (no, moderate, and intense drought) and two invasion treatments (with or without an exotic plant invasion; as described in the next two sections); the 30 replicates of the 16-species mixture were also randomly assigned to the six treatment combinations of drought and invasion, with five replicates each.

The experimental plant communities were constructed in plastic containers (72 cm long × 64 cm wide × 42 cm deep) with five draining holes at the bottom. Each container was first filled with a 27 cm layer of a soil (total N: $0.763 \pm 0.104 \text{ g kg}^{-1}$; total P: $0.216 \pm 0.047 \text{ g kg}^{-1}$, mean ± SE, $n = 10$) and then a 10 cm layer of a mixture of the soil and a nutrient-rich potting compost (Appendix S1: Table S3) at a volume ratio of 1:1 (total N: $4.612 \pm 0.456 \text{ g kg}^{-1}$; total P: $0.802 \pm 0.189 \text{ g kg}^{-1}$, mean ± SE, $n = 10$). The soil was collected in a mountain area near Taizhou, and was classified as a fine loamy mixed semiatric molic hapludult soil (Chinese Soil Taxonomy Cooperative Research Group, 1995). The potting compost was bought from Shanghai Kuheng Company, China. The soil-compost mixture layer was added to facilitate seed germination and seedling establishment.

In December 2013, we sowed a total of 800 seeds in each container and determined seed number of each species in a container by dividing 800 by species number. At 1 month after germination, vigorous seedlings of each species with similar height were selected and excess seedlings were removed. Therefore, at the start of the experiment, plant density was maintained at 32 seedlings per container, and each species was represented by the same number of seedlings (e.g., for four-species mixtures, there were eight seedlings for each species). The 32 seedlings were spatially evenly distributed in the container, and seedlings of the same species were not adjacent, if possible. In each container, we also removed undesired seedlings, that is, those not belonging to the originally sown species. All the containers were randomly placed inside a plastic rain shelter in Taizhou University, which was open at the bottom sides to allow air to be ventilated.

Using automatic drip irrigation systems, we set up three drought treatments (no, moderate, and intense drought) via the control of the irrigated time. To account for seasonal variation of evapotranspiration, soil water content of 20 containers randomly selected for each of six combined treatments were measured with a ProCheck analyzer (Decagon, Pullman, Washington, USA). Data collected using this ProCheck analyzer were adjusted based on the traditional way of measuring gravimetric soil water content. The irrigation time was adjusted based on the data

from these measurements. For the no drought treatment, the irrigation time was set to 20–35 min, and gravimetric soil water content (15.5%–19.8%) was maintained as similar to that of plant communities of the mountain areas around Taizhou. For the treatments of moderate and intense drought, the irrigation time was 50% (gravimetric soil water content ranging from 12.4% to 15.4%) and 25% (gravimetric soil water content ranging from 10.0% to 12.6%) of that in the no drought treatment, respectively. Depending on the weather conditions, plant communities in the containers were irrigated once a day between May and September, once every other day between March and April and between October and December, and once every week between January and February. The drought treatments started on 12 March 2015, that is, 16 months after the plants were initially sowed.

In December 2015, for half (150) of the experimental communities, 50 seeds of the invasive annual herb *S. subulatum* were evenly sown in each plot. We also established four monocultures of the invader under each drought treatment by sowing 50 seeds of *S. subulatum*, and all of the surviving individuals were left.

Plant community harvest and measurements

We harvested the communities in all containers in October 2016. The biomass of most species almost reached the highest value in October. In each container, aboveground living plants were sorted into species, dried to a constant mass at 80°C and weighed. As some pathogens seemed to specifically infect *Medicago sativa*, no plants of this species survived to the end of the experiment. As the monocultures of *M. sativa* had no living plants, these containers (one in each of the six treatment combinations of drought and invasion) were not included in data analysis. Consequently, there was a final sample of 49 communities (container) in each of six treatments.

Phylogenetic distance

We constructed phylogenies of the 16 resident species and the invasive species (*S. subulatum*) using three commonly sequenced genes from GenBank: *rbcL*, *matK* and *ITS* (Appendix S1: Table S4; Figure S1). We also used the gene sequences of one additional species *Amborella trichopoda* that diverged early in angiosperm evolution to serve as the out-group species (Cadotte et al., 2008). Sequences were aligned for each region independently using MUSCLE (Edgar, 2004) and combined into a single supermatrix.

