Species diversity and environmental determinants of aquatic and terrestrial communities invaded by *Alternanthera philoxeroides*

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HIGHLIGHTS

- Species diversity of *Alternanthera philoxeroides* communities in terrestrial habitats was greater than aquatic habitats.
- Aquatic plant communities were more vulnerable to the *A. philoxeroides* invasion than terrestrial plant communities.
- The major determinants of terrestrial *A. philoxeroides* invasion were nitrogen, precipitation, temperature and latitude.
- The major determinants of aquatic *A. philoxeroides* invasion were longitude, ammonia and precipitation.

GRAPHICAL ABSTRACT

ABSTRACT

The impact of invasive species on native biodiversity varies across environments, with invasion effects of amphibious plant species across terrestrial and aquatic systems especially poorly understood. In this study, we established 29 terrestrial plots and 23 aquatic plots which were invaded by the alien plant alligator weed, *Alternanthera philoxeroides* in Southern China. We measured α-species diversity (Shannon-Wiener and Simpson index), species richness and evenness, species cover and the importance value (a comprehensive index of cover, height and abundance) of *A. philoxeroides* in invaded communities in both aquatic and terrestrial habitats. We recorded seven environmental factors (longitude, latitude, elevation above sea level, temperature, precipitation, ammonia and nitrate) across habitats. We then used Redundancy Analysis (RDA) to determine which factors best explain *A. philoxeroides* invasion in either environment type. We found that terrestrial habitats had greater species diversity (Shannon index) than aquatic habitats, and the biotic resistance of aquatic plant communities to the *A. philoxeroides* invasion was weaker than terrestrial plant communities. Accumulated ammonia improved some indices of species diversity (Shannon-Weiner, Simpson) and evenness, but decreased species cover of *A. philoxeroides* in both aquatic and terrestrial environments. Precipitation increased species richness in terrestrial habitats but decreased richness in aquatic habitats. Precipitation increased *A. philoxeroides* cover in both environment types, while elevated nitrate increased *A. philoxeroides* cover in terrestrial habitats only. In aquatic habitats, species richness increased but *A. philoxeroides* cover decreased with increasing longitude. Our study indicates that increased precipitation may accelerate *A. philoxeroides* spread across aquatic and terrestrial habitats, while reducing nitrate inputs could inhibit terrestrial *A. philoxeroides* invasion. Aquatic communities appear to be

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more vulnerable to invasion by *A. philoxeroides* than terrestrial communities, likely due to low native species diversity. We need to intensify invasion assessment of water ecosystems in lower longitudinal regions of China and elsewhere where diversity is low.

1. Introduction

Biological invasions by alien species critically threaten ecosystem functioning and global species diversity (Ding et al., 2008; Hulvey and Zavaleta, 2012). Environmental heterogeneity has been identified as an important factor determining species richness and community structure (Gonzalez-Megias et al., 2007; Warren et al., 2014), and the invasion dynamics of alien species can also vary depending on the environment. For instance, in Western France, the biomass of some amphibious exotic plants (*Ludwigia* spp.) is lower in aquatic habitats than in terrestrial habitats, as the higher organic matter of terrestrial environments can create dense populations and larger amounts of roots (Haury et al., 2014). Amphibious plant removal may also be more difficult in terrestrial sites where plants can root in soil, versus aquatic sites where large portions of biomass are floating and unrooted (Lambert et al., 2010). However, climate change-associated increases in CO_2 and temperature are predicted to have a disproportionately negative impact on native aquatic species (versus invasive aquatic species or native or invasive terrestrial species), which could leave these systems open to increased invasion (Sorte et al., 2013). Moreover, the process of biological invasion and its ecological impact on native biodiversity may be restricted or enhanced by habitat heterogeneity (Pan et al., 2006; Richardson et al., 2012). This is because both regional scale differences (soil nutrients, temperature, precipitation, etc.) and landscape scale differences (latitude, elevation above sea level, etc.) in environmental variables may affect distributions and diffusions of species (Williams-Linera and Lorea, 2009; Qian and Ricklefs, 2011).

Geographical differences caused by latitudinal gradient variation can significantly affect the invasiveness and ecological effect of exotic species. Some alien grasses were found to restrain seedling germination of native plants and threaten species diversity at higher, more stressful latitudes in the western USA, however, at lower latitudes these species facilitated the establishment of native plant populations (Richardson et al., 2012). Likewise, Molina-Montenegro and Naya (2012) found greater phenotypic plasticity of the invasive *Taraxacum officinale* (such as photosynthesis, biomass, foliar angles, etc.) at higher latitudes in South America. Although higher latitudes with lower mean annual temperature may decrease invasive plant richness at large spatial scales (Schnitzler et al., 2007; Bai et al., 2013), climate change can extend suitable habitat for non-indigenous species' establishment at higher latitudes, (e.g. De Rivera et al., 2011; Lu et al., 2013; Tererai et al., 2013), and to vulnerable ecosystems (e.g. Ware et al., 2014).

As an important meteorological factor, there exists a paradox in the effect of precipitation on biological invasions. Hernández et al. (2014) found the spreading of invasive *Acacia melanoxylon* in Spain was positively associated with sufficient precipitation, but Pyšek et al. (2005) considered the plant invasion was restrained by precipitation in the Czech Republic, because they found many native species are fast growing and more competitive in wet conditions compared to invaders. Indeed, Godoy et al. (2009) found that little precipitation (approximate to drought) can aggravate plant invasion by causing an early flowering and long blooming periods of invaders, which would increase their invasiveness. In addition, precipitation usually affects plant invasion by co-varying with longitude (Jauni and Hyvönen, 2010), thus, studying the complex effects of precipitation on biological invasions is crucial.

Nitrogen deposition may also strongly influence biological invasion through disproportionally favoring weedy species, however this phenomenon is not well studied, particularly for invasive plants that inhabit both aquatic and terrestrial habitats (Cleland et al., 2011; Currie et al., 2014). Nitrogen deposition consists largely of ammonium (NH_4^+) and nitrate (NO_3^-). Since 1980s, the average annual bulk deposition of N had increased by 8 kg N ha^{-1} in China, with maximum values of 63.53 kg N ha^{-1} yr^{-1} in Southern China (Lv and Tian, 2007; Liu et al., 2013; Lu et al., 2013). Ammonium (NH_4^+) was the dominant form of N deposition in China, but nitrate (NO_3^-) had a higher rate of deposition in the past 30 years (Liu et al., 2013). Some studies found that different N forms also had dissimilar influence on plants; high concentrations of NH_4^+ was toxic to many herbaceous plants as elevated NH_4^+ can lead to cation deficiency, NO_3^- was found to stimulate plant growth (van den Berg et al., 2008). While some have argued that invasion is not consistently promoted by N enrichment due to trait dissimilarity between native and exotic communities (Cleland et al., 2011). Currie et al. (2014) demonstrated a positive feedback between invasive plants and elevated N inflows in coastal marshes, where invaders were not able to reproduce clonally at low N inflow but could successfully invade at high N inflow with negative impacts on native species diversity. However, the influence of different nitrogen forms on invasive species in various habitats is not well understood.

