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Extrinsic environmental factors, not resident diversity itself, lead to invasion of *Ageratum conyzoides* L. in diverse communities

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Abstract The relationship between diversity and invasibility might be confounded by extrinsic environmental factors and the evolutionary structure of the resident community. To examine the role of extrinsic environmental factors, species and phylogenetic diversity in regulating community susceptibility to invasion, we established 109 plots either with or without *Ageratum conyzoides* L. in Liandu, China. We identified all the species in our samples, weighed the aboveground biomass of each species, and measured environmental variables. For all species recorded in our survey, we constructed a community phylogeny using PhytoPhylo mega-phylogeny as a backbone. We selected the best-fit environment model based on the minimum corrected Akaike information criteria score to examine the effect of extrinsic environmental variables on the relative abundance of *A. conyzoides*. Relationship between biodiversity and invasion of *A. conyzoides* was examined by a multiple regression, in which extrinsic ecological factors and biodiversity were combined to predict the relative abundance of *A. conyzoides*. To reduce the number of extrinsic variables, the first six components produced by a principal component analysis of environmental variables were used as predictive variables in the multiple regression. The best-fit environment model indicated that the relative abundance of *A. conyzoides* was higher in summer and in communities with lower total organic matter and higher total nitrogen in the soil. The multiple regression indicated that only the positive relationship between the Shannon–Wiener diversity of exotics and

the relative abundance of *A. conyzoides* was significant. This result challenges the importance of diversity–resistance to plant invasion. Generalist facilitation might exist between *A. conyzoides* and other exotic species, although mechanisms for such facilitation are unclear. Overall, our finding suggests the extrinsic factors covarying with diversity are more important than diversity itself in regulating community susceptibility to invasion.

Keywords Biological invasion · Diversity-resistance hypothesis · Phylogenetic diversity · Site characteristics · Species diversity

Introduction

Long-distance dispersal of species through human activities is a major component of global change (Vitousek et al. 1997) and is broadly recognized as one of the factors having the potential to profoundly modify diversity and ecosystem functioning through strong feedback loops (Levine et al. 2003; Pejchar and Mooney 2009). Facing the severe challenge of biological invasions, ecologists have long been fascinated by the mechanisms that determine the success of exotic species in new ecosystems where they have either been introduced or are spreading. Nevertheless, the reason behind varying susceptibility to invasion among different communities remains elusive (Kennedy et al. 2002; Fridley et al. 2007; Rejmanek et al. 2013).

The classic diversity–resistance hypothesis that species diversity enhances community resistance to biological invasions is one of the most common hypotheses examined over the past six decades (Elton 1958; Fridley et al. 2007; Rejmanek et al. 2013). Although the hypothesis is supported by the results obtained from both theoretical and experimental small-scale studies, many results from large-scale observational studies tend to contradict it (reviewed by Levine and D’Antonio 1999; Fridley et al. 2007). Such conflicting results across

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studies question the existence of a general relationship between species diversity and invasibility.

One commonly cited mechanism under the diversity–resistance hypothesis is that more diverse assemblages more fully utilize the available resources, thereby leaving fewer resources available to a potential invader (Levine and D’Antonio 1999). Most authors now believe that species diversity might be a poor indicator of niche usage, particularly on a large scale (Whitfeld et al. 2014; Iannone III et al. 2016). To improve the interpretation of the diversity–resistance hypothesis, many ecologists have proposed that the phylogenetic diversity of the resident community should be considered (Bennett et al. 2015; Li et al. 2015; Lososova et al. 2015). For example, Whitfeld et al. (2014) found that communities in Minnesota, USA, with higher overall plant phylogenetic diversity harbor less *Rhamnus cathartica* (an invasive species), even though native-species richness was not significantly related to abundance of the invasive species. Lososova et al. (2015) also found that exotic species invaded more phylogenetically clustered communities. At the same time, related species are expected to reduce invasion by occupying niches similar to those of the invader, thereby increasing competition with the invader (Bennett et al. 2015). Therefore, the communities with more resident species that are closely related to the invader are thought to increase invasion resistance (Strauss et al. 2006; Bennett et al. 2015). Tan et al. (2015) demonstrated that resident–invader phylogenetic relatedness controls community invisibility, instead of resident phylogenetic diversity. This contradicting result suggests that the effects of native plant phylogenetic diversity and exotic–native relatedness on the invasibility of natural communities are not clearly understood.