To estimate phylogenetic distance, we constructed an ultrametric tree using BEAST v2.5 software (Bouckaert et al., 2019). First, we compared a 24 different nucleotide substitution model using their Bayesian Information Criterion (BIC) scores and MEGA-X version 10.1.8 (Kumar et al., 2018; Nei & Kumar, 2000); General Time Reversible (GTR) + Gamma + Invariable was selected as the best fitting model. Second, we used BEAUti v2.5 software (Bouckaert et al., 2019) to create a file that defined the sequence mutation model, molecular clock model, and parameter priors. The uncorrelated log normal relaxed clock model was applied. We set an average mutation rate as 0.001/site/million years ago, with a normal distribution for the rate prior. Six calibration points were set according to Li et al. (2019). We ran 20 million steps with sampling of the chains every 2000 steps and a burn-in of 10%. Finally, we used TRACER v1.7 software (Rambaut et al., 2018) to estimate the proper convergence and mixing of the chains. The maximum clade credibility tree was summarized using Tree Annotator v2.5 with a burn-in of 10% (Bouckaert et al., 2019).

We used Phylocom v4.2 software (Webb et al., 2008) to calculate the phylogenetic distance of *S. subulatum* to the natives. Furthermore, the above genetic distances were weighted by the relative abundance of the natives, as metrics to represent the phylogenetic distance between the invader and a recipient community (Jiang et al., 2010). The mean phylogenetic distance (MPD) was calculated as follows:

$$\text{MPD} = \sum_{i=1}^n \text{PD}_i \times \text{RPD}_i$$

where n is number of species in a native community, PD_i is phylogenetic distance of *S. subulatum* to species i , and RPD_i is relative abundance of species i in the native communities. MPD was calculated using three weighted methods: (1) MPD calculated by original planted density in April 2014; (2) MPD weighted by plant density in October 2014 (before the drought treatment and the invasion treatment), which was independent of drought and invasion treatments; (3) MPD weighted by biomass in October 2016 (at the end of the experiment). These three MPD measures were highly correlated (Appendix S1: Figure S2), and we reported the results based on MPD weighted by plant density in October 2014 in the main text. Significant correlations indicated that the gradient of phylogenetic distance persisted across the different drought treatments during the experiments. MPD was log transformed before data analysis.

Species interactions

Complementarity and selection effects

With increase in environmental stress, species interactions may shift from competition to facilitation, which can lead to the mechanism of the biodiversity effect to shift from selection to complementarity (Wang et al., 2013, 2021). The selection and complementarity effects were used to reflect the relative role of competition and facilitation with increasing drought stress. The complementarity and selection effects among native species were calculated following the additive partitioning method of Loreau and Hector (2001). The selection effect, $N_{cov}(\Delta RY, M)$, was calculated as the covariance between monoculture yield of species (M) and their change in relative yield in the mixture (ΔRY) multiplied by N of the mixture. The complementarity effect for a given number of species (N) was quantified as $N\Delta RY \bar{M}$, where \bar{M} was the mean value of monoculture yield (biomass) across all species and $\overline{\Delta RY}$ was the mean value of relative yield (aboveground biomass) across all species in the mixture.

Biomass deviation

To further quantify the interspecific interactions among natives in different drought treatments, we investigated the change in community biomass. Biomass deviation (D) of mixtures was calculated based on its monoculture biomass following the method of Loreau and Hector (2001):

$$D_j = \frac{\sum_{i=1}^n O_{ij} - \sum_{i=1}^n E_{ij}}{\sum_{i=1}^n E_{ij}}$$

where O_{ij} was observed biomass of species i in the mixture under the drought level j , E_{ij} was the expected biomass of species i in the mixture, that is, simply the monoculture biomass multiplied by the initial proportion (original planted density in April 2014) of the species in the mixture under the drought level j , and n was the number of species included in the mixture. If positive interactions are dominant in communities, then D_j will be more than 0. In contrast, if competition is through dominant interspecific interactions, then D_j will be <0.

Biomass deviation (D_i) of each dominant species (having the greatest biomass in a community) and nondominant species in mixtures was also calculated as $D_i = (O_i - E_i)/E_i$. If $D_i > 0$, the dominant or nondominant species expressed a better performance than the expected yield; if $D_i < 0$, the dominant or nondominant species

expressed a worse performance than the expected yield. The performances of dominant and nondominant species were used to reflect the change in species interactions. If species interactions shift from competition to facilitation, the values of nondominant species should shift from negative (for competition restrain by dominant species) to positive (for facilitation with dominant species).

Relative neighbor effect

To directly quantify the effect of native species on the invader performance, we investigated the effect of native species on biomass of invasive species. The relative neighbor effect (RNE) was calculated following Callaway et al. (2002):

$$RNE = [(X_t - X_c)/x]$$

where X_t is invader biomass for each container with native species in a given drought treatment, X_c is average biomass of the invader monocultures in the same drought treatment, and x is the highest value of X_t and X_c . A positive RNE value indicates that native species have a positive effect on the invader (i.e., facilitation prevails), whereas a negative RNE value indicates that native species have a negative effect on the invader (i.e., competition prevails).

