



Phylogenetic diversity is a better predictor of wetland community resistance to *Alternanthera philoxeroides* invasion than species richness

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Keywords

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ABSTRACT

- Highly biodiversity communities have been shown to better resist plant invasions through complementarity effects. Species richness (SR) is a widely used biodiversity metric but lacks explanatory power when there are only a few species. Communities with low SR can have a wide variety of phylogenetic diversities (PD), which might allow for a better prediction of invasibility.
- We assessed the effect of diversity reduction of a wetland community assemblage typical of the Beijing area on biotic resistance to invasion of the exotic weed *Alternanthera philoxeroides* and compared the reduction in SR and PD in predicting community invasibility.
- The eight studied resident species performed similarly when grown alone and when grown in eight-species communities together with the invasive *A. philoxeroides*. Variation partitioning showed that PD contributed more to variation in both *A. philoxeroides* traits and community indicators than SR. All *A. philoxeroides* traits and community indicators, except for evenness index, showed a linear relationship with PD. However, only stem length of *A. philoxeroides* differed between the one- and two-species treatments, and the diversity index of the communities differed between the one- and two-species treatments and between the one- and four-species treatments.
- Our results showed that in natural or semi-natural wetlands with relatively low SR, PD may be a better predictor of invasibility than SR. When designing management strategies for mitigating *A. philoxeroides* invasion, deliberately raising PD is expected to be more efficient than simply increasing species number.

INTRODUCTION

Habitat and diversity loss driven by invasive alien species pose a major threat to wetland communities (Zedler & Kercher, 2005; Ursino, 2010). A successful plant invader can suppress other species by competing strongly for nutrients, forming tall dense canopies that intercept light (Zedler & Kercher, 2005) and secreting allelopathic chemicals that limit the growth of other species (Lankau, 2012; Fabbro & Prati, 2014), with accompanying detrimental effects on ecosystem functioning and services (Hager, 2004; Barber *et al.*, 2017). However, generalized principles of habitat and community characteristics that determine the success of invasion remain unclear, especially genetic characteristics of the recipient community (Estoup *et al.*, 2016).

Plant communities differ markedly in their susceptibility to plant invaders because of numerous factors (Dukes, 2002; Smith *et al.*, 2015; Adomako *et al.*, 2019). Among these, biodiversity plays an important role involving the stability, productivity, trophic structure and species composition of a community (Tilman, 1999). Diverse communities can resist invasion partly due to complementarity effects that enable

plants to occupy more niche space, produce more biomass and use more resources (Fargione & Tilman, 2010). Various biodiversity metrics have been studied as potential predictors of invasibility, including species diversity (species richness) (Henriksson *et al.*, 2016), functional group diversity (Pokorný *et al.*, 2010) and phylogenetic diversity (Ketola *et al.*, 2017).

Species richness (SR) is the most widely used measure of diversity, as relationships between species richness and diversity are simple, positive and strong (Stirling & Wilsey, 2001). However, biodiversity can vary independently of SR in some cases (Stirling & Wilsey, 2001; Rychtecká *et al.*, 2014; Wang & Yu, 2018), because SR reflects only one aspect of biodiversity, and not all species are evolutionary equivalents (Whitfield *et al.*, 2014). There has been increasing evidence that biodiversity is better represented by the diversity of functional traits, niches and ecological interactions (Srivastava *et al.*, 2012). Based on the theory of niche complementarity, functional trait distinctiveness and evolutionary distinctiveness have been recently used as proxies to quantify species ecological roles (Pigot *et al.*, 2016). It has been proposed that phylogenetic distance can be related to fitness and niche differences (Cadotte

et al., 2012). For instance, alien species that are phylogenetically distant from a local community might more easily establish themselves in the community (Zheng *et al.*, 2018), and phylogenetically similar tree species could suffer from phylogenetically related parasites that make the area near a tree inhospitable for seedlings of closely related species (Liu *et al.*, 2012). This potentially powerful phylogenetic approach, however, has been intensively debated and criticized because the underlying assumptions are only weakly supported (Gerhold *et al.*, 2015; Pigot & Etienne, 2015). Contrasting evidence has been found on one of the fundamental assumptions, niche conservatism, that highlights the importance of considering appropriate niche breadth and comparing alternative evolutionary models (Münkemüller *et al.*, 2015; Olalla-Tárraga *et al.*, 2017). Therefore, the relationship between phylogenetic distance and community invasibility may depend on the mode of interspecific interactions and the resulting evolutionary trajectory of the recipient community (Jones *et al.* (2013)).

