

Linking Darwin's naturalisation hypothesis and Elton's diversity–invasibility hypothesis in experimental grassland communities

Yanhao Feng^{1,2,3} 

Timothée Donatien Fouqueray^{1,4}

Mark van Kleunen^{1,5}

¹Ecology, Department of Biology, University of Konstanz, Konstanz, Germany

²Department for Physiological Diversity, Helmholtz Centre for Environmental Research - UFZ, Leipzig, Germany

³Department for Physiological Diversity, German Center for Integrative Biodiversity Research (iDiv), Leipzig, Germany

⁴Department of Biology, Ecole Normale Supérieure de Lyon, Lyon, France

⁵Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, China

Correspondence

Yanhao Feng
Email: yanhao.feng@idiv.de

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Abstract

1. Darwin's naturalisation hypothesis posing that phylogenetic distance of alien species to native residents predicts invasion success, and Elton's diversity–invasibility hypothesis posing that diversity of native communities confers resistance to invasion, are both rooted in ideas of species coexistence. Because the two hypotheses are inherently linked, the mechanisms underlying them may interact in driving the invasion success. Even so, these links and interactions have not been explicitly disentangled in one experimental study before.
2. To disentangle the links between the two hypotheses, we used 36 native grassland herbs to create greenhouse mesocosms with 90 grassland communities of different diversities, and introduced each of five herbaceous alien species as seeds and seedlings. We used phylogeny and four functional traits (plant height, specific leaf area, leaf size, and seed mass) to calculate different measures of phylogenetic and functional *distance* and *diversity*. Specifically, we tested how the alien–native *distance* (phylogenetic or functional) and the native *diversity* (phylogenetic or functional) affected each other in their effects on germination, seedling survival, growth, and reproduction of the aliens.
3. Overall, our results supported both hypotheses. Multivariate functional distance based on four traits jointly had stronger positive effects than phylogenetic distance and the univariate ones based on each trait separately. Moreover, the aliens were more successful if they were more competitive by being taller and having larger leaves with a lower SLA than the native residents. Univariate functional diversity based on each trait separately had stronger negative effects than phylogenetic and multivariate functional diversity. Most importantly, we found that the effects of alien–native phylogenetic and multivariate functional distance became stronger as diversity increased. Our analyses with single traits also showed that the strength of the effects of both alien–native hierarchical functional *distances* (indicative of competitive inequalities) and absolute functional *distances* (indicative of niche differences) increased at higher *diversities*, where competition is more severe.
4. *Synthesis*. Our study explicitly demonstrates for the first time how the mechanisms underlying the two classical invasion hypotheses interact in driving invasion

success in grassland communities. This may help to explain some of the puzzling results of studies testing either of the two hypotheses.

KEYWORDS

biotic resistance, competitive exclusion, competitive inequality, Darwin's naturalisation conundrum, invasion ecology, modern coexistence theory, niche differences

1 INTRODUCTION

A major quest in ecology is to understand the mechanisms driving the success of alien species in native communities. While numerous invasion hypotheses have been proposed, it is suggested that the mechanisms associated with some of them may be implicitly interlinked (Catford, Jansson, & Nilsson, 2009; Jeschke, 2014). In essence, whether or not alien species invade native communities is a question of coexistence between alien species and native residents. Classical invasion hypotheses, which are often rooted in ideas of species coexistence (Levine & D'Antonio, 1999; MacDougall, Gilbert, & Levine, 2009), have long focused on identifying the characteristics predisposing alien species to become invasive and the properties that render native communities invulnerable (Richardson & Pyšek, 2006). Darwin (1859) posited that alien species will be more successful in a native community if they are phylogenetically distantly related to native residents (Darwin's naturalisation hypothesis), because phylogenetic distance may indicate niche differences favouring coexistence (Violle, Nemergut, Pu, & Jiang, 2011). Elton (1958) proposed that alien species will be less successful in more diverse native communities (Elton's diversity–invasibility hypothesis), where fewer unoccupied niches are available for newcomers (Herbold & Moyle, 1986).