Many authors have attributed these conflicting results, the so-called invasive paradox, to a combination of different processes operating on different scales (Shea and Chesson 2002; Fridley et al. 2007). The covariation of extrinsic factors with resident plant diversity and invasion, particularly in observational studies, was considered as the most likely explanation for the conflicting results (Levine and D’Antonio 1999; Naeem et al. 2000). To control the effects of the ecological factors covarying with diversity, many experimental studies were conducted in relatively homogenous experimental systems (Naeem et al. 2000; Kennedy et al. 2002; Li et al. 2015), but the relevance and importance of their results for natural communities remain controversial. Wiser et al. (1998) found that extrinsic site variables were not enough to explain the positive diversity–invasibility relationship in a New Zealand mountain beech forest. Other ecologists reported that the results of native–exotic interaction frequently vary with resource availability in the habitat (Huenneke et al. 1990; Brooker et al. 2008). The direction and strength of effects of species diversity on invasibility can sometimes change with the site of invasion and the associated environmental conditions (Von Holle 2005). Thus, it is important to explicitly account for the effects of extrinsic

ecological factors of the studied uncontrolled natural habitat to better understand the diversity–invasibility relationship (Levine 2000; Von Holle 2005). Unfortunately, few studies have reported determining a diversity–invasibility relationship through simultaneously measuring a wide variety of other habitat conditions that might influence invasion (Wiser et al. 1998; Keeley et al. 2003; Whitfeld et al. 2014).

The two objectives of this study were to assess (1) influence of extrinsic environmental variables on abundance of *Ageratum conyzoides* L. (an invasive species), and (2) the role of native species diversity, exotic species diversity, and resident phylogenetic diversity in regulating community susceptibility to invasion of *A. conyzoides*, after accounting for effects of extrinsic factors. To do this, we conducted a countywide field survey to investigate the species composition and habitat characteristics of natural communities that were either invaded or not invaded by *A. conyzoides*. First, we performed a multiple general linear regression with model selection to examine the effect of extrinsic variables (including abiotic habitat characteristics, propagule pressure, and growth season) on the relative abundance of *A. conyzoides* and constructed a phylogeny of all species that we found in the survey. Then, we included species and phylogenetic diversities in a multiple general linear regression with the first six components produced by a principal component analysis (PCA) on the extrinsic variables. This analysis allowed us to investigate the pure effect of diversity after controlling the effect of extrinsic ecological factors on invasion of *A. conyzoides*.

Materials and methods

The invasive species

Ageratum conyzoides L. is a light-demanding annual weed native to tropical America that is now naturalized in the tropics and subtropics of the Old World (Chen 2011). This species was first found in Hong Kong in the late nineteenth century; at the same time, it spread to Southwest China (Yunnan) from Southeast Asia via commercial exchange (Wu and Chen 2004). With several advantages for generating viable populations, such as massive seed production of relatively small, wind-dispersed seeds, drought tolerance, fast growth, short juvenile stage, and plenty of allelochemicals, this species can quickly occupy new habitats and has now spread throughout southern, eastern, and central China (Wu and Chen 2004; Chen 2011).

Other exotic species were determined at a country-wide level based on *The Checklist of the Chinese invasive plants* (Ma 2013). Species not included in the checklist were considered native species.