Despite these concerns, experimental evidence for the relationship between phylogenetic distance and invasion success remains relatively scarce. The phylogenetic approach might have value as a predictor of biological invasions. Among various phylogenetic measures of biodiversity, phylogenetic diversity (PD), which was originally defined by Faith (1992) as the total amount of phylogenetic distance among species in a community, is intuitive, relatively easy to calculate and similar to biodiversity metrics from the biomass allocation perspective. Mixed evidence has been reported on the relative importance of SR and PD for resistance to plant invasions in forests and grasslands. Significant negative relationships have been found between SR and invasibility (Oakley & Knox, 2013), as well as for PD and invasions (Whitfeld *et al.*, 2014; Bennett *et al.*, 2015; Selvi *et al.*, 2016). Studies of the effect of SR of grassland invasions have generally used communities composed of two to more than 30 species in both field surveys and controlled experiments (Flory & Clay, 2010; Venail *et al.*, 2015; Abernathy *et al.*, 2016). Little explanatory power of SR has been found in communities where SR is low, especially in wetlands, where SR is often <12 species (Lei *et al.*, 2006). However, these communities can have a wide variety of PD, resulting from the differentiation among species (Venail *et al.*, 2015; Wu *et al.*, 2017), which might allow for better prediction of the invasibility of such communities.

Here, we experimentally used artificial species assemblages of typical species-poor wetland communities in the Beijing area, together with a species reduction experiment to assess the relative importance of SR and PD in predicting biotic resistance to the invasion of *Alternanthera philoxeroides*. Specifically, we addressed the following questions: (i) do the selected species of the recipient community differ in performance under controlled conditions when grown alone and in mixture together with the plant invader; (ii) how do SR and PD of the recipient community affect the performance of *A. philoxeroides*; and (iii) does SR or PD more strongly affect the resistance to *A. philoxeroides* of the resident community?

MATERIAL AND METHODS

Study species

Alternanthera philoxeroides (Mart.) Griseb. is an invasive, herbaceous, perennial, semi-aquatic weed native to South

America (Xu *et al.*, 2010; Dong *et al.*, 2019b). The species reproduces both sexually and asexually. It rarely sets seed outside of its native range, and those seeds produced are often sterile, but each single stem node can serve as a vegetative propagule. Thus, it mainly spreads by clonal growth (Dong *et al.*, 2011). *Alternanthera philoxeroides* can grow in both aquatic and terrestrial habitats (Gunasekera *et al.*, 2001). The prostrate stems can develop leaves, side branches and roots at each node, and thus generate ramets that extend across bodies of water (Qin *et al.*, 2018). When introduced to a new area, its strong propagation ability propels its spread (Wang *et al.*, 2008). Across China, the species is frequent in both natural and semi-natural wetlands. Eradication of existing populations has been reported to be effective, but may be inadequate in the long term (Perry *et al.*, 2004). Clonal integration has been shown to increase its growth in both aquatic and terrestrial habitats (Wang *et al.*, 2008; Luo *et al.*, 2014). Physical and chemical methods often create disturbances that can, in turn, promote the growth of *A. philoxeroides* (Schooler *et al.*, 2008). The species also shows higher tolerance to waterlogging and higher photosynthetic capacity than its native congener *A. sessilis*, which may promote its invasion into wetlands (Chen *et al.*, 2013).

Plant sample collection

In early May 2013, we collected ramets of *A. philoxeroides* from six different sites in Xixi National Wetland Park in Hangzhou, Zhejiang Province, China. We assumed that ramets belonged to a single clone based on the relatively low genetic diversity of *A. philoxeroides* in southern China (Pan *et al.*, 2007). About 120 ramets were brought to a greenhouse at the Forest Science Co, Ltd., Beijing Forestry University, Beijing, China, and propagated vegetatively, growing from 10 cm to about 100 cm in 40 days. The soil used for propagation was a 1:1 mixture of sand and peat.

The recipient plant communities were composed of eight common wetland species that often co-occur in natural and semi-natural wetlands in the Beijing area, China (Wang *et al.*, 2004): *Acorus calamus*, *Iris wilsonii*, *Butomus umbellatus*, *Pontederia cordata*, *Lythrum salicaria*, *Sagittaria trifolia*, *Typha minima* and *Polygonum lapathifolium* (see Table 1 for details). Among them, *Pontederia cordata* is native to North America and was introduced to China as an ornamental plant and to improve water quality. There is no evidence that *Pontederia cordata* is invasive in China (www.efloras.org). All eight species, hereafter referred to as residents, can form a shallow, dense network of rhizomes (Hroudova *et al.*, 1996; Vojtiskova *et al.*, 2004; Lu & Huang, 2012). *Polygonum lapathifolium* individuals were collected from the north bank of Miyun Water Reservoir, Miyun County, Beijing, China, in June 2013. The other seven species were purchased from Tianbei Landscape Co. Ltd., Beijing. All plants were propagated in a greenhouse located on the north bank of Miyun Water Reservoir. The experimental site is in the north temperate zone.

Experimental design

We divided the experiment into two parts with 48 containers in total. Each container had 16 resident individuals and four *A. philoxeroides* individuals. All individuals were placed

Table 1. List of the eight resident species with status, height range and habitat information in China.

