RESEARCH ARTICLE

Evolution of increased intraspecific competitive ability following introduction: The importance of relatedness among genotypes

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Abstract

1. A long-standing explanation for invasion success is that invasive plants could evolve to be more competitive following introduction. This evolution of increased competitive ability (EICA) hypothesis, however, has seldom been tested with regard to intraspecific competition. Given that plants can display different responses to related and unrelated conspecifics, the evolution of intraspecific competitive ability might be specific to genotypes of different relatedness.

2. Here, we grew five native (South American) and five introduced (North American) genotypes of the clonal herbaceous invasive plant *Alternanthera philoxeroides* alone, with above-ground competition from kin (the same genotype) or from one of two types of strangers (another genotype from the same range or another genotype from the other range).

3. When grown alone, introduced and native genotypes produced similar total biomass and storage-root biomass. However, in response to intraspecific competition, introduced genotypes showed increases in total biomass and stem length, and a decrease in specific stem length, whereas native genotypes showed the opposite pattern. When grown with kin instead of strangers, introduced genotypes showed an increase in branch number, whereas native genotypes showed the opposite.

4. *Synthesis*. Our study provided evidence for evolution of increased intraspecific competitive ability in an invasive plant. We also found, for the first time, that the interactions among kin were likely to shift from competition towards facilitation following introduction.

KEYWORDS
Alternanthera philoxeroides, clonality, evolution of increased competitive ability, intraspecific competition, invasion ecology, kin selection, relatedness

1 | INTRODUCTION

The rapid rise in the number of naturalized alien plant species (Seebens et al., 2017; van Kleunen et al., 2015) has stimulated interest in the determinants of invasion success. One of the most long-standing potential explanations is that due to release from most specialist enemies, introduced genotypes of invasive plants can evolve to be less defended but more competitive (evolution of increased competitive ability, EICA hypothesis; Blossey & Nötzold, 1995). Despite evidence for the evolution of defences (Zhang et al., 2018) and the growing number of studies on the evolution of interspecific competitive ability (Blumenthal & Hufbauer, 2007; Oduor, van Kleunen, & Stift, 2017), the EICA hypothesis has seldom been tested with regard to the evolution of intraspecific competitive ability (but see Bossdorf, Prati, Auge, & Schmid, 2004).

Tests of the EICA hypothesis may depend on the index used to quantify competitive ability. Most studies measured competitive ability from performance in the absence of competition (Bossdorf et al., 2005; Felker-Quinn, Schweitzer, & Bailey, 2013). Although Blossey and Nötzold (1995), when they formulated the EICA hypothesis, argued that an increased performance would lead to an increased competitive ability, performance per se is not a direct measure of competitive ability. Studies on interspecific competitive ability face the problem of competitor choice (Bossdorf et al., 2004), because different genotypes might be locally adapted to different species (Callaway & Aschehoug, 2000; Oduor, Leimu, & van Kleunen, 2016). Studies on intraspecific competitive ability avoid arbitrary choices of competitors (Bossdorf et al., 2004). In addition, given that many invasive plants form thick monospecific stands in non-native ranges, even small evolutionary changes in intraspecific competitive ability might cause a considerable change in population growth.

Studies that tested for the evolution of intraspecific competitive ability, although few in number, also differed in their measures of competitive ability. Three studies (Lin, Klinkhamer, & Vrieling, 2015; van Kleunen & Schmid, 2003; Zou, Rogers, & Siemann, 2008) compared performance of native and introduced populations that were grown in competition with conspecifics (i.e., there were no individuals without competition). This approach, however, cannot fully capture the two components of competitive ability: competitive effect—the ability of individuals to suppress the performance of other individuals, and competitive response—the ability to tolerate competition from other individuals (sensu Goldberg, 1990). For example, in a given competition environment, an individual that has a high intrinsic growth rate but a negative competitive response would have a similar realized growth rate as an individual that has a low intrinsic growth rate but a positive competitive response. Bossdorf et al. (2004) measured the performance of individuals in both competition and competition-free environments, and compared competitive responses and effects. They found that plants from introduced populations exerted weaker competitive effects on conspecifics than those from native populations did. Nonetheless, given that competitive dominance is determined more by competitive responses than

competitive effects (Fletcher, Callaway, & Atwater, 2016; Goldberg, 1996; Hart, Freckleton, & Levine, 2018; Ridenour, Vivanco, Feng, Horiuchi, & Callaway, 2008), more studies on differences in competitive responses between introduced and native populations are needed.

Another blind spot in this research area is that the role of kin selection, the strategy to favour the fitness of an individual's kin (Hamilton, 1964), has never been investigated. Kin selection is hypothesized to be favoured if individuals mostly interact with kin (Hamilton, 1964), and has been frequently found in social animals (Clutton-Brock, 2002), and also in several plant species (Dudley & File, 2007). Due to reduced genetic diversity following introduction (Dlugosch & Parker, 2008), introduced genotypes of invasive plant species are likely to interact more frequently with kin than native genotypes do. Consequently, introduced populations have the potential for kin selection and might compete less with or even facilitate their kin.