Here, we examine *A. philoxeroides* invasion in aquatic versus terrestrial habitats due to environmental variation between these habitat types. *A. philoxeroides* is native to South America and has invaded widely in North American, Australia, New Zealand, Southeast Asian, India and China (Julien et al., 1995). Although mainly reported as invading in aquatic habitats in Australia, the USA, and New Zealand, *A. philoxeroides* was initially planted as terrestrial forage in China in the 1930s and has widely invaded both aquatic and terrestrial habitats across the mainland (Julien et al., 1995; Lu et al., 2013). *A. philoxeroides* has rapid clonal reproduction and is phenotypically plastic (leaf area, internode length, shoot diameter, etc.) (Pan et al., 2006; Geng et al., 2007). A recent study found that in the last decade this invasive weed has expanded its distribution region by 2° to the north along latitudinal gradients in mainland China (Lu et al., 2013). In 2012, we found that the invasive dominance of terrestrial *A. philoxeroides* increased with latitude from 21°N to 37°N within China (Wu et al., 2016). However, the different effects of *A. philoxeroides* invasion on biodiversity in aquatic versus terrestrial habitats and the environment factors associated with *A. philoxeroides* invasion across these two habitat types remain unexplored.

Across the vast geographic range of *A. philoxeroides* in China there are variety of microhabitat conditions (Liu et al., 2013; Zhang et al., 2015b), in addition to the significant differences in flora and plant diversity between terrestrial and aquatic ecosystems (Santamaría, 2002). In this study, we hypothesize that the heterogeneous environments may significantly affect the impact of *A. philoxeroides* on native diversity. Specifically, we addressed the following questions: (1) Do the aquatic and terrestrial communities associated with *A. philoxeroides* invasion differ in species diversity? (2) Does the effect of *A. philoxeroides* on native diversity vary across aquatic versus terrestrial habitats? (3) Do environmental factors differ in their effects on *A. philoxeroides* communities in terrestrial vs. aquatic habitats? To answer these questions, we conducted large scale surveys to sample plants across *A. philoxeroides* invasion areas that vary in environments and habitats.

2. Materials and methods

2.1. Site selection and data collection

For our sampling plots, we first conducted a reconnaissance survey during July and August 2014 to identify locations where a continuous

invasion area of *A. philoxeroides* was >100 m². From these locations, we selected our plots along five latitudinal clusters (about 2° apart) from N21° to N31° in South China. We randomly set four to six terrestrial plots (10 × 10 m, at least 10 km apart) in each latitudinal cluster, meanwhile, four to six aquatic plots were also set in the same latitudinal gradient closed to terrestrial plots. In total, we established 29 and 23 plots in terrestrial and aquatic ecosystems, respectively (see Fig. 1). We set up two 10 m transects evenly in each plot. For each transect, five quadrats (0.5 × 0.5 m) were uniformly spaced 2 m apart. Across these transects there contained gradients of invasion cover in both plots (20% to 100%, see Fig. 3) and quadrats (0% to 100%). The whole study areas covered twelve cities across five Chinese provinces.

We consulted the measurement methods of Wu et al. (2016) to record the species name, height, cover and abundance of plants in every quadrat, and we used the website 'Chinese Virtual Herbarium' (http://www.cvh.org.cn/) and 'Flora of China' (http://www.eflora.cn/) to identify unknown plants.

We recorded longitude, latitude and elevation above sea level of every plot using a handheld GPS receiver (Garmin eTrex 20, Garmin international incorporated company, Kansas, USA). We retrieved the mean annual temperature and mean annual precipitation of every sampling location in the last 50 years from the National Meteorological Center of China (http://www.nmc.gov.cn/). In addition, we also measured ammonium (NH_4^+) and nitrate (NO_3^-) in each plot. For aquatic habitats, water ammonium (NH_4^+) and nitrate (NO_3^-) were determined by using a YSI water quality analyzer (Professional Plus, YSI incorporated company, Ohio, USA) with sensor calibration of 100 mg/l and 1 mg/l before measurement. The data probes were inserted below the water at a depth of 10 cm. Data with variability 0.01 mg/l were considered stable. For terrestrial habitats, along a random transect of each plot, we selected five positions evenly to dig 0–20 cm layer soil and mixed them into a plastic bag. About 250 g of soil from every plot were collected and stored in a portable cooler at 0 °C (MobicoolCF-50DC, Dometic Group, Solna, Sweden). Inorganic nitrogen was extracted from the soil with 2 mol/l KCl and analyzed for ammonium (NH_4^+) and nitrate (NO_3^-) by an auto discrete analyzer (Easychem Plus, Systea Scientific, Oak Brook, Italy) as soon as the soil samples were brought back to the laboratory.

2.2. Data analysis

We calculated four α species diversity indices of the *A. philoxeroides* community based on Pruchniewicz and Zolnierz (2014) and Zhang et al. (2015a):

Species richness (Patrick index): $R = S$
Simpson diversity index: $\lambda = 1 - \sum P_i^2$
Shannon-Wiener diversity index: $H = -\sum P_i \ln P_i$
Species evenness (Pielou index): $E = (-\sum P_i \ln P_i) / \ln S$

Where S is the total number of species in each plot and P_i is the relative abundance of species i.