Plant species name	Status	Height range (cm)	Habitat
<i>Lythrum salicaria</i> Linn.	Native	30–150	Damp grasslands, banks
<i>Typha minima</i> Funk	Native	16–65	Shallow water of ponds and rivers
<i>Sagittaria trifolia</i> Linn.	Native	50–150	Ponds, lakes, marshes, paddy fields and channels
<i>Polygonum lapathifolium</i> Linn.	Native	40–90	Roadsides, along ditches, field margins, watersides
<i>Iris wilsonii</i> C. H. Wright	Native	45–70	Forest margins, hillsides, meadows, damp riversides
<i>Acorus calamus</i> Linn.	Native	60–150	Swamps, pond sides, standing water
<i>Butomus umbellatus</i> Linn.	Native	30–120	Still or slow-moving water of lakes, ponds and channels
<i>Pontederia cordata</i> Linn.	Introduced, non-invasive	80–150	Moist riparian habitats

Habitat information is based on the *Flora of China* (www.efloras.org).

according to the experimental design shown in Fig. 1, and their positions in each container were randomized, except for those of *A. philoxeroides*.

In part 1, we compared two different plant species diversity arrangements. We established a mixture of all eight resident species (two individuals of each of the eight species) in the presence of *A. philoxeroides* (four individuals), with eight replicates. We further established eight different two-species combinations by growing one resident species (16 individuals) in the presence of four individuals of *A. philoxeroides*. Each combination had three replicates.

In part 2, we grew four individuals of each of four randomly selected resident species or two individuals of each of two random resident species with four individuals of *A. philoxeroides*. Each treatment had eight replicates. We then used the combined one-resident species treatments from part 1 with the treatments from part 2 to form a diversity reduction line (Fig. 1).

On 6 June 2013, the axillary stems produced from each node of *A. philoxeroides* were about 20-cm long. We pruned 192 stems of similar diameter and a length of 20 cm from shoot tips of propagated *A. philoxeroides* plants and then transplanted healthy, intact individuals of all nine species into 48 opaque plastic containers (50-cm surface diameter and 100-cm depth), filled with soil to a depth of 30 cm and flooded with water to a depth of 10 cm. We simulated the water level found in areas where the plants naturally occur. The containers were placed in an open field and exposed to full sunlight and ambient temperature and precipitation. The soil was collected from the north bank of Miyun Water Reservoir (40.548° N, 117.012° E, Beijing, China) and sieved through a 4 mm mesh. The soil had an

organic carbon content of 5.681 ± 1.674 (mean \pm SE) $\text{g} \cdot \text{kg}^{-1}$, a total nitrogen content of 1.213 ± 0.012 $\text{g} \cdot \text{kg}^{-1}$, a total phosphorus content of 1.269 ± 0.015 $\text{g} \cdot \text{kg}^{-1}$ and pH of 7.9 ± 0.04 .

The resident species differed in initial size at the planting stage, which ranged from 0.3 g per individual in *Polygonum lapathifolium* to 2.7 g in *I. wilsonii*. However, the initial sizes of the individuals of a given species were similar across treatments. During the experiment, we monitored plant growth, maintained constant water level and regularly weeded the containers. Dead plants were replaced over a 7-day colonization period after transplanting. Containers were arranged randomly and rearranged monthly (twice in total) to avoid environmental heterogeneity. The mean temperature was 24.5°C and mean air humidity was 79.2% during the experimental period.

Harvest and measurements

We harvested plants in all containers on 6 September 2013. For surviving *A. philoxeroides* plants, we measured the number of ramets, number of nodes, number of leaves, leaf area and total stem length of each individual. Plants were separated into leaves, stems and roots, dried at 80°C for at least 72 h and weighed. For the resident species, we measured plant height and number of surviving individuals, separated each individual into shoots and roots, dried these at 80°C for at least 72 h and weighed them. Leaf area was measured with WinFOLIA Pro 2004a (Regent Instruments, Québec, Canada). Specific leaf area (SLA) was calculated as leaf area/leaf dry mass, and root/shoot ratio was calculated as belowground biomass/aboveground biomass.

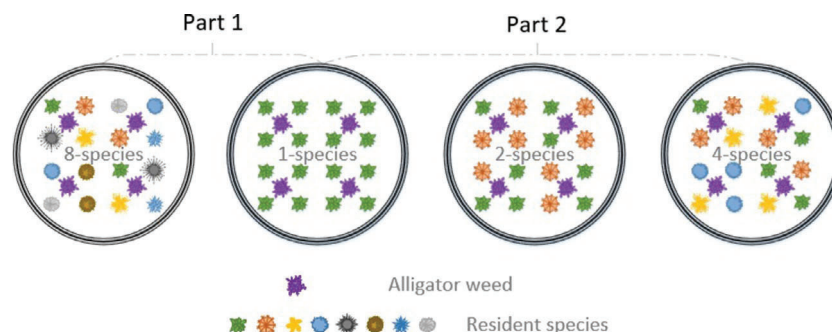


Fig. 1. Experimental design and plant arrangement. Part 1 had two diversity levels, both with four individuals of *Alternanthera philoxeroides*: (1) a mixture of all eight resident species (two individuals of each species) and (2) eight different treatments each with 16 individuals of one resident species. In part 2, we repeatedly drew four species and two species randomly from the eight-species pool of residents to establish four- and two-species recipient communities (containing four and eight individuals of each resident species, respectively) that were grown with four individuals of *A. philoxeroides*. One-species communities in part 1 were also included in analysis of part 2.