AMF colonization rates of the invader

AMF colonization rates of hyphae, vesicles and arbuscules in roots were quantified using the line-intersect method after clearing roots in 10% KOH and staining in 0.05% trypan blue (Mcgonigle et al., 1990). For *S. subulatum* in each container, at least 200 intersects of 30 root segments of ~1 cm long were scored under a light microscope at $\times 200$ magnification. AMF colonization rate was calculated by dividing the infected intersects by the observed 200 intersects. A high colonization rate meant more easily colonized by AMF. AMF colonization rate was not measured in 23 containers, as no living plants of *S. subulatum* were found.

Statistical analysis

To improve the homoscedasticity and normality, data for invader biomass, native species biomass, and AMF colonization rate were transformed to $\log(x + 1)$. We used a linear mixed model to determine the effects of drought (category factor), species richness (category factor), MPD (continuous factor), and their interactions on invader

biomass; species composition was included as a random term in this model. We used ANCOVA to test the effects of drought, MPD, and their interaction on colonization rate of AMF and RNE. Generalized least squares (GLS) estimator was also used to analyze the effect of MPD on RNE at each drought treatment (Appendix S1: Figure S3). After inverse hyperbolic sine transformation, nonparametric Kruskal–Wallis test was used to test the differences in the complementarity effect, the selection effect, and biomass deviation of communities among different drought treatments. Relationships between variables (MPD and invader biomass, MPD and RNE, MPD and AMF, AMF and RNE, and AMF and invader biomass) were also explored by simple linear regressions. One-sample *T*-test was used to test whether average values of dominant or nondominant species biomass deviation, the complementarity effect, the selection effect, and biomass deviation of communities under each level of drought were significantly higher or lower than 0. Data analyses were performed using SPSS 20.0 for windows (IBM, Armonk, NY, USA) and R (version 3.1-145; Pinheiro et al., 2018).

RESULTS

Results of the linear mixed model showed that drought and MPD had significant interactive effects on invader biomass (Table 1). Increasing phylogenetic distance between the natives and invader (*S. subulatum*) significantly increased the biomass of the invader under no drought (Figure 1a), but significantly decreased it under intense drought (Figure 1c). Because species richness also interacted with drought and MPD in influencing invader biomass, to eliminate the effect of species richness, the effects of drought and MPD on invader biomass were further analyzed at each species richness level. We found that the relationships between MPD and invader biomass shifted from positive to negative with increasing drought stress across most richness levels (Appendix S1: Figure S4).

TABLE 1 Results of a linear mixed mode for the effects of drought, species richness, and mean phylogenetic distance on invader biomass.

Effect	df	den. df	<i>F</i>	<i>p</i>
Drought (<i>D</i>)	2	85	22.49	<0.001
Richness (<i>R</i>)	4	40	6.84	<0.001
Mean phylogenetic distance (MPD)	1	85	0.57	0.452
<i>D</i> × MPD	2	85	23.34	<0.001
<i>D</i> × <i>R</i> × MPD	12	85	4.61	<0.001

Note: Species composition was included as a random factor and MPD was a continuous factor. Monocultures of *Medicago sativa* had no living plants and was not included in the data analysis, resulting in 147 plots in total. Values are in bold when *p* < 0.05. Abbreviations: den., denominator; df, degrees of freedom.

Drought had significant effects on the complementarity effect, selection effect, and biomass deviation of communities (Figure 2). The complementarity effect and biomass deviation of communities significantly increased with increasing drought stress (Figure 2a,c). Under no drought, most of the nondominant species had worse performances when growing with dominant species (mixtures) than when growing alone (monocultures), but had better performances with increasing drought stress (Figure 3; Appendix S1: Figure S5). The invader showed similar responses to increasing drought stress when growing in more closely related native plant communities, that is, had lower biomass under no drought, but had higher biomass under intense drought (Figure 4). These responses led to the MPD–RNE relationships shifting from positive to negative, and drought and MPD also had significant interactive effects on RNE ($F_{2,141} = 14.3$, $p < 0.001$).

Results of ANCOVA showed that AMF was significantly affected by MPD ($F_{1,121} = 55.8$, $p < 0.001$). Moreover, AMF colonization rate of the invader decreased with MPD under all three drought treatments (Figure 5a–c). However, AMF colonization rate of the invader was only positively correlated with RNE and biomass of invader under intense drought (Figure 5f,i). AMF colonization rate of the invader had no significant relationships with RNE under no and moderate drought, and also had no or even negative relationships with invader biomass under no and moderate drought (Figure 5d,e,g,h).