We used regression analysis to examine the relationship between invasion cover of *A. philoxeroides* and the four diversity indices. The relationships between invasive plant cover and biodiversity have been previously shown to be linearly negative, linearly positive, neutral and/or nonlinear (quadratic) for various spatial scales and ecosystems (Bangert and Huntly, 2010; Clark and Johnston, 2011; White and Shurin, 2011; Zeiter and Stampfli, 2012; Qi et al., 2014; Shah et al.,
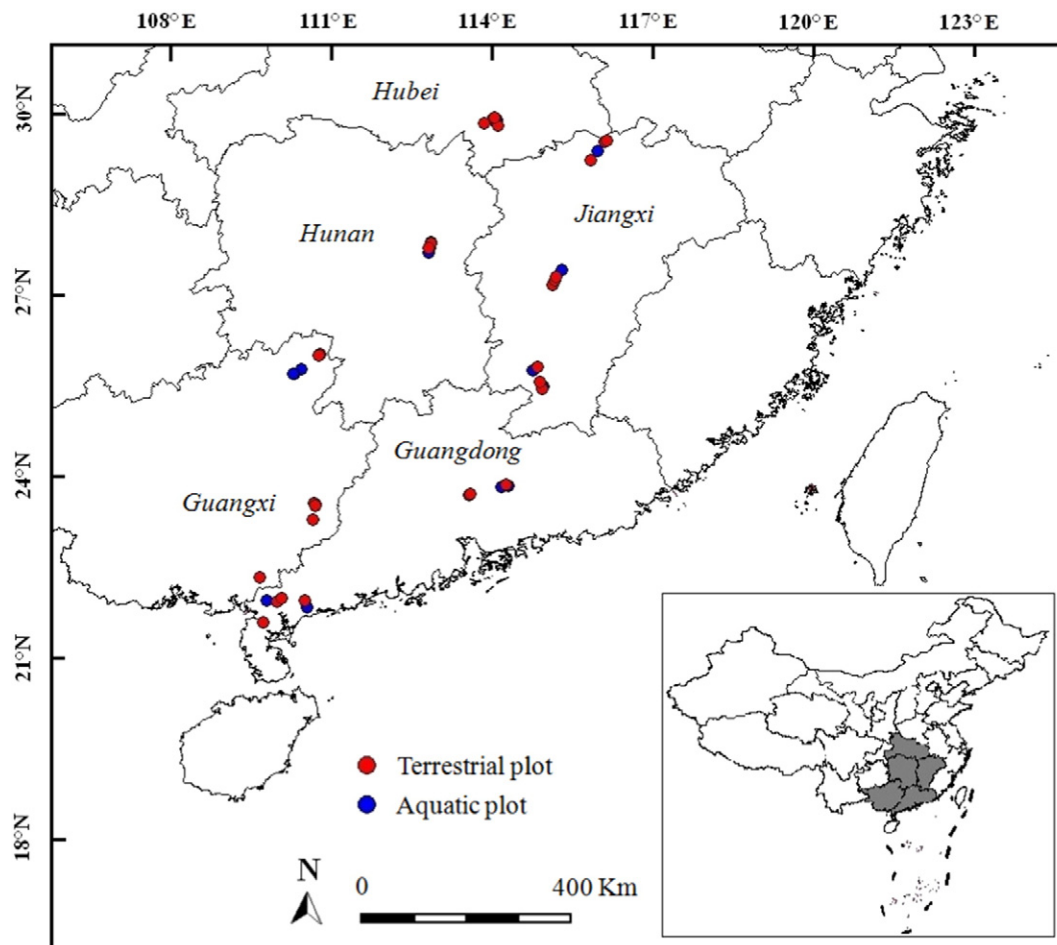

Fig. 1. Sampling plots of *A. philoxeroides* across South China along a latitudinal gradient. The field surveys were carried out during July and August 2014, covering 12 cities. A total of 52 plots (29 for terrestrial habitats and 23 for aquatic habitats) spanned five latitudinal clusters. Plot size: 10 × 10 m; Transect size: 10 m; Quadrat size: 0.5 × 0.5 m.

2014), thus, we performed the 'Linear' and 'Quadratic' models in SPSS16.0 software (SPSS Inc., Chicago, USA) in our study. We selected the best-fitting models with the lowest Akaike information criterion (AIC) values (if the models had the same AIC, then we chose the one with higher explained variances (R^2)) (Bangert and Huntly, 2010; Ren et al., 2015). In addition, we used the 'Independent-Samples t-Test' (SPSS16.0, Subset for $\alpha = 0.05$) to examine the differences of four species diversity indices between terrestrial and aquatic habitats.

Relative important value (IV) is a comprehensive quantitative index which is to measure the dominance of species in a community. It was used as data in numerical ordination of plant species distribution in our study and calculated as the following formula (Wang et al., 2007; Jing et al., 2014):

Relative IV = (relative cover + relative height + relative abundance) / 3

Where relative cover, relative height and relative abundance refer to the percentages of one species cover, mean height and abundances over the sum of all species cover, mean height and total abundances within a plot respectively.

Total IV was the sum of a plant species' relative IV in all sampling plots.

We established a community characteristic matrix containing 5 indicators (invasion cover and 4 diversity indices; 29×5 for terrestrial, 23×5 for aquatic) and an environment matrix containing 7 environmental factors (longitude, latitude, elevation above sea level, temperature, precipitation, NH_4^+ and NO_3^-; 29×7 for terrestrial, 23×7 for aquatic) to explore the effect of environmental heterogeneity on community diversity and *A. philoxeroides* invasion using the software Canoco 5.0 (Microcomputer Power, Ithaca New York, USA). We first applied detrended correspondence analysis (DCA) to examine whether unimodal or linear model would be appropriate for use. Results showed that the longest gradient lengths were all much <3 standard deviations, therefore Redundancy Analysis (RDA) was preferentially performed (Tererai et al., 2013).

We established a relative importance value matrix (29×36 for terrestrial, containing 36 main plants which had a total $IV > 0.10$, see Table S1 for plant names; 23×48 for aquatic, 48 plant names as Table S2 shown) and environment matrix (29×7 for terrestrial, 23×7 for aquatic), and used Redundancy Analysis (RDA) to explore the effect of environmental heterogeneity on species distributions. Interactive forward stepwise selection was used to choose the optimal environmental variable. The variable which had the highest explanatory contribution indicated it possessed the largest effect on community diversity and species distributions, while the variable which had the highest correlation coefficient with RDA ordination axes indicated it was the main determinant factor of this axis.

3. Results

3.1. The differences of species diversity between terrestrial and aquatic habitats

In total, 135 plant species in 45 families and 118 genera were recorded in 29 terrestrial plots (see Table S1). The Asteraceae had the greatest richness, with 17 genera and 18 species represented in our plots, followed by the Poaceae (15 genera 16 sp), Labiatae (9 genera 9 sp), Polygonaceae (3 genera 9 sp) and Leguminosae (8 genera 8 sp). *A. philoxeroides* had the largest total importance value ($IV = 15.42$), and *Digitaria sanguinalis* was the main accompanying species in our terrestrial community based on its total importance value ($IV = 1.52$). However, we only recorded 48 plant species belonging to 21 families and 42 genera in 23 aquatic plots (see Table S2). The Poaceae had the greatest richness (7 genera 7 sp), followed by the Asteraceae (4 genera 6 sp) and Polygonaceae (2 genera 5 sp). *A. philoxeroides* still had the largest total importance value ($IV = 13.50$) and *Paspalum paspaloides* ($IV = 3.53$) was the main accompanying species in aquatic community.