Molecular phylogeny

We estimated a phylogenetic tree of nine species, including the eight resident species used in the experiment and one outgroup, *Amborella trichopoda*, as the tree root (Byng *et al.*, 2016; Zheng *et al.*, 2018). For each species, we searched the NCBI nucleotide database for publicly available genetic data of *matK*, which is a plastid gene commonly used in angiosperm phylogeny (Harrington *et al.*, 2005). To represent the species with no available data (*I. wilsonii* and *T. minima*), we randomly picked two congeneric species (*Iris sanguinea* and *Typha latifolia*). Given the phylogenetic scale of the study, this was unlikely to influence the results (Zheng *et al.*, 2018). Accession numbers of the sequences used are provided in Table S1.

We conducted multiple sequence alignment on the *matK* gene using MAFFT (Kazutaka & Standley, 2013), trimmed gap columns and outlier sequences using TRIMAL (Capellagutiérrez *et al.*, 2009), performed substitution model selection using MEGA (Tamura *et al.*, 2007) and estimated a maximum likelihood phylogeny in RAXML (Stamatakis, 2006) by using a GTR + gamma model of evolution together with 1000 bootstrap replicates to gauge nodal support. Once the phylogenetic tree was completed, we re-rooted the tree to *A. trichopoda* using APE (Paradis *et al.*, 2017).

Our phylogenetic tree had the same topology as APG IV except for the clade including Asparagales (*Iris sanguinea*), Commelinales (*Pontederia cordata*) and Poales (*Typha latifolia*). Five nodes were supported by >95% bootstrap values (with three nodes 100%), one node (which was the inconsistent clade mentioned above) was supported by an 84% bootstrap value, indicating relative uncertainty in this node (see Figure S1 for details). We calculated PD and mean pairwise distance (MPD) using Picante (Kembel *et al.*, 2013) from the tree we had built and the species presence-absence data at the beginning of the experiment. The phylogenetic tree is provided in Figure S1.

Statistics

For part 1, we calculated Spearman's rank correlation coefficient, which by definition assesses how well the relationship between two variables can be described using a monotonic function, for biomass per species and root/shoot ratio of the resident species in eight-species and one-species communities. We also performed permutational multivariate analysis of variance (PERMANOVA) between one-species recipient communities and eight-species mixtures in each resident species for biomass production and root/shoot ratio, and pairwise PERMANOVA among eight one-species recipient communities and eight-species mixtures of biomass production and root/shoot ratio in *A. philoxeroides*. For part 2, we calculated a Shannon-Wiener diversity index based on dry mass of each species, using the formula $H = -\sum P_i \ln(P_i)$ ($i = 1, 2, 3 \dots, S$), in which S is the species number of the community and P_i is the biomass of species i divided by the summed biomass of all species in the community (Whittaker, 1972). We then calculated the Pielou evenness index E based on the diversity index, using $E = H/\ln(S)$ (Sheldon, 1969). To measure the community-level competitive effects of *A. philoxeroides*, we calculated the relative dominance index (RDI) of *A. philoxeroides*, where $RDI = \text{biomass of } A. philoxeroides / \text{total biomass of all plants in the invaded community}$ (Zhang *et al.*, 2017). We ran general linear mixed effect

models (GLMM) using PD as a fixed effect, species combinations as a random effect and *A. philoxeroides* traits (total mass, root mass, stem mass, leaf mass, stem length, number of nodes, SLA and number of leaves) and community indicators (diversity index, evenness index, RDI and total biomass of the resident species) as response variables. We considered SR to be a discrete variable with three levels and thus performed pairwise PERMANOVA to test effects of different SR levels (one, two and four) on *A. philoxeroides* traits and community indicators, respectively. We also performed variation partitioning analysis using standardized response variable matrices of *A. philoxeroides* growth traits and community indicators to quantify the contribution of SR and PD to data variation. Shapiro-Wilk normality tests were used to verify the normality of residuals of all linear models; no violation of assumptions was found. The P -values for multiple comparisons were adjusted using the 'fdr' method (Benjamini & Hochberg, 1995). Data analyses were conducted with vegan, tidyverse, MASS, lme4 and ggpmisc in R (R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Performance of the resident species (Part 1)