DISCUSSION

Our study investigated how phylogenetic distance covaries with native species richness to impact invasion success. Under no drought, invader biomass significantly increased with its phylogenetic distance to native communities, which supports DNH. In contrast, under intense drought, invader biomass significantly decreased with its phylogenetic distance to native communities,

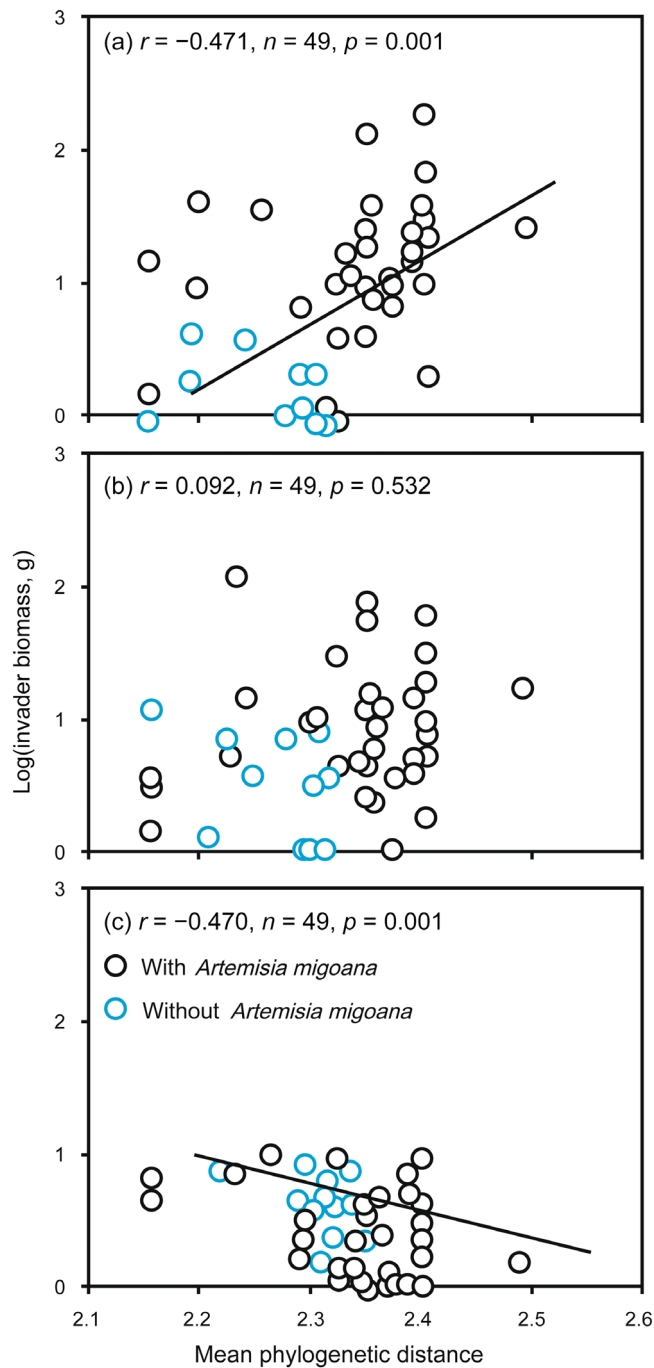


FIGURE 1 Relationships between biomass of *Symphyotrichum subulatum* and mean phylogenetic distance between the invader and native communities under (a) no, (b) moderate, or (c) intense drought. Significant relationships were represented by regression lines. Small circles represent data from each community.

which supports PAH. We further showed that the change of the effect of phylogenetic distance on invasion was related to the change in species interactions from competition to facilitation along the drought gradient. These findings, therefore, provide a novel explanation to reconcile DNC.