Plant species richness in terrestrial habitats was significant higher than in aquatic habitats ($t = 6.67$, $P < 0.0001$). The averaged species numbers in terrestrial and aquatic plots were 13 and 6 (Fig. 2a) respectively. This trend held true for the Shannon-Wiener index of species diversity ($t = 2.93$, $P = 0.005$) (Fig. 2b). But there was no significant difference between terrestrial and aquatic habitats for the Simpson index of species diversity ($t = 1.78$, $P = 0.080$) nor for species evenness ($t = -0.43$, $P = 0.669$) (Fig. 2c, d).

3.2. Effect of A. philoxeroides invasion on species diversity in different habitats

The optimal fitting relationships between *A. philoxeroides* cover and Simpson index ($F_{2, 26} = 13.39$, $P < 0.0001$ for terrestrial; $F_{2, 20} = 11.20$, $P = 0.001$ for aquatic), Shannon-Wiener index ($F_{2, 26} = 5.43$, $P = 0.011$ for terrestrial; $F_{2, 20} = 7.34$, $P = 0.004$ for aquatic), Pielou index ($F_{2, 26} = 10.66$, $P < 0.0001$ for terrestrial; $F_{2, 20} = 10.96$, $P = 0.001$ for aquatic) across our habitat types were all quadratic equations (Table S3 and Fig. 3). With increase in invasion cover, these three diversity indices showed a downward tendency after initially rising, suggesting that a slight invasion of *A. philoxeroides* could improve community diversity and evenness, but weakened diversity dramatically when *A. philoxeroides* invaded massively, however, the invasion cover thresholds of each diversity index were different (Simpson 0.48, Shannon 0.48, Pielou 0.38 for terrestrial; Simpson 0.35, Shannon 0.40, Pielou 0.38 for aquatic; as the black arrow showed in Fig. 3). *A. philoxeroides* cover did not affect Patrick richness index in either terrestrial or aquatic communities ($F_{2, 26} = 0.60$, $P = 0.556$ for terrestrial; $F_{2, 20} = 0.32$, $P = 0.732$ for aquatic).

3.3. Effect of environmental heterogeneity on species diversity

The RDA results showed that the cumulative percentage variance of species diversity-environment relation of the first two canonical axes in terrestrial habitat was 99.5% (69.0% for axis 1 and 30.5% for axis 2, respectively, see Fig. 4a). However, in aquatic habitat, the cumulative percentage variance was 84.2% (75.5% for axis 1 and 8.7% for axis 2, respectively, see Fig. 4b).

In terrestrial habitats (Table 1 and Fig. 4a), 'forward selection' indicated that the NO_3^- possessed the highest explanation contributions (40.5%) while NH_4^+ and precipitation also possessed substantial contributions (22.6% and 15.8%, respectively). NO_3^- was significantly related to the first two axis (coefficient = 0.42 for axis 1, coefficient = 0.50 for axis 2, Table 2), NH_4^+ and precipitation were both significantly related to the second axis (coefficient = -0.48 for NH_4^+, coefficient = 0.50 for precipitation, Table 2). NO_3^- was highly positively correlated with Patrick index and *A. philoxeroides*' species cover. NH_4^+ was positively correlated with Pielou index and strongly negatively with invasive cover. Mean annual precipitation was highly positively correlated with *A. philoxeroides* cover. Other environmental factors (mean annual temperature, latitude, longitude, elevation above sea level) contributed less to invasive cover and species diversity.

The effects of these environmental factors on aquatic species diversity showed some differences compared to the terrestrial habitat (Table 1 and Fig. 4b). For aquatic invasion, longitude had the greatest contribution (26.9%) and was significantly related to the first two axes (coefficient = 0.44 for axis 1, coefficient = -0.53 for axis 2, Table 2). NH_4^+ and precipitation also had higher contributions (24.8% and 24.1%, respectively). NH_4^+ was positively related to the second axis (coefficient = 0.73) while precipitation was negatively related to the first axis (coefficient = -0.431). Longitude was positively correlated with plant species richness. Similar to terrestrial habitats, NH_4^+ was also strongly positively correlated with plant species evenness but negatively with *A. philoxeroides* cover in aquatic habitats, while precipitation was still positively correlated with the aquatic invasion cover.
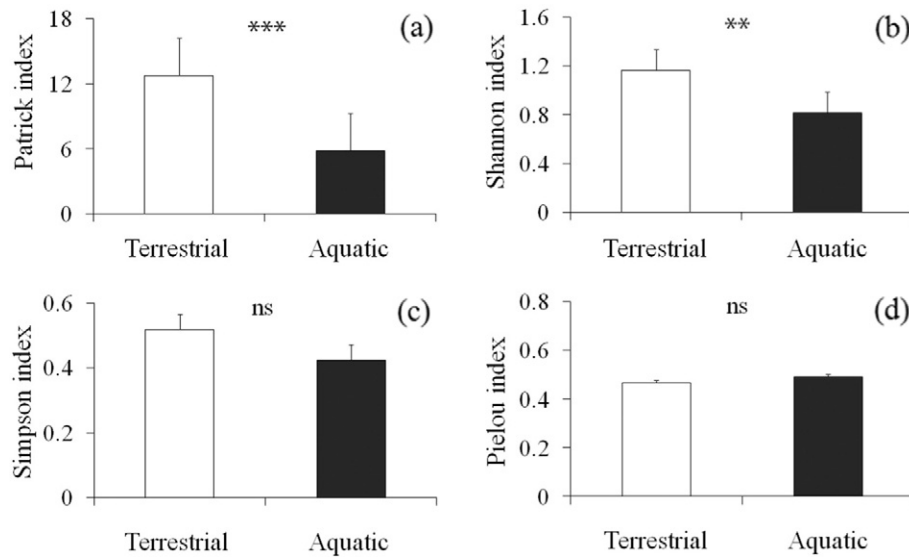
Fig. 2. Comparison of species diversity of *A. philoxeroides* community in terrestrial and aquatic habitats. Values are means + 1 SE. The differences of species diversity between terrestrial and aquatic habitats were examined by the 'Independent-samples *t*-test'. ** $P < 0.01$ level; *** $P < 0.001$ level; ns, no significant differences.