Here, we conducted a greenhouse study with the clonal herb *Alternanthera philoxeroides*, which is native to South America and invasive in many parts of the world. Five native and five introduced genotypes of *A. philoxeroides* were grown alone, with kin (i.e., the same genotype), or with one of two types of strangers (other genotypes, either from the same range or from the other range). We focused on above-ground competition rather than on below-ground competition because above-ground competition might have a greater effect on species dominance (Kiaer, Weisbach, Weiner, & Gibson, 2013). We asked the following two questions. (a) Whether introduced genotypes of *A. philoxeroides* have evolved increased competitive ability to conspecific plants than the native genotypes? We expected, according to the EICA hypothesis, that introduced genotypes would have better competitive ability than native genotypes. (b) Whether the evolution of competitive ability is specific to different categories of intraspecific competitors (i.e., kin, strangers from the same range, and strangers from the other range)? We expected that evolution of competitive ability would be more apparent for competition among kin than competition among strangers.

2 | MATERIALS AND METHODS

2.1 | Study species

Alternanthera philoxeroides (alligator weed, Amaranthaceae) is a stoloniferous perennial species of both terrestrial and aquatic environments. The height of its natural stands varies from 10 to 60 cm (Wu, Carrillo, & Ding, 2016). *Alternanthera philoxeroides* is native to South America from the Buenos Aires province (39°S), Argentina, to southern Brazil (18°S), and is now naturalized and invasive in many parts of the world (Reed, 1970). In the United States, it was first introduced in 1897, probably through ballast water. It rapidly spread into wetlands of the northeastern US and also invaded California (Reed, 1970).

Plants of *A. philoxeroides* typically emerge from buds on storage roots and stem fragments in spring, then spread vegetatively in summer, and finally overwinter as storage roots. Native genotypes of *A. philoxeroides* can reproduce and spread through seeds. However, introduced genotypes strongly depend on vegetative reproduction due to extremely low seed outputs and low germination rates of seeds (Vogt, Quimby, & Kay, 1992). As a consequence, biomass allocation to storage roots plays a major role in the population growth of *A. philoxeroides*, particularly for introduced genotypes (Pan et al., 2007). Moreover, due to the predominant mode of vegetative reproduction in the introduced ranges, competition among kin (i.e., competition among ramets of the same genotype) is very likely to occur there. In previous studies, we found that native genotypes were highly branched and grew more frequently at low abundance, while introduced genotypes were less branched and usually formed dense, monospecific stands (Pan, Weiner, & Li, 2013; Zhang, Pan, Zhang, He, & Li, 2015; Figure S1).

2.2 | Plant material collection and experimental set-up

Stem fragments of plants of *A. philoxeroides* were collected from five locations in the United States (introduced range) and five locations in Argentina (native range) in 2005 and 2006, respectively (Table S1; Figure S2). In a previous study, we found that each of the sampled plants was characterized by a unique multilocus genotype (Geng et al., 2016). The sampled genotypes were transplanted in a greenhouse and vegetatively propagated three times to remove potential differences due to environmental maternal carry-over effects (Schwaegerle, McIntyre, & Swingley, 2000).

The experiment was conducted in a greenhouse on the Jiangwan campus of Fudan University (Shanghai, China). On 6 July 2016, we placed 150 stem fragments (with one node, 2 cm in length) of each genotype into Petri dishes filled with moist tissue paper at 25/28°C (12/12 hr) to promote root and shoot development. On 22 July 2016, we transferred 48 plantlets of similar size (*c*. 3 cm tall with two pairs of leaves) per genotype separately into 0.3-L square plastic pots filled with commercial potting compost (Beilei Organic Fertilizer Co., Ltd., Zhenjiang, China).

Four different above-ground competition treatments were set as follows (Figure 1). (a) Competition-free (alone treatment): plants of the same genotype were grown alone in a row of four pots containing one seedling each. The distances between the pots were at least 20 cm to avoid above-ground competition. (b) Competition with kin (kin treatment): plants of the same genotype were grown in a row of eight pots containing one seedling each. (c) Competition with strangers from the same range (intrarange treatment): plants of two different genotypes from the same range were grown alternatingly in a row of eight pots. (d) Competition with strangers from the other range (interrange treatment): plants of two different genotypes, one from each range, were grown alternatingly in a row of eight pots. In the kin, intrarange and interrange treatments, we arranged pots side by side so that each individual was in above-ground competition
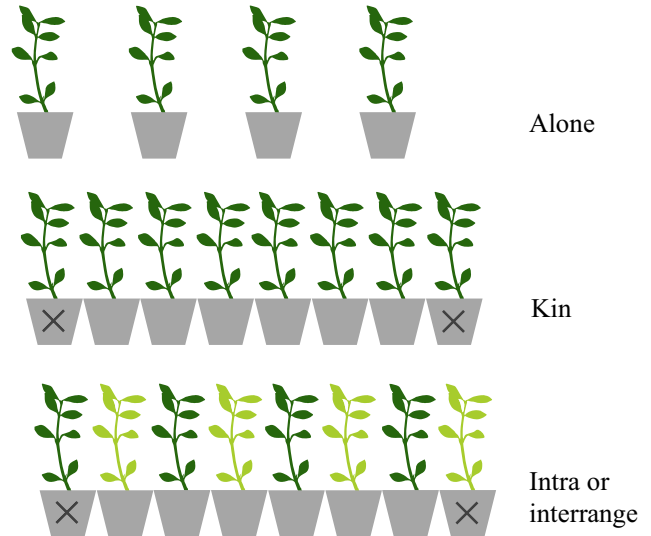

