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

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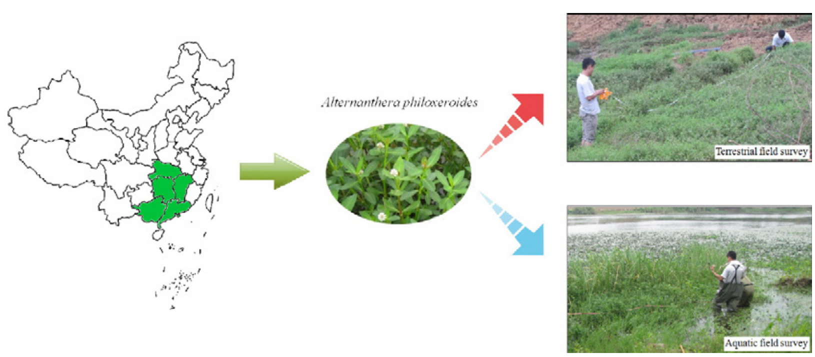
HIGHLIGHTS

- 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



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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