Notably, the effects of precipitation on species richness were different across habitats, as elevated precipitation inhibited plant species richness of aquatic *A. philoxeroides* community but promoted terrestrial species richness to some extent (Fig. 4). In addition, NH_4^+ was positively correlated with plant species evenness but negatively correlated with *A. philoxeroides* cover in both terrestrial and aquatic habitats, suggesting that a higher concentration of NH_4^+ in the invaded community habitats may be conducive to improve community evenness and reduce *A. philoxeroides* occurrence.

3.4. Effect of environmental heterogeneity on species distributions

The ordinations of plant species in both terrestrial and aquatic *A. philoxeroides* community along the environmental gradients are presented in the RDA biplot (Fig. Fig. 5). For terrestrial habitat, the first two canonical axes cumulatively explained 56.2% variance of the species distribution-environment relations (32.0% for axis 1 and 24.2% for axis

2, Fig. Fig. 5a), and the cumulative percentage variance in aquatic habitat was 65.7% (41.7% for axis 1 and 24.0% for axis 2, Fig. Fig. 5b).

In our analyses, dominant factors that determined species distribution in terrestrial habitats were mean annual temperature, NH_4^+ and latitude (Table 1), and these three environmental factors were all significantly positively related to the first axis (Table 2). NO_3^- was significantly related to the second axis but its percentage contribution was smaller (11.0%). Temperature was positively correlated with the plant species *Digitaria sanguinalis* (2), *Alternanthera sessilis* (19) and *Monochoria vaginalis* (15), NH_4^+ was positively correlated with *Kalimeris indica* (14), *Setaria viridis* (11) and *Artemisia argyi* (10), while the plants which were primarily associated with latitude were *Humulus scandens* (3) and *Polygonum orientale* (29).

For aquatic habitats, NH_4^+ and precipitation mainly determined species distribution (Table 1). NH_4^+ was the most important environmental variable which explained the variation of species distribution along the first axis (coefficient = 0.88), while precipitation was significantly
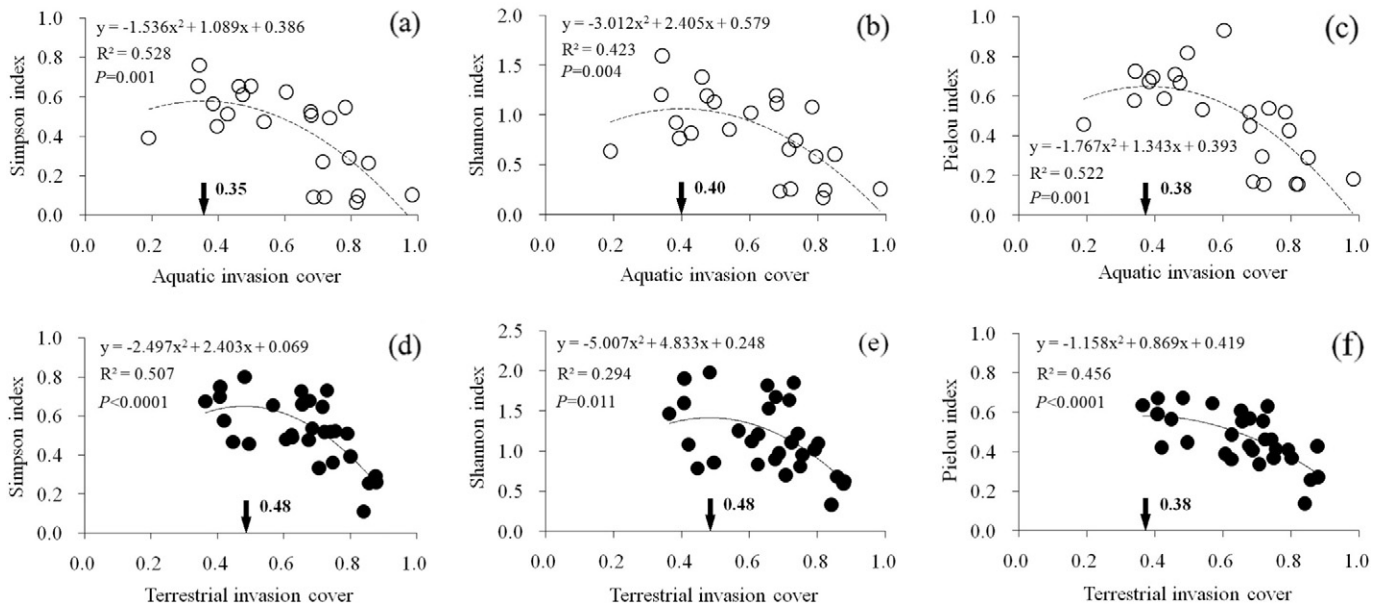