Data collection

Our survey was conducted in Liandu district, a prefecture of Lishui, in Zhejiang Province, China (28°06'N to 28°44'N latitude and 119°32' E to 120°08' E longitude). Within the target region, we randomly chose 84 administrative villages distributed throughout the district. In each village, we first surveyed the abundance class (dominant: ≥ 1000 plants hm^{-2} ; abundant: 500–999 plants hm^{-2} ; frequent: 100–499 plants hm^{-2} ; sparse: 30–99 plants hm^{-2} ; rare: 10–29 plants hm^{-2} ; very rare: 1–9 plants hm^{-2}) of *A. conyzoides* and other exotic plant species in the villages chosen for our investigation. We obtained samples from roadside habitats, abandoned farmland, and riverside or forests margins in these villages by setting up $1 \times 1\text{-m}^2$ plots. No more than three plots were set up in each administrative village. Distances between any plots within the same village were more than 200 m. During growing seasons (May to November) of *A. conyzoides* in 2014, 2015, and 2016, we investigated the species composition and habitat characteristics within 109 plots with or without *A. conyzoides*. In each plot, we harvested all aboveground plant material, sorted it to determine species (or subspecies or varieties), and weighed fresh biomass (as abundance). Species were determined according to *Flora of China* (Wu and Chen 2004).

Soil samples up to 10-cm deep were collected from the four corners and the center of each plot and were mixed together as the soil sample of the plot. Soil samples were pooled across the 109 plots, air-dried, and passed through a 1-mm sieve (0.25-mm sieve for organic matter and total nitrogen analyses). The soil chemical composition for organic matter (potassium dichromate oxidation), pH (potentiometry), total nitrogen (Kjeldahl distillation), hydrolyzable nitrogen (alkaline hydrolysis diffusion), available phosphorus (Olsen's method), and available potassium (ammonium acetate extraction) was analyzed at the Ecological Experiment Center in Lishui University. We measured the area of the geographic location (portable Global Positioning System [GPS]), slope inclination (clinometer), slope aspect (compass), altitude (portable GPS), and sunlight reception rate. All the above-mentioned soil analyses were performed according to the relevant methods compiled in the technical manual of soil analysis (National Agricultural Technology Extension Service Center 2006). The sunlight reception rate is defined as the light intensity (luminometer) above the vegetation of a plot divided by the light intensity of full sunlight nearby. We estimated the soil moisture of the plots using five criteria (wet, moist, medium, dry, and arid) based on soil texture, topographies, and shade status of the monitored plots.

Phylogeny construction

Before constructing our phylogeny, we combined all infraspecific taxa in the species list with their parental

species (279 species remained). Using Qian and Jin's (2015) PhytoPhylo mega-phylogeny as a backbone, we assembled phylogeny of the 279 species recorded in our survey. The backbone of the supertree was the Zanne et al. (2014) phylogeny, which is the largest and most up-to-date time-calibrated species-level phylogeny of seed plants and uses seven gene regions in addition to fossil data. We applied the S.PhyloMaker function in R software using the phytools (Revell 2012) to generate phylogenies based on Scenario 3: adding genera or species to their families or genera with the same approach used in Phylomatic and BLADJ (<http://www.phylodiversity.net/phyloomatic/>). The phylogenetic tree was used for the analyses of the phylogenetic properties of communities.

Measurements of diversity and phylogenetic relatedness

We used the mean pairwise phylogenetic distance (MPD) among native species in each plot to determine the phylogenetic diversity of resident communities (Webb 2000). This metric takes into account pairwise phylogenetic distances between all native species in a sample and provides an overall measure of phylogenetic diversity. Many studies have reported that resident-invaser phylogenetic relatedness and phylogenetic diversity usually show different effects on plant invasions (Whitfield et al. 2014; Tan et al. 2015). To test the importance of relatedness, we calculated the mean phylogenetic distance (PD) between *A. conyzoides* and native species recorded within a sample. MPD and PD were abundance weighted and estimated using the Picante package (Kembel et al. 2010) implemented in R. In this study, we used the Shannon–Wiener index (Pielou 1975) to assess species diversity of native/exotic species. MPD, PD, and the Shannon–Wiener index (*H*) were calculated as follows:

$$MPD = \sum_{i=1}^{s-1} \sum_{j=i+1}^s \left(d_{ij} \cdot \frac{n_i}{N} \cdot \frac{n_j}{N} \right)$$

$$PD = \sum_{i=1}^s \left(d_i \cdot \frac{n_i}{N} \right)$$

$$H = - \sum_{i=1}^s \left(\frac{n_i}{N} \cdot \ln \frac{n_i}{N} \right)$$

where d_{ij} is the branch length between species *i* and species *j*, d_i is the branch length between *A. conyzoides* and species *i*, *s* is the number of species in a sample, n_i and n_j are the abundance of species *i* and *j*, respectively, and *N* is the total abundance of *s* species in the sample.

Statistical analyses

We used a multiple generalized linear model (GLM) with an inverse link function and gamma distribution to examine the relative importance of propagule pressure,

growth season, and abiotic plot characteristics that could potentially either promote or inhibit the establishment and invasion of *A. conyzoides*. The relative abundance, defined as the proportional aboveground fresh weight (hereafter “biomass”) of *A. conyzoides* compared to total plot biomass, was used as the dependent variable in the model. To guarantee the dependent variable > 0 , we added the value of $0.1/1656.9$ to all the relative abundances of *A. conyzoides* (0.1 is precision of our investigation, 1656.9 is the mean total biomass of all plots). The predictive factors included abiotic plot characteristics (soil chemical composition, tangent-transformed slope, cosine-transformed aspect, altitude, reception rate of sunlight, and degree of soil moisture), the abundance class of *A. conyzoides* in the target villages, and survey date (growth season). Considering that the seeds of *A. conyzoides* are easy diffused, village-scale propagule availability of *A. conyzoides* should be positively correlated with density of *A. conyzoides* in the whole village. In this study, we used the abundance class of *A. conyzoides* in the villages where the plots were located as an estimate of village-scale propagule availability (propagule pressure) for each plot. Considering the seasonal rotation, we transformed the survey date using the equation $d = \cos(r/365 \times 2 \times \pi)$, where r is the rank of survey date in a year, taking February 3, the beginning of spring (the traditional Chinese calendar), as the first day of a year. All continuous variables were centralized and standardized, while variables of the ordered abundance class of *A. conyzoides* in the villages and the degree of soil moisture were converted into dummy variables before they were used in the model. The best-fit model was chosen based on the minimum corrected Akaike information criteria (AICc) score. The analogous R^2 , similar to the coefficient of determination in a linear model, was calculated for the best-fit GLM model using the following equation:

$$R^2 = 1 - (L_0/L_s)^{\frac{2}{n}}$$

where L_0 and L_s are likelihoods of the best-fit model and the null model (i.e., no independent variable in the model), respectively, and n is the sample size (Magee 1990).

To control the effects of extrinsic variables (i.e., environmental factors, village-scale *A. conyzoides* abundance class, survey date) that influence native and/or exotic species, we integrated information of these extrinsic variables into a multiple general linear regression with species and phylogenetic diversities of native and/or exotic species (except *A. conyzoides*) as predictive factors to predict the relative abundance of *A. conyzoides*. To reduce multi-collinearity and the number of extrinsic variables, we performed a PCA on 13 extrinsic variables. The first six components produced by the PCA accounted for 75.72% of the variance in the 13 variables we used. As we were interested in the effect of species and phylogenetic diversity/relatedness on *A.*

conyzoides invasion, we ruled out 20 plots that were dominated by exotic species in the diversity–invasibility relationship analysis. R software (R Core Team 2017) was used to perform all statistical analyses.