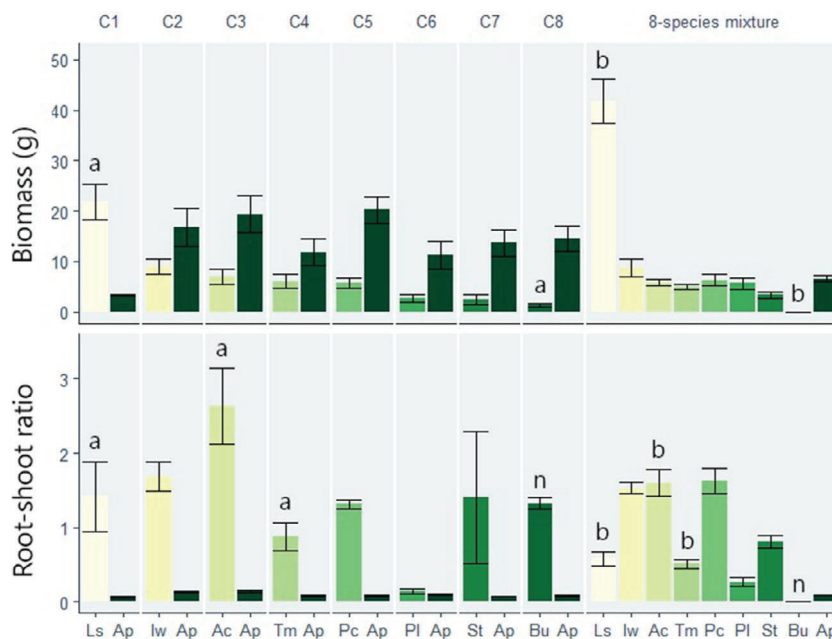
Biomass of *L. salicaria*, *B. umbellatus* and *A. philoxeroides* differed significantly between the one-species and eight-species communities (*L. salicaria*, $df = 1, 9$, $P = 0.030$; *B. umbellatus*, $df = 1, 9$, $P < 0.001$; *A. philoxeroides*, $df = 1, 30$, $P < 0.001$). *Lythrum salicaria* biomass in the one-species communities was significantly less than in the eight-species communities, whereas biomass of *B. umbellatus* was higher. No difference in biomass between one- and eight-species communities was found in any of the other six resident species. The rank correlation of the biomass per species in the one-species and eight-species recipient communities was highly significant ($\rho = 0.881$, $P = 0.007$). Root/shoot ratio of *L. salicaria*, *Acorus calamus* and *T. minima* differed between the one-species and eight-species communities ($df = 1, 9$ for all treatments; *L. salicaria*, $P = 0.024$; *Acorus calamus*, $P = 0.031$; *T. minima*, $P = 0.038$), but root/shoot ratio of other resident species did not. The rank correlation of the root/shoot ratio in the one-species and eight-species recipient communities was not significant ($\rho = 0.607$, $P = 0.167$; Fig. 2).

Detailed results of pairwise PERMANOVA of *A. philoxeroides* are given in Table S2. All one-species resident communities, except for that with *L. salicaria*, had higher mean *A. philoxeroides* biomass than the eight-species communities (Fig. 2, Table S2).

Performance of SR and PD in predicting invasion susceptibility (Part 2)

The SR and PD had a strong linear relationship (Fig. 3C), but PD explained more variation in the growth traits of *A. philoxeroides* (Fig. 3A; for pure effects of PD: $R^2 = 0.22$; for pure effects of SR: $R^2 = 0.05$; for unexplained effects: residuals = 0.75; shared effects are not shown because the value is < 0) and in community indicators (Fig. 3B; for pure effects of PD: $R^2 = 0.17$; for pure effects of SR: $R^2 = 0.07$; for unexplained effects: residuals = 0.79; shared effects are not shown because the value is < 0). All *A. philoxeroides* traits showed a linear relationship with PD (Fig. 4; total mass, $R^2 = 0.25$,

Fig. 2. Comparison of biomass per individual of each resident species when grown in one-species and in the eight-species mixtures, all with *Alternanthera philoxeroides* (upper panel). Comparison of root/shoot ratio of each resident species when in one-species and in the eight-species mixtures (lower panel) with *A. philoxeroides*. Ls = *Lythrum salicaria*, lw = *Iris wilsonii*, Ac = *Acorus calamus*, Tm = *Typha minima*, Pc = *Pontederia cordata*, Pl = *Polygonum lapathifolium*, St = *Sagittaria trifolia*, Bu = *Butomus umbellatus* and Ap = *A. philoxeroides*. Letters above bars indicate results of pairwise PERMANOVA tests on each resident species between one-species and eight-species mixtures. For bars of the same species, letters 'a' and 'b' indicate a significant difference between one-species recipient community and eight-species mixture; 'n' indicates not available. Data are mean \pm SE ($n = 3$ in one-species communities, and $n = 6$ in eight-species mixtures).