Fig. 3. The effect of *A. philoxeroides* invasion on community species diversity in terrestrial and aquatic habitats. The values of black arrows are the thresholds of invasion cover.
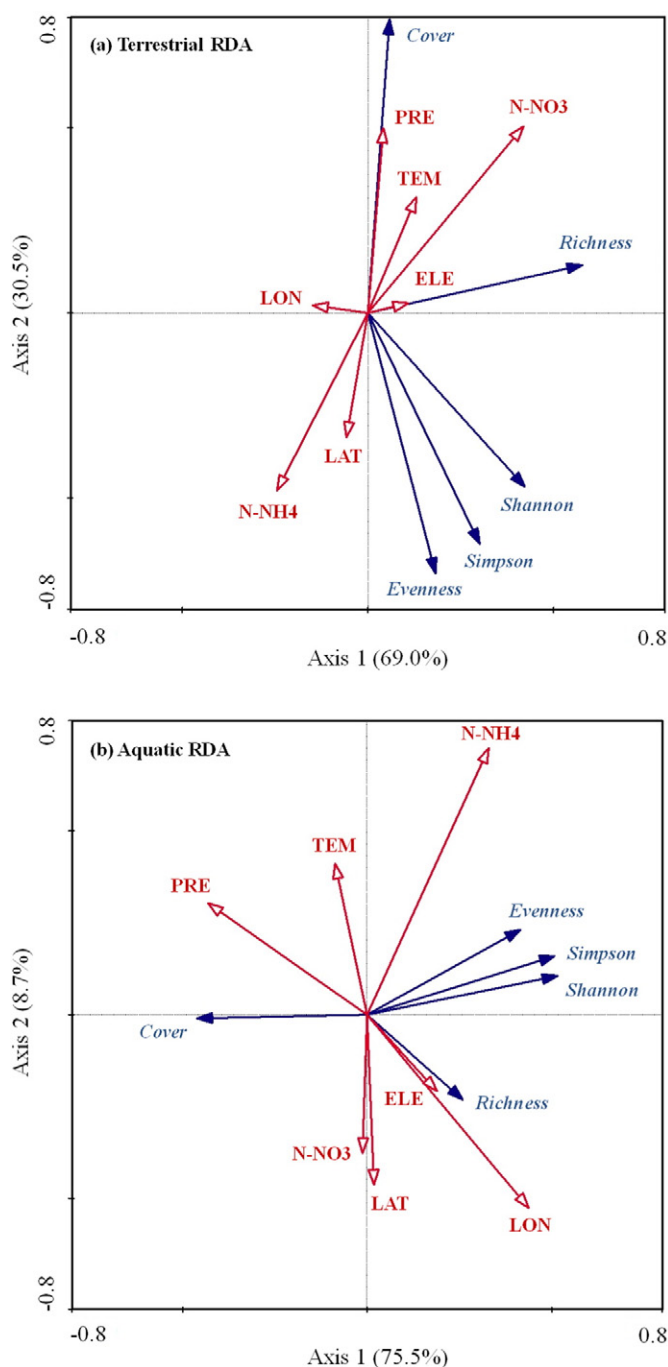
Fig. 4. RDA ordination diagram of *A. philoxeroides'* cover and community species diversity in different habitats. The N-NO₃, N-NH₄, PRE, TEM, LAT, LON, ELE represents nitrate (NO₃⁻), ammonia (NH₄⁺), mean annual precipitation, mean annual temperature, longitude, latitude and elevation above sea level, respectively. Hollow red vectors represent seven environmental variables, solid blue vectors represent the four species diversity indices and species cover of *A. philoxeroides*. Arrow indicates direction of increase in variables from ordination center. Angle between the variables represents their correlations, the smaller the angle, the greater the correlation.

Table 1
Forward selection results for the Redundancy Analyses (RDA) on diversity index and species distribution. The N-NO₃, N-NH₄, PRE, TEM, LAT, LON, ELE in this table represents nitrate (NO₃⁻), ammonia (NH₄⁺), mean annual precipitation, mean annual temperature, longitude, latitude and elevation above sea level, respectively.

Name	Explains (%)	Contribution (%)
Interactive-forward-selection for terrestrial diversity index		
N-NO₃	7.7	40.5
N-NH₄	4.3	22.6
PRE	3.0	15.8
TEM	1.6	8.4
LAT	1.4	7.4
LON	0.6	3.2
ELE	0.4	2.1
Interactive-forward-selection for aquatic diversity index		
LON	3.9	26.9
N-NH₄	3.6	24.8
PRE	3.5	24.1
ELE	1.3	9.0
LAT	0.8	5.5
TEM	0.8	5.5
N-NO₃	0.6	4.1
Interactive-forward-selection for terrestrial species distribution		
TEM	9.0	19.1
N-NH₄	8.8	18.7
LAT	8.4	17.9
PRE	6.3	13.4
N-NO₃	5.1	11.0
LON	5.0	11.0
ELE	4.4	9.4
Interactive-forward-selection for aquatic species distribution		
N-NH₄	9.2	31.7
PRE	4.7	16.2
N-NO₃	3.4	11.7
LON	3.3	11.4
TEM	3.1	10.7
LAT	3.0	10.3
ELE	2.3	7.9

aquatic habitats, *A. philoxeroides* (1) was positively correlated with NO₃⁻ but negatively with NH₄⁺ (Fig, Fig. 5).

4. Discussion

We found that plant species diversity in terrestrial invaded communities was higher than in aquatic communities and that aquatic habitats were more vulnerable to *A. philoxeroides* invasion. Small scale *A. philoxeroides* invasion appeared to increase diversity in both aquatic and terrestrial habitats, but in general *A. philoxeroides* invasion decreased species diversity. The major determinants of *A. philoxeroides* community diversity and species distribution in terrestrial habitats were nitrogen, precipitation, temperature and latitude, while in aquatic habitats, longitude, ammonia and precipitation were most important.

Although aquatic plant species generally have broader distributions than their terrestrial congeneric species (Santamaría, 2002; Landeiro et al., 2014), aquatic floras are a smaller proportion (1–2%) of vascular plants (Cook, 1990). Indeed, terrestrial ecosystems in general have much higher indices of endemicity and plant species richness (Santamaría, 2002). In this study, we found that the species richness and Shannon diversity index of terrestrial *A. philoxeroides* communities were all significant higher than in aquatic habitats. We found that the Simpson index (representing the concentration of species dominance; Lu et al., 2008) was similar between terrestrial and aquatic habitats, as *A. philoxeroides* had similar dominance (relative importance value) in both environments (see Fig. S1). Invaders have been shown to disturb habitat heterogeneity and decreased species evenness sharply by their strong competitiveness, thus leading to smaller variation in species evenness across different habitats (Tererai et al., 2013; Mandal and Joshi, 2014); our results were consistent with these findings.

related to the second axis (coefficient = −0.69). Longitude, temperature and latitude also showed significant correlations with the second axis, however, their percentage contributions were smaller (Table 2). *Monochoria vaginalis* (5) and *Erigeron annuus* (14) were highly positively correlated with NH₄⁺, but most of the remaining plant species were negatively with NH₄⁺. The species which strongly corresponded with high precipitation were *Wedelia chinensis* (32), *Colocasia esculenta* (22), *Limnophila sessiliflora* (31). However, in both terrestrial and

Table 2

Correlations between the seven environmental factors and first two RDA axes. The N-NO₃, N-NH₄, PRE, TEM, LAT, LON, ELE in this table represents nitrate (NO_3^-), ammonia (NH_4^+), mean annual precipitation, mean annual temperature, longitude, latitude and elevation above sea level, respectively.