Results

Effects of extrinsic variables on the relative abundance of *A. conyzoides*

The best-fit GLM predicting the relative abundance of *A. conyzoides* by extrinsic variables based on minimum AICc scores included the survey date, soil organic matter, and soil total nitrogen. Results of *t*-tests for the significance of these selected parameters indicated that the survey date and soil organic matter significantly reduced the relative abundance of *A. conyzoides*, while soil total nitrogen significantly increased the relative abundance of *A. conyzoides* (Table 1). Because these predictive variables were centralized and standardized, the absolute values of the three coefficients showed that the effects of soil total nitrogen were much stronger than were the effects of survey date and soil organic matter. The R^2 of the best-fit GLM was 0.19, indicating that only approximately 19% of the variation in *A. conyzoides* invasion in our survey plots could be explained by the extrinsic variables.

Diversities and their effects on invasion of *A. conyzoides*

Among the 109 sampled plots, we recorded 285 species (including six varieties) of vascular plants, with 251 and 34 species of native and exotic origin, respectively. Sixty-eight families were recorded across the plots. The most species-rich families were Poaceae (37 species), Asteraceae (34 species), Polygonaceae (17 species), and Lamiaceae (13 species). All species we recorded from Poaceae, Polygonaceae, and Lamiaceae were native species. There were 14 invasive species from Asteraceae, while other invasive species belonged to Amaranthaceae (six species), Scrophulariaceae (three species), Caryophyllaceae (two species), Euphorbiaceae (two species), Chenopodiaceae (one species), Convolvulaceae (one species), Cyperaceae (one species), Geraniaceae (one species), Phytolaccaceae (one species), Rubiaceae (one species), and Solanaceae (one species). The native-species richness per plot ranged from 3 to 37 species and the invasive species richness ranged from 0 to 7. There were eight plots without exotic species. *A. conyzoides* was the dominant species in 18 plots, while each of other two exotic species, *Alternanthera philoxeroides* and *Crassocephalum crepidioides*, dominated another plot, respectively. Each of the remaining 99 plots was dominated by one of the 37 native species (18 perennials and 19 annuals), which dominated no more than six plots each (mostly one or two). The two species that domi-

Table 1 Results of a best-fit generalized linear model showing relationships between the relative abundance of *Ageratum conyzoides* and environmental variables that were chosen from 13 abiotic variables based on AICc score

Variable	Estimate	SE	<i>t</i> value	<i>P</i> (> <i>t</i>)
Survey date	− 1.97	0.73	− 2.69	0.009
Organic matter	− 2.63	0.85	− 3.11	0.003
Total nitrogen	4.03	1.22	3.28	0.001

Table 2 Relationships between the relative abundance of *Ageratum conyzoides* and diversity variables by multiple generalized linear regressions combining diversity variables and the first six PCA axes of extrinsic variables as predictive factors simultaneously

Variable	Estimate	<i>P</i> (> <i>t</i>)
Shannon–Wiener diversity index of natives	0.19	0.85
Shannon–Wiener diversity index of exotics except <i>A. conyzoides</i>	0.76	0.05
The mean phylogenetic distance from <i>A. conyzoides</i> to natives	− 0.32	0.47
The mean pairwise phylogenetic distance among natives	0.46	0.64

nated six plots each were perennial plant (Table S1, see online supplementary information).

The multiple regression model showed that only the Shannon–Wiener diversity index of exotics was significantly correlated with the relative abundance of *A. conyzoides*, while neither the Shannon–Wiener diversity index of natives nor the *PD* from *A. conyzoides* to natives and the *MPD* among natives were significantly correlated with the relative abundance of *A. conyzoides* (Table 2). Analysis of deviance for the multiple regression indicated that the first six components produced by the PCA explained 10.82% of the null deviance.

Discussion

The effect of species diversity on the susceptibility of biotic communities to invasion has been debated for decades (Elton 1958; Bennett et al. 2016; Nunez-Mir et al. 2017). In this study, the disentanglement of the confounding effects of the main extrinsic factors provides insights about the effect of diversity on the invasibility of the community. By integrating habitat heterogeneity, survey date, and propagule pressure with the examination of the diversity–invasibility relationship in natural communities, our study suggests that neither species diversity nor phylogenetic diversity of the resident community is significantly related to invasion after accounting for extrinsic condition variations. Our results show that the net diversity–invasibility relationship in natural communities would be misguided, if extrinsic condition variations such as habitat heterogeneity and growth season variation were not considered properly.