FIGURE 1 Graphical illustration of the experimental design for the different competition treatments. In the alone treatment, plants of the same genotype were grown in rows without physical contact among plants (i.e., without competition). In the kin treatment, plants of the same genotype were grown in rows with above-ground interaction among plants. In the intrarange treatment, two different genotypes (represented by different shades of green) from the same range were grown in rows with physical contact among plants. In the interrange treatment, two different genotypes, each from a different range were grown in rows with physical contact among plants. Plants at the ends of the rows of the kin, intrarange and interrange treatments (represented by pots with crosses) were used as buffer plants only and not included in the analyses [Colour figure can be viewed at wileyonlinelibrary.com]

with its neighbours (plants at the ends of the rows functioned as buffer plants only, and were not included in the analyses).

We included all 10 genotypes in the kin treatment and all possible pairwise combinations of genotypes in the intrarange and interrange treatments. This resulted in a total of 65 rows (10 for the competition-free treatment, 10 for the kin treatment, 20 for the intrarange treatment, 25 for the interrange treatment) and 480 pots. We did not replicate the combinations of genotypes (i.e., rows). However, because we had multiple genotypes per range within each competition treatment, we did have proper replicates for the range-by-competition treatment combinations. The distances between rows were at least 30 cm to avoid shading between different rows. The rows were randomly arranged on tables, and rerandomized once during the experiment. Plants were watered as needed. Because each individual was grown in a separate pot, below-ground competition was avoided and the differences among competition treatments must have resulted from above-ground interactions.

2.3 | Measurements

We harvested all plants on 18 August 2016. For each plant, we counted the number of branches with at least one node, and measured the length of the main stem with a ruler, and total leaf area with

a leaf-area meter (Li-3100; Li-Cor Inc., Lincoln, NB, USA). Above-ground parts were separated into leaves, main stem, and branches. Below-ground parts were carefully washed, and then divided into the storage roots and fine roots. Subsequently, biomass of each plant part was weighed after being dried to constant mass at 70°C. We calculated the specific stem length (SSL) by dividing the main stem length by its dry mass, and the specific leaf area (SLA) by dividing total leaf area by total leaf dry mass.

2.4 | Statistical analyses

To test whether introduced and native genotypes of *A. philoxeroides* differed in their growth performance (expressed as total biomass and storage-root biomass) and functional traits (branch number, stem length, SSL, and SLA) when grown alone, we carried out a series of analyses with the dataset that only included plants grown alone with the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015) in r 3.4.0 (R Development Core Team, 2017). Branch number was analysed using generalized linear mixed models with a Poisson error distribution, and the other traits were analysed using linear mixed models. SSL data were natural log-transformed to meet the assumption of a Gaussian distribution of the residuals. We included range (introduced vs. native genotypes) as the fixed effect, and genotype as the random effect. The significance of fixed effects in the mixed models was assessed with likelihood-ratio tests when comparing models with and without the effect of interest (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

To make a direct comparison with previous studies which inferred competitive ability from performance of plants that were grown in competition environments (Lin et al., 2015; van Kleunen & Schmid, 2003; Zou et al., 2008), we tested whether the introduced and native genotypes of *A. philoxeroides* showed different growth performance and functional traits when grown in competition environments. We carried out a series of analyses with the subset of data that only included plants grown in the kin, intrarange, or interrange treatments. Storage-root biomass data were natural log-transformed to meet the assumption of a Gaussian distribution of the residuals. We included range as the fixed effect, and genotype of the target plants and genotype of the neighbouring plants as the random effects. Data in our analyses were not independent because each individual was used both as a target and a neighbouring plant in each row. To account for nonindependence of individuals in the same row, we also added row as a random effect. As mentioned above, data of buffer plants positioned at the ends of the rows were excluded to eliminate edge effects.

To test whether introduced and native genotypes of *A. philoxeroides* showed different responses of growth performance and functional traits (a) when grown in competition with conspecifics (irrespective of relatedness) compared to when grown alone, (b) when grown in competition with kin (i.e., plants of the same genotype) compared to when grown with strangers (i.e., plants of different genotypes), and (c) when grown in competition with strangers from the same range compared to when grown with strangers from the other range, we carried out a series of analyses with the full dataset using specified contrasts (see below). Storage-root biomass data were natural log-transformed to meet the assumption of a Gaussian distribution of the residuals. We used the optimizer "bobyqa" and set the maximum number of iterations to 9,999 if a model failed to converge. We included range, competition treatment (alone, kin, intrarange, and interrange), and their interaction as fixed effects. We created three dummy variables to split up the competition treatment into three a priori contrasts (Schielzeth, 2010; see Liu & van Kleunen, 2017 for another example) that tested for differences between plants grown alone and the mean of the other three treatments with competition (C1), between competition with kin and the mean of the two competition with strangers treatments (C2), and between intrarange stranger and the interrange stranger treatments (C3). We included genotype of the target plants, genotype of the neighbouring plants and row as random effects.