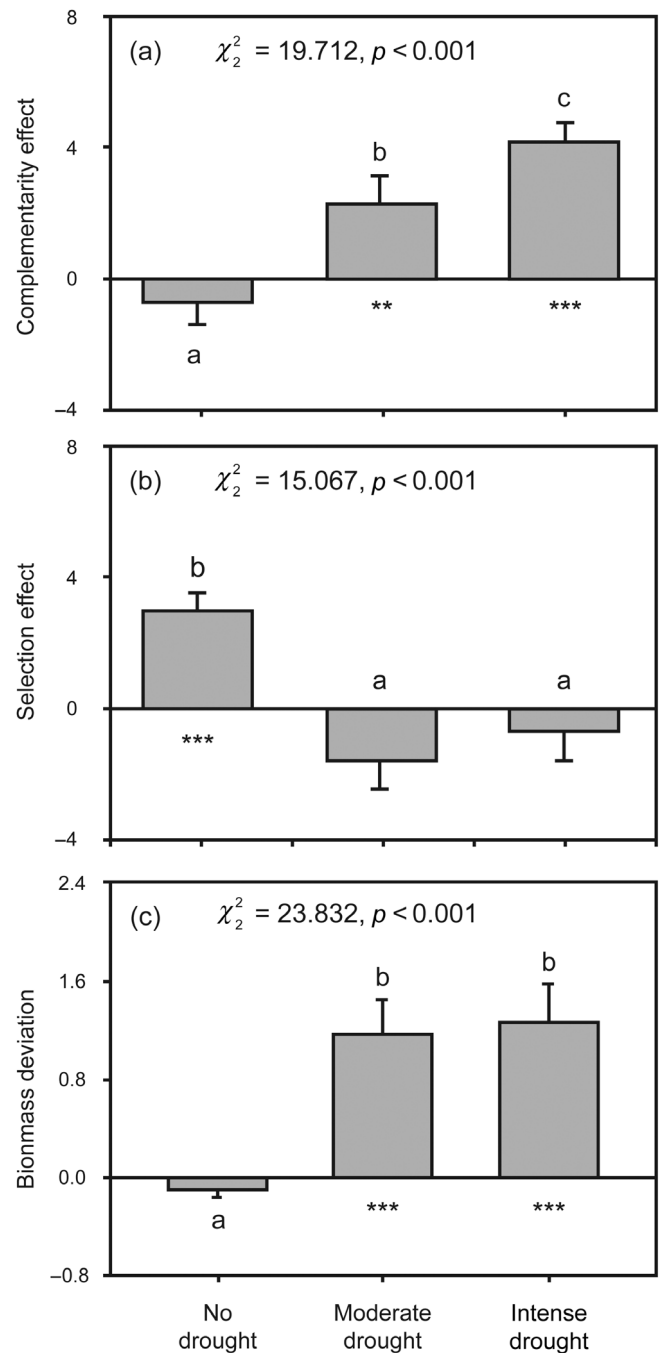


FIGURE 2 The complementarity effect (a), selection effect (b), and biomass deviation of invaded communities (c) under no, moderate, or intense drought. Significant difference from zero was indicated by asterisks (*** $p < 0.001$; ** $p < 0.01$); different letters indicate significant differences among the three drought treatments.

Consistent with prior studies (Bertness & Callaway, 1994; He et al., 2013; Lortie & Callaway, 2006; Silliman et al., 2015), we found that interspecific interactions shifted from competition to facilitation with increasing drought stress. Under no drought, competitive advantages of dominant species led to nondominant

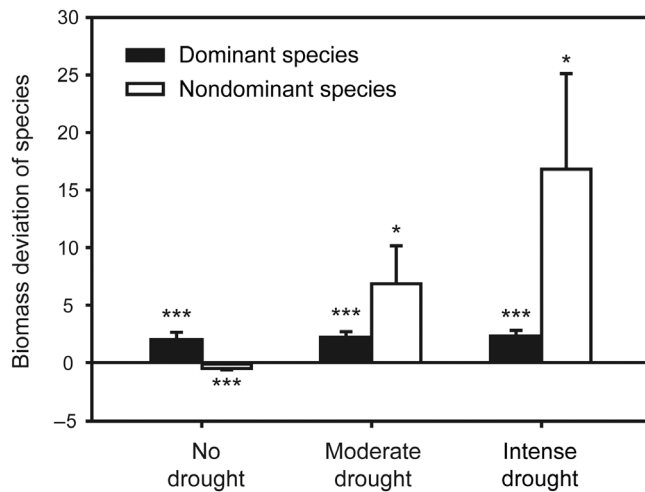


FIGURE 3 Biomass deviation of dominant and nondominant native species in invaded communities under no, moderate, or intense drought. Significant difference from zero was indicated by asterisks (***) $p < 0.001$; (*) $p < 0.05$.

species to perform worse in mixtures than in monocultures. However, under intense drought, the better performances of the nondominant species indicated the benefits from living with the dominant species by facilitation (Sotomayor et al., 2021; Wang et al., 2013). With increasing drought stress, more species had better performances, suggesting the increasing role of facilitation, which led to the increase in the complementarity effect (Appendix S1: Figure S5, Wang et al., 2021, Wright et al., 2021). Under no and moderate drought, RNE values were negative, indicating that the invader was inhibited by competing with native species (Shen et al., 2021; Zhi et al., 2007). Moreover, under no drought, the lower negative values of RNE in closely related native communities (Figure 4a) indicated that stronger competition was imposed on the invader, which supported DNH. However, under intense drought, positive values of RNE in closely related native communities indicated that the invader was promoted through facilitation with closely related native species (Figure 4c; Shen et al., 2021; Zhi et al., 2007), which supports PAH. Consequently, DNH and PAH may apply to different environmental conditions, such as those along a drought stress gradient, as increasing drought stress led to the shift in interspecific interactions between closely related native and invader species from competition to facilitation.