Effects of extrinsic factors

Our results show that the relative abundance of *A. conyzoides* was positively affected by the soil total nitrogen. After examining the nutrient contents of the soil samples, we found that, according to the nutrient classification criteria of the second general detailed soil survey in China (The Office of National Soil Survey 1993), only the concentrations of soil total nitrogen were relatively low, while the levels of other nutrients were either medium or high [Fig. S1, see electronic supplementary material (ESM)]. This indicates that nitrogen is an important limiting abiotic factor for plant growth in the region. Competition for nitrogen limited invasion in the natural community. Increasing the nitrogen concentration in the soil in a low-soil-nitrogen community could confer a competitive advantage on annual fast-growing plants such as invasive species (Heckman and Carr 2016). Huenneke et al. (1990) proposed that increasing nutrient availability without physical disturbance of the soil and native vegetation can favor the invasion and success of non-native species in an ecosystem in which there is reduced availability of natural resources.

Besides soil total nitrogen, our best-fit extrinsic factor model included the transferred survey date and soil organic matter with negative effects. This suggested that the relative abundance of *A. conyzoides* was higher in summer (June to August) and in plots with lower total organic matter in the soil. The result was consistent with that of a previous observation showing that *A. conyzoides* grows vigorously in Lishui during June and July but more slowly both before and after this period (Jiang 2004). This may be because *A. conyzoides* is a tropics-originating exotic annual plant that positively revels in heat. The negative relationship between the relative abundance of *A. conyzoides* and soil total organic matter was consistent with the finding that *Hieracium lepidulum*, an invasive perennial herb, tends to invade habitats with lower carbon:nitrogen ratios in New Zealand (Wiser et al. 1998). Previous studies have shown that improving carbon content (e.g., organic matter) is the most reliable approach for lowering nitrogen availability (reviewed by Perry et al. 2010). Briefly, higher soil organic matters can increase heterotrophic soil microbial biomass and activity, which leads to greater microbial nitrogen uptake, thus lowering soil nitrogen availability. Invasive species would lose their advantages over native species in habitats with lower nitrogen availability (Huenneke et al. 1990; Heckman and Carr 2016).

Some ecologists have suggested that, in disturbed environments, invasion is more affected by abiotic than biotic factors (Levine et al. 2004; Von Holle 2005). Considering that all habitats (i.e., roadside habitats, abandoned farmland, and riverside or forests margins) of our sampled communities experienced some degree of disturbance, we expected that abiotic factors would be more important in regulating invasions in these communities. However, our best-fit GLM indicated that

only approximately 19% of the variation in the invasion of *A. conyzoides* in the disturbed plots could be explained by the extrinsic environmental variables we studied. This suggested that extrinsic factors did not determine the overall pattern of invasibility in these communities.

Earlier studies have shown that both increased precipitation and light availability can promote plant invasion (Duggin and Gentle 1998; Davis et al. 2000). However, our results did not show any significant effect of water and light availability on the relative abundance of *A. conyzoides*. Chen (2011) demonstrated that *A. conyzoides* could grow well under a wide range of water potential (0–500 mmol L⁻¹ polyethylene glycol) and light (75% shading to full sunlight). The non-significant result would be easy to accept if we consider the biological features of *A. conyzoides* together with the fact that the reception rate of sunlight at most sites was > 50% (Fig. S2c in ESM), and the annual precipitation was 1395.5 mm in this region. It is more important to consider the match between the invader and the invaded community, rather than the traits of invaders and invaded communities in isolation, to obtain a better insight into the process of invasion (Strauss et al. 2006).