3 | RESULTS

3.1 | Mean values in competition-free and competition environments

When grown alone (i.e., in competition-free environments), introduced genotypes of *A. philoxeroides* had fewer branches (−55.86%) than native genotypes (Table S2; Figure 2). However, they did not differ significantly in total biomass, storage-root biomass, stem length, SSL, and SLA (Table S2; Figure 2). When grown in competition environments, introduced genotypes tended to produce more storage-root biomass. These differences, however, were not statistically significant (Table S3; Figure 2 and Figure S2). Introduced and native genotypes significantly differed in a few functional traits. Introduced genotypes had fewer branches (−52.04%) than native genotypes when grown with strangers (i.e., different genotypes), and had a lower SLA (−8.59%) when grown with strangers from the other range (Table S3; Figure 2 and Figure S2). When analysed across all treatments, introduced genotypes still had significantly fewer branches than native genotypes, and they also had a significantly lower SLA (Table 1; Figure 2).

3.2 | Responses to competition

When grown in competition with conspecifics compared to when grown alone, native genotypes showed a decrease in total biomass (−15.25%), whereas introduced genotypes showed an increase in total biomass (+10.87%; Figure 2 left panels). The difference in these opposing trends, however, was marginally nonsignificant (R × C1 interaction in Table 1). Introduced and native genotypes significantly differed in their responses of stem length and SSL to the presence of competitors (significant R × C1 interactions in Table 1). Introduced genotypes showed an increase in stem length (+14.68%) and a decrease in SSL (−18.85%) in response to the presence of competitors, whereas native genotypes showed a decrease in stem length (−3.98%) and an increase in SSL (+3.73%; Figure 2 left panels).

When grown in competition with kin (i.e., the same genotype) compared to grown with strangers (i.e. different genotypes), introduced genotypes showed an increase in branch number (+11.31%), whereas native genotypes showed a decrease in branch number (−29.21%; Figure 2 right panels; significant R × C2 interaction in Table 1). However, none of other traits measured in the present study showed significant R × C2 interactions. For plants grown in competition with strangers, none of the traits measured was significantly affected by range of the competitor (intra vs. interrange stranger, C3), and neither showed significant R × C3 interactions (Table 1; Figure S3).
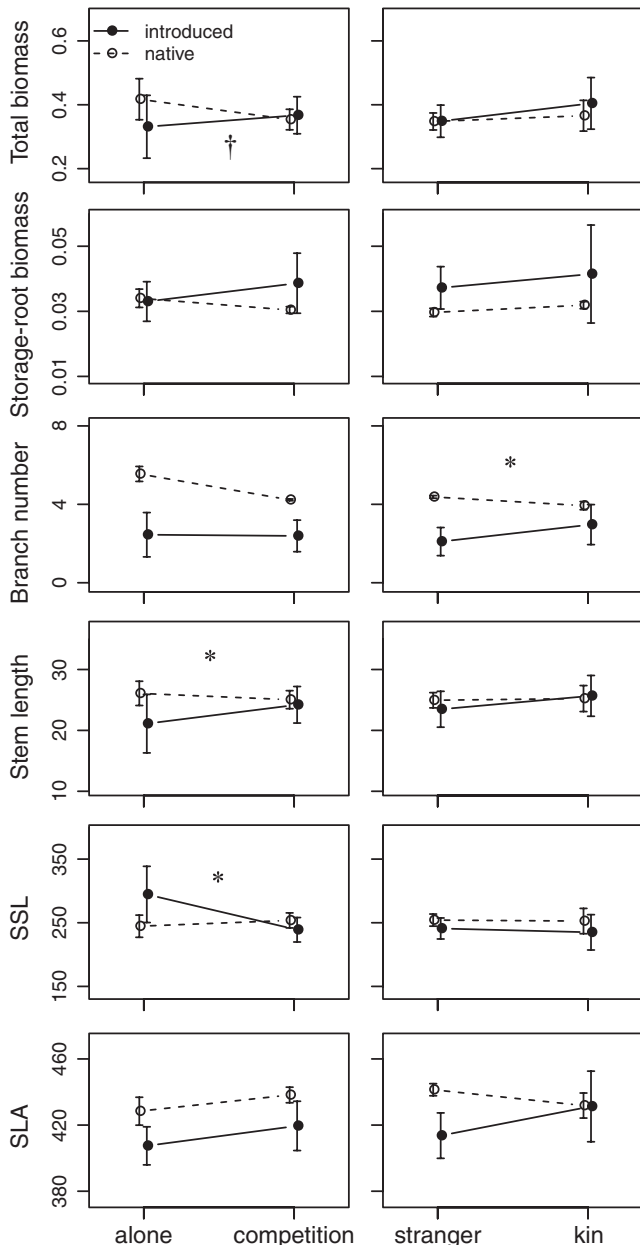