Name	Axis 1	Axis 2
Correlations between environment and terrestrial diversity index		
N-NO₃	0.42*	0.50**
N-NH₄	−0.25	−0.48**
PRE	0.04	0.50**
TEM	0.13	0.31
LAT	−0.06	−0.33
LON	−0.15	0.02
ELE	0.11	0.03
Correlations between environment and aquatic diversity index		
LON	0.44*	−0.53**
N-NH₄	0.33	0.73**
PRE	−0.43*	0.30
ELE	0.19	−0.21
LAT	0.02	−0.46*
TEM	−0.09	0.41*
N-NO₃	−0.01	0.38
Correlations between environment and terrestrial species distribution		
TEM	−0.74**	0.32
N-NH₄	0.75**	0.23
LAT	0.70**	−0.22
PRE	−0.59**	−0.20
N-NO₃	−0.17	−0.54**
LON	0.26	−0.25
ELE	−0.08	−0.11
Correlations between environment and aquatic species distribution		
N-NH₄	0.88**	−0.37
PRE	−0.32	−0.69**
N-NO₃	−0.21	−0.19
LON	0.02	0.54**
TEM	0.14	−0.59**
LAT	−0.17	0.51**
ELE	−0.08	0.29

* $P < 0.05$ level.
** $P < 0.01$ level.

Biological invasion usually reduces biodiversity at global scales, but it improves species diversity at regional scales (Gaertner et al., 2009; Timsina et al., 2011). The positive effect of small scale invasion on native diversity had been demonstrated in *Sargassum muticum*, *Sphagneticola trilobata* and other many exotic plants (White and Shurin, 2011; Tererai et al., 2013; Qi et al., 2014). This is because alien species may optimize microhabitats as pioneer species at the initial invasion stage and provide 'associational plant refuge' facilitating native species (White and Shurin, 2011; Lososová et al., 2012). *A. philoxeroides* may also function to improve habitat suitability, as we also found that low level *A. philoxeroides* invasion improved species diversity across habitat types. However, as populations of *A. philoxeroides* grow, it is likely that species diversity is diminished through either allelopathy of the invasive and/or resource competition (Zhou et al., 2012; Zuo et al., 2012a). This phenomenon was similarly found in our 2012 terrestrial survey, however, thresholds of invasion cover in 2012 was lower than that in 2014, perhaps due to the former survey spanning a wider latitudinal gradient (21°N−37°N vs. 21°N−31°N) (Wu et al., 2016). These results implied that the effects of *A. philoxeroides* on native species diversity are both invasion density and time dependent, but, overall, negative (Fig. 4).

We found aquatic communities were more vulnerable to *A. philoxeroides* invasion than terrestrial communities, as the cover thresholds of Simpson and Shannon index in aquatic habitats were lower (Fig. 3). On the one hand, greater biodiversity could increase resistance to invasion by non-residents (biotic resistance hypothesis, BRH), as communities with high species richness are thought to be more resistant to invasion through direct competition from natives for limiting resources, and a lack of vacant niches for new invaders' establishment (Stachowicz et al., 1999; Funk et al., 2008). In our survey, terrestrial plant richness
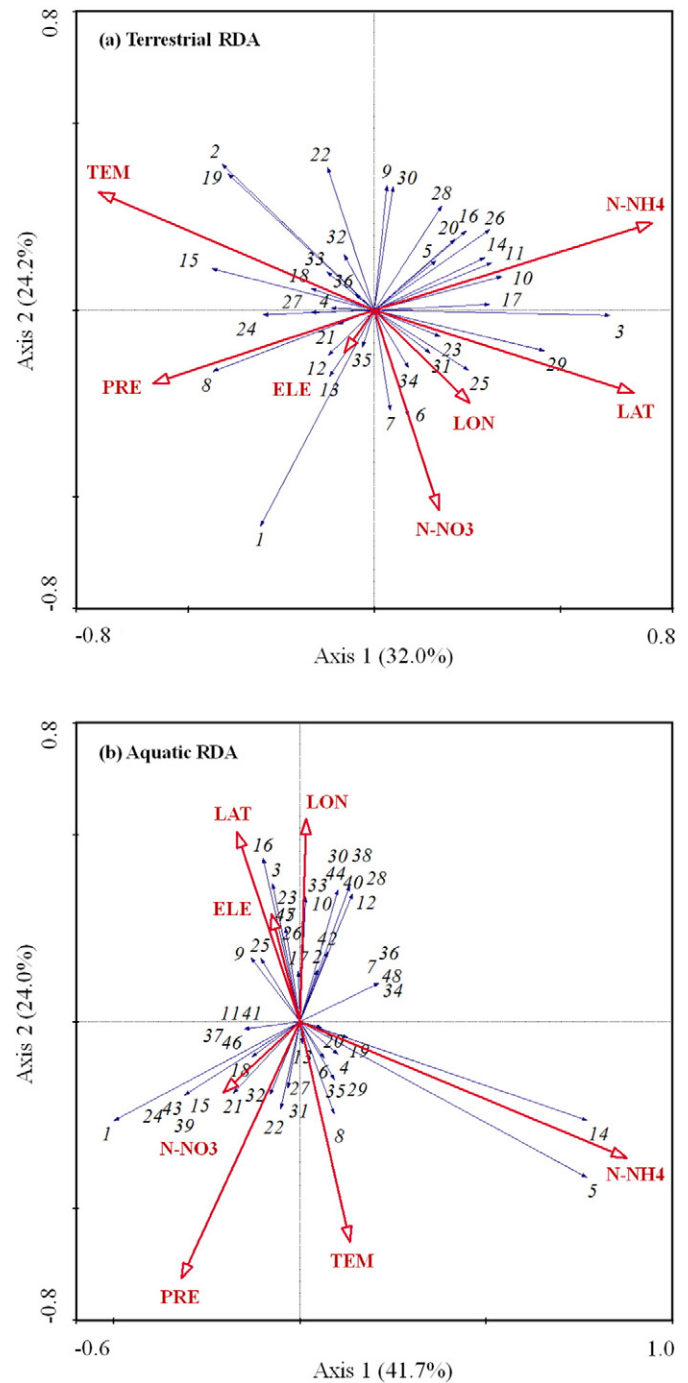

Fig. 5. RDA ordination diagram of species distributions of *A. philoxeroides* community in different habitats. The N-NO₃, N-NH₄, PRE, TEM, LAT, LON, ELE represents nitrate (NO_3^-), ammonia (NH_4^+), mean annual precipitation, mean annual temperature, longitude, latitude and elevation above sea level, respectively. Hollow red vectors represent seven environmental variables, solid blue vectors represent plant species. Arabic numbers are codes of plant species (as Table S1 and Table S2 shown for terrestrial and aquatic habitats, respectively). Arrow indicates direction of increase in variables from ordination center. Angle between the variables represents their correlations, the smaller the angle, the greater the correlation.