Facilitation and competition between species occurred simultaneously, with potential net effects being competition, facilitation, or neutral (Bornette & Pujalon, 2011; Bruno et al., 2003; Zhang & Wang, 2016). Closely related species can frequently generate facilitation by sharing similar AMF symbiosis partners (Beltrán

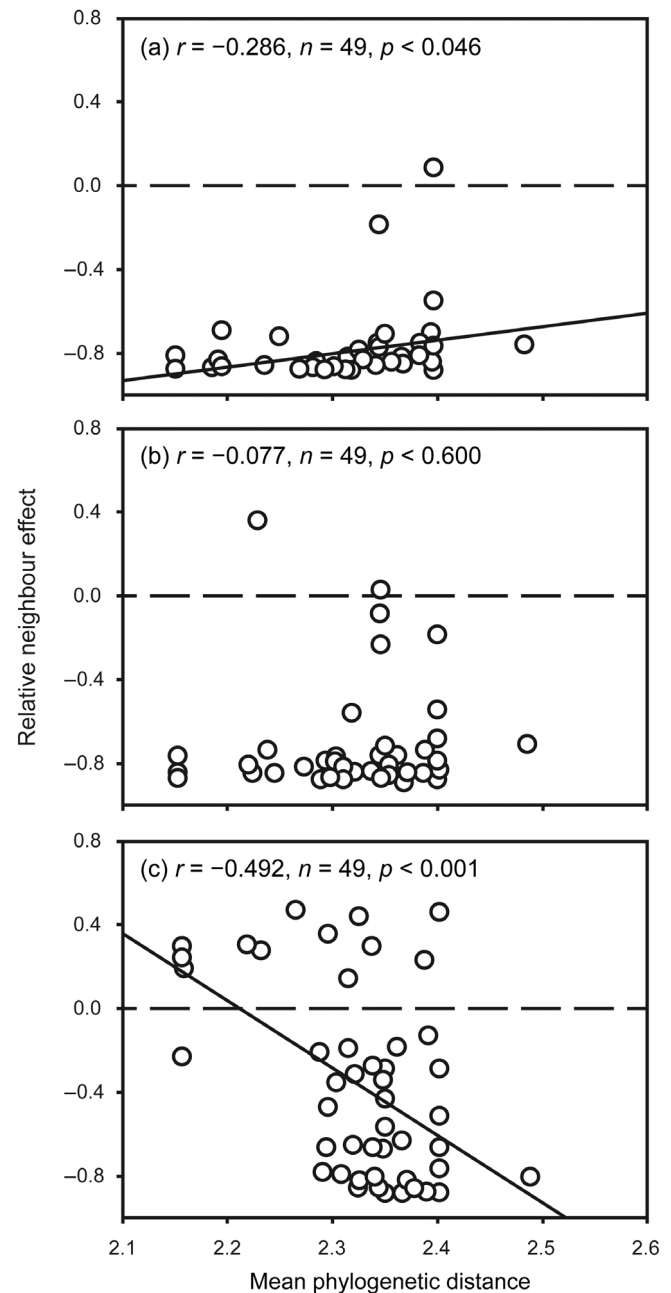


FIGURE 4 Relationships between relative neighbor effect on the invader and mean phylogenetic distance between the invader and native communities under (a) no, (b) moderate, or (c) intense drought. Small circles represent data from each community.

et al., 2012; Bukowski et al., 2018; Montesinos-Navarro et al., 2015). However, only under intense drought, AMF infection (i.e., colonization rate) had a positive effect on invader biomass (Figure 5i). In previous studies, AMF infection was also found to benefit host plants under drought stress, but these benefits disappeared in benign environments (Basyal & Emery, 2020; Duan et al., 2021; Jayne & Quigley, 2014). AMF could confer plants with a great tolerance to drought stress by increasing the