FIGURE 2 Responses of introduced (solid lines) and native (dashed lines) genotypes of *Alternanthera philoxeroides* when grown with competition compared to when grown alone, and when grown with kin (plants of the same genotype) compared to when grown with strangers (plants of different genotypes). SSL, specific stem length (cm/g); SLA, specific leaf area (cm²/g). Dots and error bars indicate means and standard errors, respectively, across five genotypes. Asterisks (*) indicate significant differences in responses between introduced and native genotypes. Daggers (†) indicate marginally significant differences in responses between introduced and native genotypes

4 | DISCUSSION

Evolution of increased competitive ability (i.e., the EICA hypothesis) has since long been viewed as a potential explanation for the invasion success of some alien plants (Blossey & Nötzold, 1995). We found that, in the absence of competition, introduced and native genotypes of *A. philoxeroides* showed no differences in fitness-related traits. However, when competing above-ground with conspecifics, introduced genotypes tended to increase biomass, whereas natives decreased it. Moreover, while introduced genotypes increased their stem length and decreased SSL in response to competition, native genotypes showed the opposite. Unlike previous studies, we additionally investigated whether introduced and native genotypes showed different responses when competing with kin compared to when competing with strangers. This revealed the first evidence that above-ground interactions among kin, as inferred from changes in branch number, might shift from competition towards facilitation following introduction.

4.1 | Evolution of competitive responses to conspecifics

Our finding that introduced genotypes tended to produce greater total biomass when grown in competition with conspecifics compared to when grown alone, while native genotypes showed the opposite trend, suggests that introduced genotypes might have evolved a better competitive response. This is in line with one of the predictions of the EICA hypothesis. Previous studies mainly inferred competitive ability from performance of individuals in competition environments. Studies with *Jacobaea vulgaris* and *Triadica sebifera* found that introduced populations or genotypes achieved greater performance in competition environments (Lin et al., 2015; Zou et al., 2008). However, in agreement with a study of *Solidago canadensis* (van Kleunen & Schmid, 2003), we found that, when we only analysed the plants grown in competition, introduced and native genotypes of *A. philoxeroides* showed similar competitive ability. We argue that, performance in competition environments, although providing some insights into the competitive outcome (i.e., which species or genotype might "win" or "lose"), is insufficient to capture competitive effects and responses due to lack of a competition-free control or gradients of densities (see Hart et al., 2018; Weigelt & Jolliffe, 2003 for detailed reviews on quantifying competitive ability). Our study measured the performance of individuals in both competition and competition-free treatments, and thus provided a more direct test of evolution of increased intraspecific competitive ability in invasive plants.

TABLE 1 Results of (general) linear mixed effects models testing the effects of range (i.e., introduced vs. native), competition (planned contrasts C1–C3), and their interactions on total biomass, storage-root biomass, branch number, stem length, specific stem length (SSL), and specific leaf area (SLA) of *Alternanthera philoxeroides*. C1, individuals grown in competition with conspecifics vs. grown alone; C2, individuals grown in competition with kin vs. those with strangers; C3, individuals grown in competition with strangers from the same range (intrarange) vs. those with strangers from the other range (interrange). Significant effects are marked in bold. Marginally significant effects are marked in italics and bold

Fixed effects	Total biomass χ^2	P	Storage-root biomass χ^2	P	Branch number χ^2	P	Stem length χ^2	P	SSL χ^2	P	SLA χ^2	P
Range (R)	0.01	0.927	1.07	0.301	6.04	**0.014**	0.22	0.639	0.31	0.576	4.10	**0.043**
C1 (alone vs. competition)	0.22	0.641	0.05	0.831	3.69	*0.055*	1.01	0.315	2.28	0.131	0.88	0.349
C2 (kin vs. stranger)	1.75	0.185	0.17	0.681	0.67	0.412	1.72	0.190	0.07	0.785	0.20	0.656
C3 (intra vs. interrange stranger)	0.00	0.996	0.45	0.504	0.02	0.902	0.18	0.668	0.10	0.750	1.60	0.206
R:C1	2.97	*0.085*	2.18	0.140	1.64	0.201	4.32	**0.038**	4.70	**0.030**	0.01	0.909
R:C2	0.52	0.471	0.57	0.451	7.79	**0.005**	1.17	0.279	0.03	0.864	2.36	0.124
R:C3	0.82	0.365	2.02	0.155	0.77	0.379	0.40	0.528	1.00	0.317	2.19	0.139
Random effects	*SD*		*SD*		*SD*		*SD*		*SD*		*SD*	
Genotype (target)	0.094		0.254		0.480		5.270		30.535		18.299	
Genotype (neighbour)	0.000		0.000		0.000		0.000		0.000		2.647	
Row	0.063		0.154		0.000		1.930		26.736		19.148	
Residual	0.122		0.356		0.970		4.624		72.651		45.673	

Unlike our results, Bossdorf et al. (2004) found that native populations of *Alliaria petiolata* could exert stronger competitive effects and outperformed their introduced populations. Based on their findings, Bossdorf et al. (2004) hypothesized that if there was more intraspecific competition and less interspecific competition in non-native ranges, introduced genotypes could evolve towards having decreased intraspecific competition (evolutionary reduced competitive ability, ERCA hypothesis). Here, we argue that if introduced genotypes are less competitive than native genotypes, they may be easily replaced by genotypes that newly arrive from the native range. Therefore, the ERCA hypothesis is more likely to hold for invasive species for which multiple introductions are less likely.