Numerous studies have tested Darwin's naturalisation hypothesis, but the results are mixed (Diez, Sullivan, Hulme, Edwards, & Duncan, 2008; Duncan & Williams, 2002; Feng & van Kleunen, 2016; Finerty et al., 2016; Jiang, Tan, & Pu, 2010; Li, Cadotte, et al., 2015; Strauss, Webb, & Salamin, 2006; Yannelli, Koch, Jeschke, & Kollmann, 2017). Potential explanations are that the studies differ in the spatial and phylogenetic scales considered (Thuiller et al., 2010) and stages of invasions (Cadotte, Campbell, Li, Sodhi, & Mandrak, 2018; Li, Guo, et al., 2015), and are based on observations rather than experiments. Furthermore, the mixed findings may be because phylogenetic distance could indicate not only niche differences favouring coexistence but also competitive inequalities (i.e., species' differences in competitive ability) driving competitive exclusion (Chesson, 2000; Godoy, Kraft, & Levine, 2014). Here, we argue that the mixed results might also result from the potential confounding of phylogenetic distance with diversity of native communities. For instance, phylogenetic distance may have stronger effects as native diversity increases and thereby more niche space is occupied. However, very few studies have considered the potential confounding effects of native diversity when testing for Darwin's naturalisation hypothesis (but see Tan, Pu, Ryberg, & Jiang, 2015).

Observational studies frequently reported a positive association between the diversity of native communities and the likelihood of being invaded (e.g. Loiola et al., 2018; Stohlgren, Barnett, & Kartesz, 2003). However, with a few exceptions (Robinson & Dickerson, 1984), studies with experimentally constructed communities that tested for Elton's diversity–invasibility hypothesis often found evidence that diversity is a barrier to species invasions (e.g. Kennedy et al., 2002; Prieur-Richard, Lavorel, Grigulis, & Santos, 2000; Tilman, 1997). Despite these findings, an unresolved but critical question is to what degree the diversity effect is affected by phylogenetic distance between alien species and native residents. Some studies have implicitly recognised this by emphasising that not only the diversity but also alien species' identity (which affects alien–native phylogenetic distance) determines invasion success (e.g., Byun, de Blois, & Brisson, 2013; Crawley, Brown, Heard, & Edwards, 1999; Tan et al., 2015). However, a clear understanding of how the effect of diversity depends on alien–native phylogenetic distance is lacking.

The use of functional traits may help unravel mechanisms underlying the potential linkages between the two hypotheses, because traits are claimed to capture species' differences in niches and competitive ability (Kraft, Godoy, & Levine, 2015; Kunstler et al., 2012; McGill, Enquist, Weiher, & Westoby, 2006). Potentially important traits include plant height, specific leaf area, leaf size, and seed mass, which are at the core of plant strategies relevant to growth, survival, and reproduction (Díaz et al., 2016; Westoby, 1998). Plant height increases the ability to compete for light, leaf size is relevant for light interception and affects the leaf energy and water balance, SLA reflects a trade-off between carbon gain and longevity, and seed mass reflects a trade-off between seedling survival and colonisation ability (Díaz et al., 2016).

To disentangle the implicit linkage and potential interactions between the mechanisms underlying Darwin's and Elton's invasion hypotheses, we sowed seeds and planted seedlings of 5 alien herbaceous species into pot-mesocosms with native grassland communities of different diversities assembled with 36 native herbaceous species to test the success of alien species at different life stages. We used a phylogeny of all 41 study species and measured four of their functional traits (height, specific leaf area, leaf size, and seed mass) to quantify alien–native phylogenetic and functional distances, and phylogenetic and functional diversities of the native communities. We used these distance and diversity measures to test the following hypotheses: (a) alien–native phylogenetic and functional distances have a positive effect on the success of alien species (as predicted by Darwin's naturalisation hypothesis), (b) native phylogenetic and

functional diversities have a negative effect on the success of alien species (as predicted by Elton's diversity–invasibility hypothesis), and (c) the effect of alien–native phylogenetic and functional distances becomes stronger at higher native diversities, where niche availability is likely lower and results in more severe competition.