Many studies have demonstrated that propagule pressure is an important factor that strongly influences the success of plant invasion (Von Holle and Simberloff 2005; Brooks and Jordan 2013). In this study, we used the abundance class of *A. conyzoides* in the villages to estimate propagule availability for each plot, and we found that the propagule availability had no influence on the relative abundance of *A. conyzoides* in those communities. This conflict might be explained by the fact that the invasion of *A. conyzoides* in Lishui is at the late stage of the outbreak (Jiang 2004). Wiser et al. (1998) showed that propagule pressure explained invasions only during the early invasion stages, when propagule availability was limited. However, the abundance classes of *A. conyzoides* in villages were all higher than “frequent,” which ensured that enough seeds reached the plots we surveyed. At the outbreak stage, the propagule availability of *A. conyzoides* in every village had increased to a point high enough to support the populations of *A. conyzoides*.

Effects of native species and phylogenetic diversity

In this study, after controlling the effects of extrinsic ecological factors by using a multiple GLM, we did not observe any significant relationship between the relative abundance of *A. conyzoides* and the species diversity of natives (also see Table S2 in ESM). This runs counter to the classic diversity–resistance hypothesis (Elton 1958). It is important to note, however, if we did not control the effects of extrinsic ecological factors, relationship between the relative abundance of *A. conyzoides* and the species diversity of natives could become significantly positive (Table S2 in ESM). This result suggested that

the positive diversity–invasibility relationship found in some observational study not controlling the effects of extrinsic ecological factors may be entirely a consequence of correlations between species diversity and other biotic or abiotic factors (Levine et al. 2004; Fridley et al. 2007; Zeiter and Stampfli 2012). The factors controlling native diversity similarly controlled invaders here; thus, native species diversity was an indicator of either biotic or abiotic conditions favorable to invasion (Levine and D’Antonio 1999; Fridley et al. 2007).

Resource use complementarity is often proposed as the underlying mechanism responsible for the diversity–resistance hypothesis (Levine and D’Antonio 1999). Increased diversity should lead to increased resource capture by the community, thus leaving fewer resources available to a potential invader (e.g., MacArthur 1970; Naeem et al. 2000). So, an implicit assumption of the diversity–resistance hypothesis is a positive relationship between diversity and resource capture. To competitively resist invaders, native species need to build sufficient biomass or cover to exhaust (or at least limit) plant resources (Nunez-Mir et al. 2017). Above-ground biomass is an easily measured integration of the resource (e.g., light, nutrients, water, and space) captured by a plant community (Cleland et al. 2004). Our study revealed that community invasibility is negatively related with plant biomass, but not with biodiversity. We found that the aboveground *A. conyzoides* biomass was negatively correlated with the native aboveground biomass (Spearman’s correlation test, $\rho = -0.43$, $P < 0.01$). This suggested that in those communities with high native plant biomass, competition between natives and an invader was likely to be strong, thus displaying high resistance to *A. conyzoides* invasion. However, multiple regression analysis demonstrated that the relative abundance of *A. conyzoides* was not affected by native species diversity and *MPD* of the community (even including other exotic species, also see Table S2 in ESM). Additionally, we found that the total above-ground biomass of native species significantly decreased with their Shannon–Weiner’s diversity, Simpson’s diversity, and *MPD* (Fig. S3 a, b, d in ESM), and was not significantly correlated with native species richness (Fig. S3c in ESM). This suggested that high biodiversity did not give rise to high resource capture and subsequent strong competition in these places, which contradicted the prerequisite of the diversity–resistance hypothesis (Levine and D’Antonio 1999; Cleland et al. 2004). Lack of complementary effects in a community with high diversity in this region should explain the result that there was no net relationship between biodiversity and the relative abundance of *A. conyzoides*. Resident biomass is more important than diversity in suppressing the dominance of invasive species (Bennett et al. 2016; Iannone III et al. 2016).