A caveat of our study is that we focused on above-ground interactions only. As below-ground processes may cause negative interactions among individuals, the introduced genotypes are unlikely to expand indefinitely. Nonetheless, above-ground interactions are reported to have great effects on species dominance (Kiaer et al., 2013). In addition, competition for below-ground resources may ultimately result in increased above-ground competition (Hautier, Niklaus, & Hector, 2009). Consequently, the evolution of above-ground interactions among conspecifics might be sufficient to allow for denser monocultures in introduced genotypes than in native genotypes of *A. philoxeroides*. Another potential limitation of our study is that we only included five genotypes for each range, which is a relatively small sample size. Studies with a larger number of genotypes are needed to provide more robust evidence.

Increased stem length and SSL in response to competition are two well-documented shade-avoidance responses (Poorter et al., 2012;

Schmitt, Dudley, & Pigliucci, 1999; van Kleunen & Fischer, 2001). Our study found that, when grown in competition with conspecifics compared to when grown alone, introduced genotypes increased their stem length, whereas native genotypes decreased it. This suggests that introduced genotypes might have better shade-avoidance responses to competition from conspecifics than native genotypes. Unexpectedly, native genotypes showed a slightly increased SSL in response to competition, whereas introduced genotypes showed a decreased SSL. This suggests that the stem elongation of introduced genotypes in response to competition was not at the cost of stem thickness but actually coincided with thicker stems. Because stem fragmentation is an important component of vegetative reproduction and spread of *A. philoxeroides*, especially for the introduced genotypes (Pan et al., 2007), increased SSL in the presence of competition, which indicates more slender and weaker stems, might be selected against in introduced genotypes. Whatever the exact reason for decreased SSL in response to competition in introduced genotypes, our findings for the stem traits suggest that introduced genotypes of *A. philoxeroides* have evolved a greater ability of vertical growth and are able to allocate more biomass to the main stem under intraspecific competition. Possibly, this led to the higher competitive ability and greater biomass production under competition.

4.2 | Evolution of competitive responses to kin

Another interesting finding of our study is that introduced genotypes of *A. philoxeroides* showed an increase in branch number when grown in competition with kin compared to when grown

with strangers, whereas native genotypes showed the opposite. This might indicate that interactions among kin have shifted from competition towards facilitation following introduction. Facilitation among kin could be selected for where individuals frequently interact with kin (Hamilton, 1964). Given losses of genetic diversity during introduction (i.e., founder effects; Dlugosch & Parker, 2008, Colautti, Eckert, & Barrett, 2010), genetic diversity within introduced population is expected to be lower than that within native population. In addition, unlike native genotypes that produce viable seeds, introduced genotypes of *A. philoxeroides* solely depend on clonal propagation for reproduction (Vogt et al., 1992), and thus might be mainly surrounded by kin. Consequently, it seems plausible that kin selection could occur in introduced genotypes of *A. philoxeroides*. It has been shown that *Arabidopsis thaliana* can distinguish related and nonrelated neighbours via red/far-red light and blue light profiles and then decrease mutual shading among kin (Crepy & Casal, 2015). Therefore, mechanistic studies of how introduced genotypes reduce above-ground competition among kin can further our understanding of evolution of competitive ability.

Branching is usually at a cost of vertical growth, and could be selected against in environments with strong competition (Schmitt & Wulff, 1993). Therefore, it could be argued that increases in branch number in responses to competition from kin may constrain the performance of introduced genotypes under competition. This, however, is unlikely in our study system because branch number of introduced genotypes, despite its increases in response to kin, was lower than that of native genotypes. Still, future research is needed to assess whether mean values of traits and their responses contribute to fitness (i.e., are adaptive; van Kleunen & Fischer, 2005), or are just correlated with fitness.

5 | CONCLUSIONS

Our study tested the EICA hypothesis with regard to changes in performance in response to intraspecific competition with kin and with strangers. In support of the EICA hypothesis, introduced genotypes showed better competitive responses, as indicated by total biomass, to intraspecific competition than native genotypes did. Furthermore, we provide the first evidence, although tentative, that above-ground interactions among kin may shift from competition towards facilitation following introduction, probably due to the higher frequency of interactions among kin in introduced genotypes than in native genotypes. Because of the prevalence of uniparental reproduction, or even shifts to uniparental reproduction, in alien plant species (Razanajatovo et al., 2016; Zhang, Zhang, & Barrett, 2010), and losses of genetic diversity following introduction, kin selection might be common in invasive plants. Finally, as Modern Coexistence Theory claims that an important mechanism for species coexistence is that species are more limited by themselves than by other species (stabilizing niche difference sensu Chesson, 2000), evolution of increased competitive responses to intraspecific competition and kin selection is likely to allow invasive plants to be released from intraspecific competition and then to outcompete native species.