2 MATERIALS AND METHODS

2.1 Study species

We selected five alien species and 36 native species from the herbaceous flora of Germany (see Appendix S1 for the complete list of study species). The five alien species were *Bidens frondosa* (Asteraceae), *Senecio inaequidens* (Asteraceae), *Ambrosia artemisiifolia* (Asteraceae), *Epilobium ciliatum* (Onagraceae), and *Veronica persica* (Plantaginaceae), which are all native to non-European countries and are now invasive or widely naturalised in Europe (Appendix S1). The selection of the alien species reflects the fact that compared to other families, Asteraceae has the largest number of naturalised and invasive species (Pyšek et al., 2017). We selected 36 native herbaceous species that naturally occur in grasslands in Germany (Kühn, Durka, & Klotz, 2004) from six families (six species per family) (Appendix S1): Rosaceae, Asteraceae, Caryophyllaceae, Poaceae, Lamiaceae, and Plantaginaceae. We purchased seeds of the 36 native species from a commercial seed company (Rieger-Hofmann GmbH, Blaufelden, Germany), which produces seeds for restoration purposes and for creation of meadows and pastures on agricultural land. We obtained seeds of the five alien species from botanical gardens in Germany.

2.2 Design of native communities

We used the pool of 36 native species to design 90 native communities, including 36 monocultures, 36 three-species polycultures and 18 six-species polycultures. In three-species and six-species polycultures, we created a gradient of phylogenetic diversity by drawing species from a single family, partly different families or all different families (for details, see Appendix S1). This way, our design of communities could cover most of the phylogenetic space that the 36 native species could create. In this design, each of the 36 native species is equally represented in each level of species richness (but see a seed-contamination issue below).

2.3 Experimental setup

On 8 February 2015, we sowed c. 500 seeds of each of the 36 native species separately into trays (46 cm * 31 cm * 6.5 cm) filled with a standard potting soil (Gebr. Patzer GmbH & Co. KG, Sinntal, Germany), and then put all the trays in growth chambers (16 hr daylight, 21°C day/17°C night). Two weeks later, we did the same for each of the five alien species. They were sown later because we wanted to simulate invasion by alien species into already existing

native communities. On 23 February 2015, we filled 1,020 pots ($\varnothing = 18$ cm; H = 14 cm) with a 2:1 mixture of sand and standard potting soil enriched with 6.25 g slow-release fertiliser (Osmocote Pro 3–4 months; Everris GmbH, Nordhorn, Germany). Directly after this, we transplanted seedlings of the 36 native species into pots to assemble 11 copies of the 90 native communities (Appendix S1): five for testing success of the five alien species during early establishment (i.e., germination and survival of emerged seedlings; *sowing experiment*), five for testing success of growth and reproduction (*growth experiment*) of the five alien species, and one as the control of native communities without alien species. In each of these 990 pots, we transplanted a total of six native seedlings as illustrated in Figure S1 of Appendix S1. In addition, we had six control pots, each transplanted with a single alien plant without native residents (see below), for each of the five alien species (30 control pots in total) (Figure S1). Note that the alien and native control pots were not part of the sowing and growth experiments, but were only used to measure functional traits (see below).

Directly after transplanting, we randomly assigned the 450 pots for the *sowing experiment* to four tables, and the 450 pots for the *growth experiment*, as well as the 90 control pots without aliens and the 30 control pots without native residents, to another five tables, in three greenhouse compartments (21°C day/18°C night). One month after transplanting, we discovered that, due to contamination of one of the seed lots, about 43% and 10% of the supposed *Festuca ovina* were *Festuca pratensis* (not in our species pool) and *Poa pratensis* (in our species pool) respectively. We therefore used the actual composition of the contaminated communities in the data analyses.