Phylogenetic diversity has been seen as a better measure than is species diversity for reflecting niche usage (Iannone III et al. 2016). However, our result showed that neither phylogenetic diversity nor species

diversity of native species has truly influenced the relative abundance of *A. conyzoides*. This confirmed that niche usage is not related to diversity in those communities. In this study, we also observed no significant relationship between the relative abundance of *A. conyzoides* and the *PD* from *A. conyzoides* to natives (or all non-*A. conyzoides* species, also see Table S2 in ESM). This indicated that competition might not be stronger between *A. conyzoides* and related species due either (1) to the species competitive abilities not being conserved in this system or (2) to the interspecific competitions in these communities being diffuse (Bennett et al. 2015). Alternatively, our result might reflect the overall effects of phylogenetic relatedness at different stages of invasion, even though the phylogenetic relatedness might significantly influence *A. conyzoides* establishment and growth. Li et al. (2015) documented that phylogenetic relatedness has opposite effects at different life-stages of invasion. In this study, we used aboveground biomass, which indicates the cumulative effect on establishment and growth, to describe the invasion of *A. conyzoides*. If the opposite effects at the establishment and growth stages also existed in invasion of *A. conyzoides*, the relationship between the relative abundance of *A. conyzoides* and the *PD* from *A. conyzoides* to other species could be not significant.

Effects of exotic species diversity

In this study, we found that there was a positive relationship between the relative abundance of *A. conyzoides* and the Shannon–Wiener’s diversity index of non-*A. conyzoides* exotics. A positive relationship was also observed between the relative abundance of *A. conyzoides* and the Simpson’s diversity index/species richness of non-*A. conyzoides* exotics, whether or not we controlled effects of extrinsic factors (see also Table S2 in ESM). One explanation for this positive relationship between the diversity of non-*A. conyzoides* exotics and the dominance of *A. conyzoides* is that all invaders generally prefer similar (usually resource-rich) conditions. However, the results of multiple regressions controlling effects of extrinsic factors indicated that variation in extrinsic environmental conditions among plots cannot completely explain the positive relationship between the diversity of non-*A. conyzoides* exotics and the dominance of *A. conyzoides*. We do not believe that we missed other variables that predispose sites to invasion because we included the major categories of the site conditions used to explain plant invasion (Wiser et al. 1998). Another explanation for this positive relationship between the diversity of non-*A. conyzoides* exotics and the dominance of *A. conyzoides* is generalist facilitation (Simberloff and Von Holle 1999; Fridley et al. 2007). Through facilitation interactions, an introduced plant population can enhance invader success for subsequently introduced plants (Mitchell et al. 2006). A variety of mechanisms for such facilitation have been

reported (Simberloff and Von Holle 1999). For instance, introduced plants can modify habitat (e.g., by ameliorating microclimatic and soil conditions, or protecting invaders from herbivory) to favor other introduced plants over natives (Simberloff 2006). More often, facilitation in communities with more exotic species may also operate by means of a higher probability that a new invader will share compatible symbiotic organisms (e.g., mycorrhizal fungal and nitrogen-fixing bacteria) with previous invasive species (Richardson et al. 2000; Zeiter and Stampfli 2012).

Conclusion

In this study, we found no relationship between phylogenetic diversity/relatedness and the relative abundance of *A. conyzoides*, but a significant positive correlation with exotic species diversity. Correlations between species diversity and extrinsic environmental factors (mainly total soil nitrogen, total organic matter, and growth season) in this area could result in a false positive relationship between native diversity and invasion of *A. conyzoides*, if the effects of these extrinsic environmental factors were not controlled properly in data analysis. Due to lack of a complementary effect in communities with high diversity, the hypothesis of diversity–resistance to plant invasion does not work in this region. Although there was no truly significant effect of native biodiversity on invasion of *A. conyzoides*, native species diversity was an indicator of either biotic or abiotic conditions favorable to invasion. Our finding suggests that managers should increase their invasion monitoring and removal efforts in the most diverse habitats within this region.

This analysis found that high exotic species diversity co-occurred with more *A. conyzoides*, even though the effects of extrinsic ecological factors were controlled. This suggested that generalist facilitation might exist among exotic species. As potentially influential processes are unclear, future studies should elaborate mechanisms and impacts for such facilitation in this system (Simberloff 2006).

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