was far greater than aquatic plant richness (Fig. 2a), indicating the higher terrestrial biodiversity may create resistance to *A. philoxeroides* invasion. Other recent studies have documented similar patterns of increased diversity increasing resistance to invasion, for instance, compared to the communities with a single native plant species, higher planted species richness could increase the resistance to invasion in

grasslands of Virginia, USA (Oakley and Knox, 2013). Henriksson et al. (2016) also found that a higher weighted species richness reduced the relative frequency and invasion success of non-residents in Swedish lakes. On the other hand, the relative cover, canopy height and stem diameter of *A. philoxeroides* have all been shown to be higher in aquatic versus terrestrial habitats in China (Pan et al., 2006). Furthermore, aquatic *A. philoxeroides* also had higher levels of allelopathic effect, activity of protective enzymes and mats of entangled stems compared with its terrestrial ecotype (Zuo et al., 2012b; Chatterjee and Dewanji, 2014). These superior attributes might help this invader to pose more serious threats to native plant diversity in aquatic community.

NO_3^- is usually conducive for promoting grass growth, especially for enhancing aboveground biomass, while the high concentrations of NH_4^+ can be toxic to many herbaceous plants through cation deficiency, uncoupling of electron transport and membrane dysfunction (De Graaf et al., 1998; Krupa, 2003; Falkengren-Grerup and Schöttelndreier, 2004; Kleijn et al., 2008; van den Berg et al., 2008). In our survey, only a few terrestrial Poaceae and Asteraceae weeds showed strong positive NH_4^+ dependencies (Fig. Fig. 5). *A. philoxeroides* cover was inhibited by increased NH_4^+ (Fig. 5), thus, the positive relationship between species evenness and NH_4^+ could be due to increased space for other plant species (Fig. 4). NO_3^- simultaneously improved *A. philoxeroides* cover and species richness in terrestrial habitat and reducing nitrate input in terrestrial ecosystem may constrain *A. philoxeroides* spread. But NO_3^- only weakly affected the aquatic community, potentially due to the liquid connectivity of water accelerating NO_3^- transport and reducing its limitation on aquatic plant growth (Gao et al., 2014). In addition, Zhang et al. (2014) found the NO_3^- absorption capacity of *A. philoxeroides* was lower than some other wetland plants compared to NH_4^+. Therefore, we considered that nitrogen deposition may not promote *A. philoxeroides* invasion persistently, as it likely depends on the growth responses of accompanying plants to different nitrogen forms and the deposition ratio of NH_4^+/NO_3^-.

Low latitude usually has higher mean annual temperature and lower thermal seasonality, thus this higher environment stability could support greater plant species (Clarke and Gaston, 2006; Jablonski et al., 2006). We found only very few Poaceae and Asteraceae weeds showing positive correlations with increasing latitude in our terrestrial plots, while most accompanying plants preferred warmer areas with lower latitude (Fig. Fig. 5a). However, the distribution of *A. philoxeroides* was not restricted by latitude (indicated by almost vertical vector arrows in the RDA biplot, Fig. Fig. 5a). Furthermore, rising temperatures could facilitate terrestrial *A. philoxeroides* expanding to historically cooler areas (Lu et al., 2013). Thus, the invasion threat in higher latitude terrain will likely be aggravated by the lack of native biodiversity and rapid spreading of *A. philoxeroides* under climate warming. However, latitude and temperature weakly affected the biodiversity and species distribution of aquatic *A. philoxeroides* community (Table 1), possibly because the higher thermal conductivity of water can buffer temperature fluctuations and provide more stable habitats for hydrophyte growth (Santamaría, 2002; Landeiro et al., 2014).

Species richness usually increases with precipitation in terrestrial ecosystems, as precipitation improves moisture availability to terrestrial plants (Palpurina et al., 2015). But precipitation can increase flooding frequency in aquatic systems under climate change (Dokulil, 2016) and it may wash away many small hydrophytes. Indeed, the species diversity of aquatic *A. philoxeroides* community was negatively associated with high precipitation (Fig. 4b). Only a few macrophyte such as *C. esculenta* or stoloniferous plant such as *L. sessiliflora* could remain in the invaded community with high precipitation. However, aquatic *A. philoxeroides* could increase growth through connected basal parts in terrestrial habitats and form a stable floating mat (Wang et al., 2009), which further reduced the aquatic species richness. In addition, we found a negative relationship between longitude and species richness within aquatic communities, which is consist with Li et al. (2006) which stated that the flora and taxa of hydrophyte decreased from

southeast to northwest with decreasing longitude in China. We expect that, with increasing precipitation, aquatic *A. philoxeroides* invasion may be rapidly aggravated in western regions due to a lack of native hydrophytic competitors.

Extreme climatic events, such as floods, will become more frequent and intense with ongoing climate change in high northern latitudes, which include large portions of China (Diez et al., 2012). This may not only provide more aquatic environments for the spread and establishment of *A. philoxeroides* in northern China, but also increase the spread of *A. philoxeroides* from aquatic habitats onto land. In our study, native plant diversity in aquatic habitats was more vulnerable to *A. philoxeroides* invasion than in terrestrial habitats based, perhaps due to low native diversity in these habitats. So with a rapidly changing climate, we will also need to intensify the risk assessment and biodiversity protection of aquatic ecosystems, to better manage the spread and invasion of aquatic *A. philoxeroides* and other invasive plants with aquatic and terrestrial growth habitats.

In conclusion, we found environmental determinants of aquatic and terrestrial communities invaded by *A. philoxeroides*. Increased precipitation may accelerate the invader' spread across aquatic and terrestrial habitats, and low nitrate inputs could inhibit *A. philoxeroides* invasion in terrestrial habitats. In our study we used *A. philoxeroides* which can invade various habitat types and has become widely distributed across the world, as a model species to examine how heterogeneous environments affect invasive plant impact on native diversity. Our findings may also expand to other invasive plants and associated communities, because many other important invaders also share the ability to grow from land to water and vice-versa. For example, *Ipomoea aquatica*, native to southeastern Asia and invasive in the United States (Lin et al., 2012), and *Ludwigia grandiflora*, an undershrub native to South America and now massively invading into various environments of France (Haury et al., 2014), both share the ability to prosper in aquatic and terrestrial environments. Exploring the environmental determinants and ecological effects of these amphibious invaders in different habitats is crucial for predicting their future distribution and prioritizing management efforts (Catford and Downes, 2010).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2016.12.177.

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