$P = 0.001$; root mass, $R^2 = 0.28$, $P = 0.001$; stem mass, $R^2 = 0.24$, $P = 0.001$; leaf mass, $R^2 = 0.18$, $P = 0.006$; stem length, $R^2 = 0.17$, $P = 0.008$; number of nodes, $R^2 = 0.14$, $P = 0.019$; SLA, $R^2 = 0.24$, $P = 0.001$; number of leaves, $R^2 = 0.10$, $P = 0.044$). The relationship was positive for SLA (Fig. 4G) and negative for all other traits (Fig. 4A–F, H). The

PD generally explained a relatively low proportion of variance, indicating that other unknown processes might also play a role. Diversity index and total biomass of the resident species showed a positive relationship with PD (diversity index, $R^2 = 0.14$, $P = 0.017$; total biomass, $R^2 = 0.19$, $P = 0.006$; Fig. 5A and D), while RDI of *A. philoxeroides* showed a

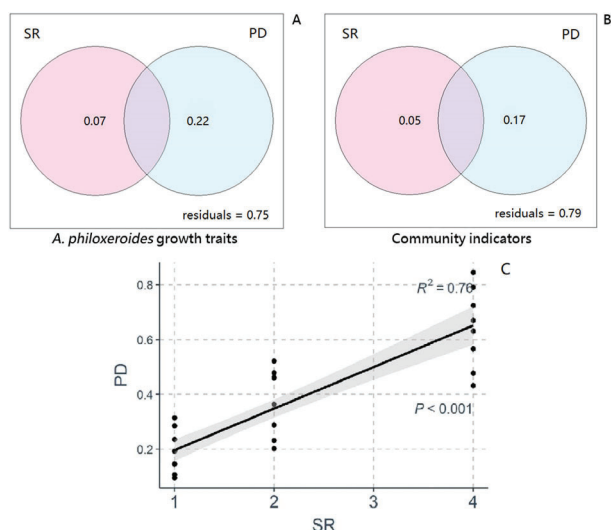


Fig. 3. Variation partitioning showing the contribution of species richness (SR) and phylogenetic diversity (PD), respectively, to variation in *Alternanthera philoxeroides* growth traits and community indicators. A: *A. philoxeroides* growth traits. B: Community indicators. C: Linear correlation between SR and PD among all communities. Pink circles represent SR and light blue circles represent PD in both panels. Values in the centre of the circles are proportion of variation in response matrices explained by the explanatory variables. Bounding rectangles are total variation and the shared partitions are variation explained by both SR and PD. Values that < 0 are not shown in the figure.

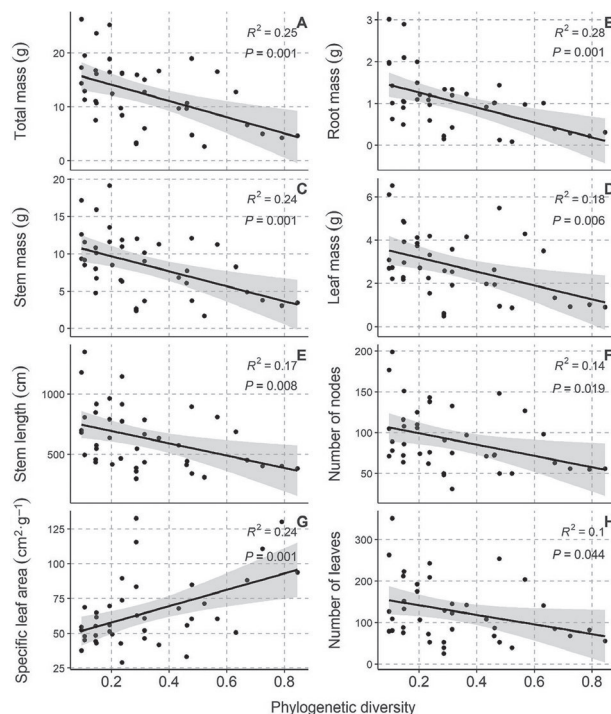


Fig. 4. Linear relationships of phylogenetic diversity with (A–D) biomass, (E) stem length, (F) number of nodes, (G) specific leaf area and (H) number of leaves of *Alternanthera philoxeroides*, with species combination as a random effect.

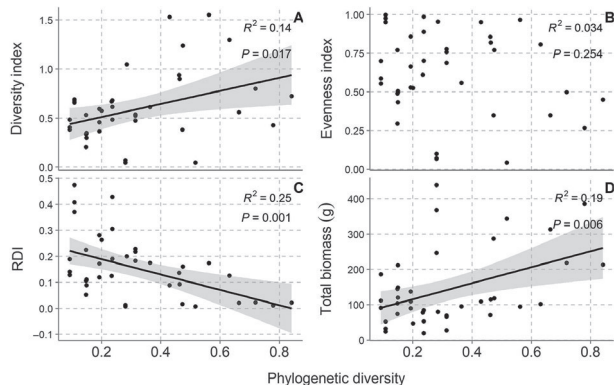


Fig. 5. Linear relationships of phylogenetic diversity with (A) Shannon-Wiener diversity index, (B) Pielou evenness index, (C) relative dominance index (RDI) and (D) total biomass of the communities, with species combination as a random effect.