2.4 Sowing experiment

About 3 weeks after transplanting (18–20 March 2015), for each of the five alien species separately, we sowed one seed into each of 25 positions in each native community (90 native communities \times 5 alien species, totalling 450 pots). The sowing was carried out using a mould with 25 holes (2 cm apart and arranged in a 5 \times 5 grid; see Figure S1 in Appendix S1). We watered the pots regularly to keep the soil moist. We checked germination of each seed about every 3 days until very few new germination happened (16 April 2015). On 13 May 2015, we scored survival of each emerged seedling. For each pot, we then calculated (a) germination rate, that is, the number of germinated seeds/25, and (b) survival rate, that is, the number of surviving seedlings/the number of germinated seeds. As germination of *B. frondosa* was overall very poor (only 5% of the pots showed some germination), we excluded *B. frondosa* from the respective analyses (i.e., for germination rate and seedling survival rate, see below).

2.5 Growth experiment and control pots

About 2 weeks after transplanting the native species (10 March 2015), we transplanted a single seedling of one of the five alien species in the centre of each of the 90 native communities (Figure S1 in Appendix S1; 90 communities \times 5 alien species, totalling 450 pots).

The same was done for each of the five alien species in the control pots (i.e., no native residents; 30 control pots in total), where we transplanted a single seedling of the respective alien species (Figure S1). In each of the 90 control native communities, we did not transplant any alien plant. Two days after transplanting, we counted the number of leaves of each alien seedling to estimate its initial biomass using a regression equation established for each alien species (biomass = coefficient * number of leaves + intercept) in a harvest of seedlings randomly selected from the germination trays on 15 March 2015 (for details, see Appendix S2). From 18 May to 4 June 2015, we harvested all alien plants in the *growth experiment* table by table. For each alien plant, we harvested above-ground biomass, and counted the total number of reproductive units (buds, flowers, and fruits) as a measure of reproduction. *Epilobium ciliatum* did not produce any reproductive units during the experimental period, so we excluded it from the analyses of reproduction.

2.6 Distance and diversity measures

For the calculation of functional distances and diversities, we measured vegetative height, and determined size and SLA of the largest healthy leaf (Pérez-Harguindeguy et al., 2013) for each plant in the 90 control native communities and the 30 alien control pots during the harvest (from 18 May to 4 June 2015). Leaves were digitised with a scanner (Expression 10000XL; Epson, Suwa, Japan), and we determined their areas (i.e., leaf sizes) with ImageJ (Abràmoff, Magalhães, & Ram, 2004). We then calculated SLA by dividing the area of each leaf by its dry mass. All the biomass was dried at 70°C for 72 hr prior to weighing. In addition, we determined seed-mass values of each species on five samples of 100 seeds that had been randomly selected from the same seed lots used for sowing our study species.

We calculated different measures of alien–native distance and native diversity based on phylogeny and functional traits. As phylogenetic measures, we calculated mean (Euclidean) phylogenetic distance between alien species and native residents (PDist), and phylogenetic diversity of native communities (PDiv, i.e., total branch length of the phylogenetic tree connecting all native residents within a community) (Faith, 1992), using the “*picante*” R package (Kembel et al., 2010). Details on the phylogenetic tree of all the study species are provided in Appendix S3.

As functional measures, we calculated mean multivariate (Euclidean) functional distance between alien species and native residents (FDist), and multivariate functional diversity of native communities (FDiv, i.e., total branch length of the dendrogram connecting all individuals of native residents within a community) (Cianciaruso, Batalha, Gaston, & Petchey, 2009), based on all four functional traits measured, using the “*vegan*” R package (Oksanen et al., 2017). Following the recommendations of Swenson (2014), we first log-transformed all traits to make them normally distributed, and then scaled them. After that, we did principal component analysis (PCA) to get orthogonal trait axes, and used the resulting three PCA axes to do the FDist and FDiv calculations.