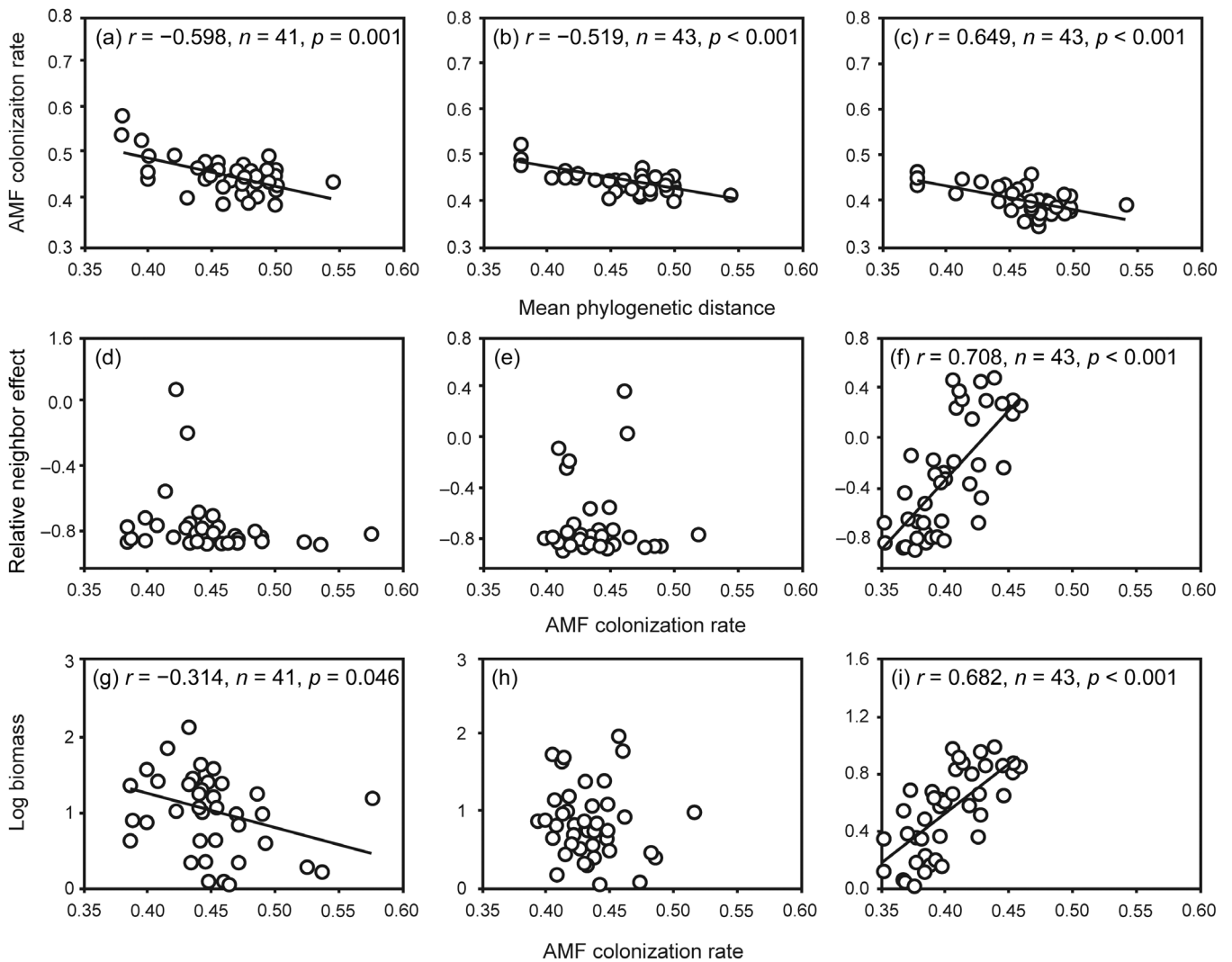


FIGURE 5 Relationships of arbuscular mycorrhizal fungi (AMF) colonization rate of the invader with mean phylogenetic distance between the invader and native communities, relative neighbor effect on the invader and invader biomass under (a, d, g) no, (b, e, h) moderate, or (c, f, i) intense drought. Small circles represent data from each community.

root-to-shoot ratio of plants (Basyal & Emery, 2020; Veresoglou et al., 2012), stimulating lateral root formation (Oláh et al., 2005), and increasing root length and root diameter (Hetrick et al., 1988; Zou et al., 2017). However, under no drought, AMF may provide no additional benefits to plants that are able to access water on their own under no drought (Basyal & Emery, 2020). This is because maintaining AMF colonization may lead to unnecessary carbon output (Duan et al., 2021; Johnson & Graham, 2013), which led to no significant and even negative effects of AMF on invader biomass. Consequently, closely related native species may share a similar AMF symbiosis with invaders (Montesinos-Navarro et al., 2012, 2015), and the effect of closely related native species on invaders may relate to the role of AMF. If AMF has a negative effect on invaders, such as that under no drought, then DNH will apply; if AMF has a

positive effect on invaders, such as that under intense drought, then PAH will apply.