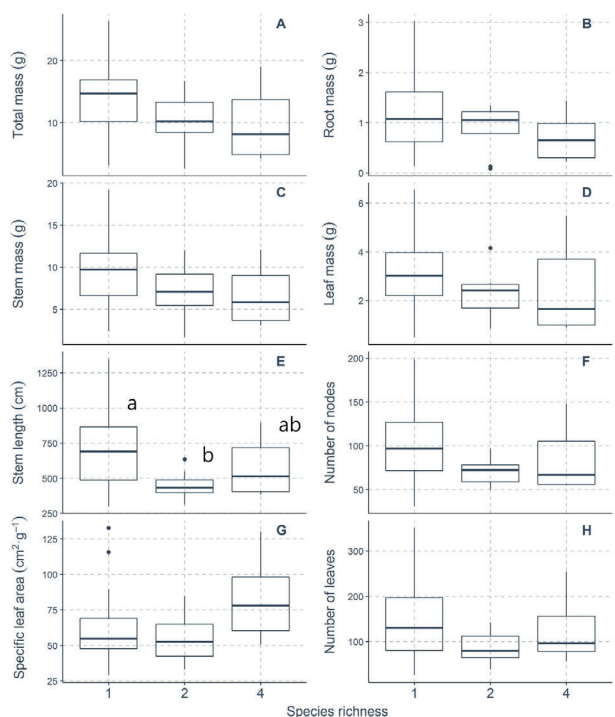


Fig. 6. Effects of species richness on (A-D) biomass, (E) stem length, (F) number of nodes, (G) Specific leaf area and (H) number of leaves of *Alternanthera philoxeroides*. Different lowercase letters indicate significant difference.

negative relationship with PD ($R^2 = 0.25$, $P = 0.001$; Fig. 5C), and the evenness index showed no relationship ($R^2 = 0.03$, $P = 0.254$; Fig. 5B).

Analysis of effects of SR on *A. philoxeroides* traits showed that only stem length differed between the richness levels, with stem length being significantly smaller in the two-species than in the one-species communities (Fig. 6, Table S3 for details). Also, only the diversity index differed between the one- and two-species communities and between the one- and four-species communities (Fig. 7, Table S4 for details).

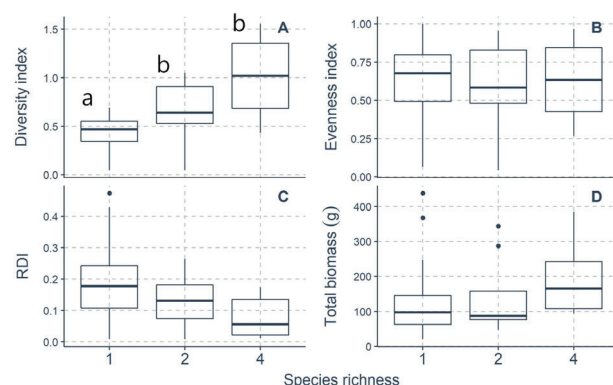


Fig. 7. Effects of species richness on (A) Shannon-Wiener diversity index, (B) Pielou evenness index, (C) relative dominance index (RDI) and (D) total biomass of the communities. Different lowercase letters indicate significant difference. Bars with different letter a and b between SR level 1, 2 and 4 indicates significant difference in diversity index.

DISCUSSION

Species performance at different SR levels

Biomass production reflects not only resource use efficiency but also resource availability, and both are associated with the plant diversity of a community through species complementarity (Cardinale *et al.*, 2007). Accordingly, as found in part 1 described above, rank performance of the resident species as measured by biomass was similar at different SR levels (see Fig. 2). This result indicates that resource competition was the major driver, because we did not observe an obvious effect of species combination that might change the biomass ranks. Since resource availability was identical and limited in all pots in the experiment, and the density of invaders was also identical, the biomasses of the resident species reflect their resource use and competition status in trait space (Bitttebiere *et al.*, 2019). *Lythrum salicaria* was found to be the strongest competitor when grown with the plant invader, as shown by doubled (92% higher) individual biomass in the mixtures (under interspecific competition) as compared to combinations with *A. philoxeroides* (under intraspecific competition). *Alternanthera philoxeroides* individual biomass in the mixtures was significantly higher than that in combinations with *L. salicaria*, but significantly lower than that in other combinations with one resident species (Fig. 2, Tables S2, S3). Thus, both complementarity effect and interspecific competition affected *A. philoxeroides* growth performance.

Plants tend to allocate more resources to roots in nutrient-poor environments, and therefore retain a higher proportion of biomass in roots rather than shoots (Pérez-Harguindeguy *et al.*, 2013; Wang *et al.*, 2019; Dong *et al.*, 2019c). However, root allocation can be highly plastic under different conditions (Gedroc *et al.*, 1996; Portela *et al.*, 2019), such as under drought stress (Xu *et al.*, 2015) or when fertilized (Wang *et al.*, 2013; Dong *et al.*, 2019a). In our experiment, rank correlations of the root/shoot ratio of the resident species were not significant between the different SR levels. Instead, three of the eight resident species decreased their root/shoot ratio significantly (Fig. 2). These

resident species may have benefited from augmented resource use efficiency and resource availability through complementarity effects from roots.