AUTHORS' CONTRIBUTIONS

Z.Z., F.Z., and X.P. conceived and designed the experiment; F.Z. performed the experiment; Z.Z. analysed the data and led the writing, with major inputs from X.P. and M.v.K., and further inputs from F.Z., M.L. and B.L.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5m5dr78 (Zhang, 2018).

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REFERENCES

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 48.

Blossey, B., & Nötzold, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants – A hypothesis. *Journal of Ecology*, *83*, 887–889. https://doi.org/10.2307/2261425

Blumenthal, D. M., & Hufbauer, R. A. (2007). Increased plant size in exotic populations: A common-garden test with 14 invasive species. *Ecology*, *88*, 2758–2765. https://doi.org/10.1890/06-2115.1

Bossdorf, O., Auge, H., Lafuma, L., Rogers, W. E., Siemann, E., & Prati, D. (2005). Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, *144*, 1–11. https://doi.org/10.1007/s00442-005-0070-z

Bossdorf, O., Prati, D., Auge, H., & Schmid, B. (2004). Reduced competitive ability in an invasive plant. *Ecology Letters*, *7*, 346–353. https://doi.org/10.1111/j.1461-0248.2004.00583.x

Callaway, R. M., & Aschehoug, E. T. (2000). Invasive plants versus their new and old neighbors: A mechanism for exotic invasion. *Science*, *290*, 521–523. https://doi.org/10.1126/science.290.5491.521

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Clutton-Brock, T. (2002). Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science*, *296*, 69–72. https://doi.org/10.1126/science.296.5565.69

Colautti, R. I., Eckert, C. G., & Barrett, S. C. (2010). Evolutionary constraints on adaptive evolution during range expansion in an invasive

plant. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 1799–1806. https://doi.org/10.1098/rspb.2009.2231

Crepy, M. A., & Casal, J. J. (2015). Photoreceptor-mediated kin recognition in plants. *New Phytologist*, *205*, 329–338. https://doi.org/10.1111/nph.13040

Dlugosch, K. M., & Parker, I. M. (2008). Founding events in species invasions: Genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology*, *17*, 431–449. https://doi.org/10.1111/j.1365-294X.2007.03538.x

Dudley, S. A., & File, A. L. (2007). Kin recognition in an annual plant. *Biology Letters*, *3*, 435–438. https://doi.org/10.1098/rsbl.2007.0232

Felker-Quinn, E., Schweitzer, J. A., & Bailey, J. K. (2013). Meta-analysis reveals evolution in invasive plant species but little support for Evolution of Increased Competitive Ability (EICA). *Ecology and Evolution*, *3*, 739–751. https://doi.org/10.1002/ece3.488

Fletcher, R. A., Callaway, R. M., & Atwater, D. Z. (2016). An exotic invasive plant selects for increased competitive tolerance, but not competitive suppression, in a native grass. *Oecologia*, *181*, 499–505. https://doi.org/10.1007/s00442-016-3584-7

Geng, Y., van Klinken, R. D., Sosa, A., Li, B., Chen, J., & Xu, C.-Y. (2016). The relative importance of genetic diversity and phenotypic plasticity in determining invasion success of a clonal weed in the USA and China. *Frontiers in Plant Science*, *7,* 213. https://doi.org/10.3389/fpls.2016.00213

Goldberg, D. E. (1990). Components of resource competition in plant communities. In J. B. Grace, & D. Tilman (Eds.), *Perspectives on plant competition* (pp. 27–49). San Diego, CA: Academic Press.

Goldberg, D. E. (1996). Competitive ability: Definitions, contingency and correlated traits. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *351*, 1377–1385.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*, 1–16. https://doi.org/10.1016/0022-5193(64)90038-4

Hart, S. P., Freckleton, R. P., & Levine, J. M. (2018). How to quantify competitive ability. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.12954

Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, *324*, 636–638. https://doi.org/10.1126/science.1169640

Kiaer, L. P., Weisbach, A. N., Weiner, J., & Gibson, D. (2013). Root and shoot competition: A meta-analysis. *Journal of Ecology*, *101*, 1298–1312. https://doi.org/10.1111/1365-2745.12129

Lin, T., Klinkhamer, P. G., & Vrieling, K. (2015). Parallel evolution in an invasive plant: Effect of herbivores on competitive ability and regrowth of *Jacobaea vulgaris*. *Ecology Letters*, *18*, 668–676.

Liu, Y., & van Kleunen, M. (2017). Responses of common and rare aliens and natives to nutrient availability and fluctuations. *Journal of Ecology*, *105*, 1111–1122. https://doi.org/10.1111/1365-2745.12733

Oduor, A. M. O., Leimu, R., & van Kleunen, M. (2016). Invasive plant species are locally adapted just as frequently and at least as strongly as native plant species. *Journal of Ecology*, *104*, 957–968. https://doi.org/10.1111/1365-2745.12578

Oduor, A. M. O., van Kleunen, M., & Stift, M. (2017). In the presence of specialist root and shoot herbivory, invasive-range *Brassica nigra* populations have stronger competitive effects than native-range populations. *Journal of Ecology*, *105*, 1679–1686.