Although our study clearly demonstrated that the effect of invader–native phylogenetic distance on invader performance depended on environmental stress, as the effect of closely related native species on the invader shifted from negative to positive with increasing drought, two points are worth noting. The potential effect of species richness should be considered for its positive effect on native community biomass (Appendix S1: Table S5, Figure S6), and its potential effects on exotic plant invasions should be considered. In this study, MPD and species richness had no close link before the drought treatments were applied ($r = -0.093$ to -0.031 for three drought intensities; $p > 0.05$). Moreover, at each species richness level, the effect of MPD on invader biomass exhibited similar changes (from positive to negative) with

increasing drought stress (Appendix S1: Figure S4). Therefore, the change of species richness did not influence the effect of MPD on exotic plant invasions in this study. The role of species identity in affecting invasions should also be considered. *A. migoana* is usually a dominant species of native communities in the area and also had great biomass in the experiment, and it is closely related to the invader. Compared with plant communities without *A. migoana*, the presence of *A. migoana* significantly affected the biomass of the invader (Figure 1) and the native communities (Appendix S1: Figure S7). The presence of *A. migoana* significantly decreased the invader biomass under no drought but significantly increased it under intense drought (Appendix S1: Figure S8). In contrast, *Cichorium intybus* is also a native species closely related to the invader, but had no great biomass. The presence of *C. intybus* had little effect on invader biomass (Appendix S1: Figure S9). Another interesting result was that the dominant species of each mixture had consistent biomass changes under all three drought treatments (Figure 3), indicating that dominant species may be important in the stability of communities in response to invasion and drought stress. Consequently, the phylogenetic distance of dominant species and their effect on invaders in response to increasing drought stress may potentially affect the relationship between MPD and invader biomass, which should be investigated in future studies.

Although we detected a significant interactive effect of drought and MPD on invader biomass (Table 1), other covariates such as soil organic matter, light, and soil microorganisms of native communities were not considered in this study. These factors may also covary with MPD and potentially affect exotic plant invasions (Karim & Nwadiuto, 2016; Renteria et al., 2021; Zhang & Suseela, 2021). Therefore, future studies should consider these factors to better explore the effect of phylogenetic distance on invasions. We also found that four closely related native species (*A. migoana*, *C. intybus*, *E. prostrate*, and *B. pilosa*; most germination happened before 20 March) and the invader *S. subulatum* (germination began on 24 March) germinated early in all drought treatments. Similar germination time may lead to competition at early growth stages, and how competition between young seedlings affects the effect of phylogenetic distance on invasions should be further explored.

Overall, our study demonstrated that the effect of phylogenetic distance on exotic plant invasions can change along a gradient of environmental stress such as drought, which is related to the change of species interactions. When competition plays a dominant role under no drought, the invader performed worse in their closely related native communities, supporting DNH. When facilitation plays a dominant role under intense drought,

the invader closely related to native communities had a higher biomass, supporting PAH. Our findings, therefore, provide a way to resolve DNC by considering the shift in species interaction along an environmental gradient. Our findings will provide important clues for invasion management. How native and exotic species interact at different invasion stages and what their roles are in phylogenetic distance effects on invasion success should be further investigated. In the future, higher temperatures associated with climate change are expected to lead to more frequent and severe drought conditions (Liu & Chen, 2021; Renne et al., 2019). With increased drought stress, interactions between native species and closely related invasive species may shift to facilitation and to promote invasions. These pieces of information will provide support to meet the future challenge of invasion pressure brought about by global change.

AUTHOR CONTRIBUTIONS

Jiang Wang and Fei-Hai Yu designed the experiment. Jiang Wang, Yuan Ge, Song Gao, and Tong Chen perform the experiment. Xiao-Yan Wang performed phylogenetic analyses. Jiang Wang, Shao-Peng Li, and Fei-Hai Yu conducted the data analysis. Jiang Wang and Shao-Peng Li wrote the first draft of the manuscript. Shao-Peng Li and Fei-Hai Yu contributed substantially to revision.

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CONFLICT OF INTEREST

Authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Wang et al., 2022) are available in Dryad at <https://doi.org/10.5061/dryad.05qftf4p>.

ORCID

Jiang Wang  <https://orcid.org/0000-0001-9269-0894>

Shao-Peng Li  <https://orcid.org/0000-0002-1730-3433>

Yuan Ge  <https://orcid.org/0000-0003-0234-5638>

Fei-Hai Yu  <https://orcid.org/0000-0001-5007-1745>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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