Augmentation of PD can suppress *A. philoxeroides* invasion

The management of invasive plants is a challenging task in restoration practices. The use of herbicides for invasive weed control in grasslands can have harmful consequences, such as water pollution, especially in wetlands (Kettenring & Adams, 2011). Invasive weeds are often observed to outcompete native species through resource depletion, impacting the diversity and stability of the resident communities (Michelan *et al.*, 2010; Wang *et al.*, 2017; Wang *et al.*, 2019). A recent study showed that aquatic communities appear to be more vulnerable to invasions by *A. philoxeroides* than terrestrial habitats, likely due to low native species diversity in the former (Wu *et al.*, 2017). Although Oakley & Knox (2013) reported a negative effect on plant invaders of increasing SR in grassland communities, Grace *et al.* (2017) found that SR had little effect on biotic resistance to invasion. Generally, invasion–diversity relationships are complex and can vary among conditions, such as habitat types (Jan *et al.*, 2010).

Our results support a positive relationship between diversity and resistance to invasion using PD, but not when using SR, likely because PD explained more variation in both the traits of *A. philoxeroides* and the community indicators than SR (Fig. 3). When PD increased, biomass of all parts of *A. philoxeroides* (total mass, root mass, stem mass and leaf mass) significantly decreased (Fig. 4); however, similar effects were not found when SR increased. As discussed above, a reduction in biomass production reflects suppression by PD of *A. philoxeroides* growth performance. Moreover, highly plastic traits, such as stem length, number of nodes and number of leaves of the invader, also had significant negative relationships with PD. Harsh habitats can reduce stem growth in *A. philoxeroides* (Pan *et al.*, 2006). Furthermore, the production of nodes is necessary for the dispersal and development of *A. philoxeroides* ramets (Erwin *et al.*, 2013). These findings suggest that the development of *A. philoxeroides* in our experiment is indeed constrained by PD. The SLA of *A. philoxeroides* had a significant positive relationship with PD (Fig. 4G). In our experiment, the increase in SLA can be interpreted as the result of narrowed niche spaces available for *A. philoxeroides*, as species that live in shaded and resource-limited places tend to have high SLA (Pérez-Harguindeguy *et al.*, 2013).

Previous studies posit that communities with larger SR can exploit larger amounts of resources, subsequently promoting the community's biomass accumulation and resistance to invasion (Kennedy *et al.*, 2002; Reich *et al.*, 2004). A positive relationship between biodiversity and biotic resistance has also been documented in more recent studies (Scherber *et al.*, 2010; Cardinale *et al.*, 2012). Although studies focusing on the PD–invasion relationship are still relatively scarce, we can also hypothesize that communities with higher SR tend to have higher PD due to the strong correlation between SR and PD (Venail *et al.*, 2015), occupying more complementarity niches and therefore better resisting plant invaders. In our study, total biomass of the resident species had a positive relationship with PD (see Fig. 5A and D), which is in line with previous studies (Whitfield *et al.*, 2014; Bennett *et al.*, 2015; Selvi *et al.*, 2016).

Augmentation of PD possibly improved resource use by the resident species and therefore biomass production. This explanation is supported by the observed negative relationship between RDI and PD. Significant negative relationships were also found between *A. philoxeroides* growth traits (except for SLA) and MPD of the resident species, which reflect phylogenetic structure of the resident communities, and *A. philoxeroides* performed worse in the communities with phylogenetic overdispersion (Figure S2). If niche conservatism obtains, phylogenetic overdispersion of the resident species may result in wider occupation of niche space, thus leaving less space for the invader.

In the field, *A. philoxeroides* spreads mainly through clonal growth, and its genetic diversity is very low across China (Pan *et al.*, 2007). Since niche conservatism can occur intraspecifically in the spread of invasive species (Wiens *et al.*, 2010), we infer that revegetation with resident species may effectively control *A. philoxeroides*, at least on a small scale of implementation. This may also apply to invasive weeds similar to *A. philoxeroides*.

CONCLUSIONS

We conclude that in natural or semi-natural wetlands with relatively low SR, PD is a better predictor of invasibility than SR. This fact should be considered when establishing and managing plant communities to resist invasions by invasive alien plants.

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SUPPORTING INFORMATION

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

Table S1. Accession numbers of sequences used.

Table S2. Letter-based representation of the results of pairwise PERMANOVA of *Alternanthera philoxeroides*.

Table S3. Results of pairwise PERMANOVA for effects of SR levels on *Alternanthera philoxeroides* growth traits.

Table S4. Results of pairwise PERMANOVA for effects of SR levels on community indicators.

Figure S1. Phylogenetic relationship among the resident species using molecular phylogenetic analysis by Maximum Likelihood method.

Figure S2. Linear relationships between MPD and *Alternanthera philoxeroides* growth traits, with species combination as a random effect.

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