Pan, X. Y., Geng, Y. P., Sosa, A., Zhang, W. J., Li, B., & Chen, J. K. (2007). Invasive *Alternanthera philoxeroides*: Biology, ecology and management. *Acta Phytotaxonomica Sinica*, *45*, 884–900. https://doi.org/10.1360/aps06134

Pan, X. Y., Weiner, J., & Li, B. (2013). Size-symmetric competition in a shade-tolerant invasive plant. *Journal of Systematics and Evolution*, *51*, 318–325. https://doi.org/10.1111/jse.12001

Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., & Mommer, L. (2012). Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. *New Phytologist*, *193*, 30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x

R Development Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Razanajatovo, M., Maurel, N., Dawson, W., Essl, F., Kreft, H., Pergl, J., … van Kleunen, M. (2016). Plants capable of selfing are more likely to become naturalized. *Nature Communications*, *7*, 13313. https://doi.org/10.1038/ncomms13313

Reed, C. F. (1970). *Selected weeds of the United States. U.S. Department of Agriculture Handbook 366*. Washington, DC: Government Printing Office.

Ridenour, W. M., Vivanco, J. M., Feng, Y., Horiuchi, J.-I., & Callaway, R. M. (2008). No evidence for trade-offs: *Centaurea* plants from America are better competitors and defenders. *Ecological Monographs*, *78*, 369–386.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*, 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Schmitt, J., Dudley, S. A., & Pigliucci, M. (1999). Manipulative approaches to testing adaptive plasticity: Phytochrome-mediated shade-avoidance responses in plants. *The American Naturalist*, *154*, S43–S54.

Schmitt, J., & Wulff, R. D. (1993). Light spectral quality, phytochrome and plant competition. *Trends in Ecology & Evolution*, *8*, 47–51. https://doi.org/10.1016/0169-5347(93)90157-K

Schwaegerle, K. E., McIntyre, H., & Swingley, C. (2000). Quantitative genetics and the persistence of environmental effects in clonally propagated organisms. *Evolution*, *54*, 452–461. https://doi.org/10.1111/j.0014-3820.2000.tb00048.x

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435. https://doi.org/10.1038/ncomms14435

van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., … Pysek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, *525*, 100–103. https://doi.org/10.1038/nature14910

van Kleunen, M., & Fischer, M. (2001). Adaptive evolution of plastic foraging responses in a clonal plant. *Ecology*, *82*, 3309–3319. https://doi.org/10.1890/0012-9658(2001)082[3309:AEOPFR]2.0.CO;2

van Kleunen, M., & Fischer, M. (2005). Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist*, *166*, 49–60. https://doi.org/10.1111/j.1469-8137.2004.01296.x

van Kleunen, M., & Schmid, B. (2003). No evidence for an evolutionary increased competitive ability in an invasive plant. *Ecology*, *84*, 2816–2823. https://doi.org/10.1890/02-0494

Vogt, G. B., Quimby, P. C., & Kay, S. (1992). Effects of weather on the biological control of alligatorweed in the lower Mississippi Valley region, 1973–83. Technical bulletin/United States Department of Agriculture (USA).

Weigelt, A., & Jolliffe, P. (2003). Indices of plant competition. *Journal of Ecology*, *91*, 707–720. https://doi.org/10.1046/j.1365-2745.2003.00805.x

Wu, H., Carrillo, J., & Ding, J. (2016). Invasion by alligator weed, *Alternanthera philoxeroides*, is associated with decreased species diversity across the latitudinal gradient in China. *Journal of Plant Ecololy*, *9*, 311–319.

Zhang, Z. (2018). Data from: Evolution of increased intraspecific competitive ability following introduction: The importance of relatedness among genotypes. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.5m5dr78

Zhang, Z., Pan, X., Blumenthal, D., van Kleunen, M., Liu, M., & Li, B. (2018). Contrasting effects of specialist and generalist herbivores on resistance evolution in invasive plants. *Ecology*, *99*, 866–875. https://doi.org/10.1002/ecy.2155

Zhang, Z., Pan, X., Zhang, Z., He, K., & Li, B. (2015). Specialist insect herbivore and light availability do not interact in the evolution of an invasive plant. *Plos One*, *10*, e0139234. https://doi.org/10.1371/journal.pone.0139234

Zhang, Y., Zhang, D., & Barrett, S. C. H. (2010). Genetic uniformity characterizes the invasive spread of water hyacinth (*Eichhornia crassipes*), a clonal aquatic plant. *Molecular Ecology*, *19*, 1774–1786.

Zou, J., Rogers, W. E., & Siemann, E. (2008). Increased competitive ability and herbivory tolerance in the invasive plant *Sapium sebiferum*. *Biological Invasions*, *10*, 291–302. https://doi.org/10.1007/s10530-007-9130-0

Zuur, A., Ieno, E., Walker, N., Saveliev, A., & Smith, G. (2009). *Mixed effects models and extensions in ecology with R*. In M. Gail, K. Krickeberg, J. M. Samet, A. Tsiatis, & W. Wong (Eds.). New York, NY: Spring Science and Business Media.

SUPPORTING INFORMATION

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