In addition, to better understand the role of each single trait, we calculated mean alien–native univariate hierarchical functional distance (hFDist) and univariate absolute functional distance (aFDist), and univariate native functional diversity (FDiv), based on each single trait separately. For each trait, the hFDist was calculated as the trait value of the alien individual minus the trait mean of the six native individuals in a pot, and the aFDist was the mean Euclidean trait distance between the alien individual and the six native individuals. We calculated both hFDist and aFDist under the assumption that hFDist may capture competitive inequalities and aFDist may capture niche differences between alien species and native residents (see also Conti et al., 2018). This is based on the idea that competitive inequalities are directional whereas niche differences are directionless (Chesson, 2000, 2013).

Measures of alien–native phylogenetic and functional distances overall varied independently of measures of diversity of native communities ($|\text{Pearson correlation } (r)| < 0.50$, see Figures S3–S5 in Appendix S4), which helps avoid collinearity problems in the data analyses (see below). We also calculated minimum values of PDist, FDist, hFDist, and aFDist between alien species and native residents, but their effects (Appendix S5) were very similar to those of the mean values that we presented in the Section . Moreover, we also calculated mean phylogenetic distance (MPD), mean functional distance (MFD), mean nearest taxon distance (MNNTD), and mean nearest functional distance (MNF), as phylogenetic and functional diversity measures, but the results (see Appendix S6) were generally similar to those for the measures presented in Section Results. Especially, as MPD and MFD are strongly correlated with PDiv and FDiv, respectively ($r > 0.93$), the results based on these different measures were very similar (for details, see Appendix S6).

Trait values for height, leaf size, and SLA were determined as described above in the harvest at the end of the experiment. However, for the analysis of germination, which happened when the native competitors were still small, we calculated functional distance and diversity measures based on height, leaf size, and SLA as measured for each species on left-over seedlings randomly selected from the germination trays at the start of the experiment (for details, see Appendix S2). To test whether the traits are phylogenetically conserved, we calculated different measures of phylogenetic signal for each trait using the mean value of each trait of the study species (Appendix S7) (Münkemüller et al., 2012).

2.7 Data analysis

We used linear or generalised linear mixed-effects models (LMM or GLMM) to test how the response variables were affected by an alien–native distance measure, a native diversity measure, and their interaction. As response variables, we used germination rate and seedling survival rate (binomial GLMMs), natural log-transformed biomass (LMM), and number of reproductive units (GLMM with a Poisson-error structure), of alien species. In a first set of analyses, we used as explanatory variables phylogenetic distance (PDist), phylogenetic diversity (PDiv) and their interaction. In a second set of

TABLE 1 Results of mixed-effects models testing the effects of phylogenetic distance between alien species and residents (PDist), phylogenetic diversity of native communities (PDiv), and their interaction (PDist × PDiv) on germination rate, seedling survival rate, biomass, and reproduction of alien species. Up and down arrows next to significant ($p < 0.05$, in bold) p -values indicate positive and negative effects respectively

	df	Germination rate		Seedling survival rate		Biomass		Reproduction	
		χ^2	p	χ^2	p	χ^2	p	χ^2	p
Fixed									
Initial biomass	1	–	–	–	–	0.00	0.938	20.25	<0.001
PDist	1	0.16	0.687	3.84	0.049 ↑	4.69	0.030 ↑	10.17	<0.001↑
PDiv	1	2.62	0.104	2.68	0.101	1.30	0.252	216.52	<0.001↓
PDist × PDiv	1	0.17	0.679	0.37	0.540	1.16	0.281	9.29	0.002
Random									
		Variance		Variance		Variance		Variance	
Alien identity		0.87		0.00		1.26		0.43	
Compartment		0.00		0.00		0.00		0.12	
Table		0.01		0.00		0.00		0.14	

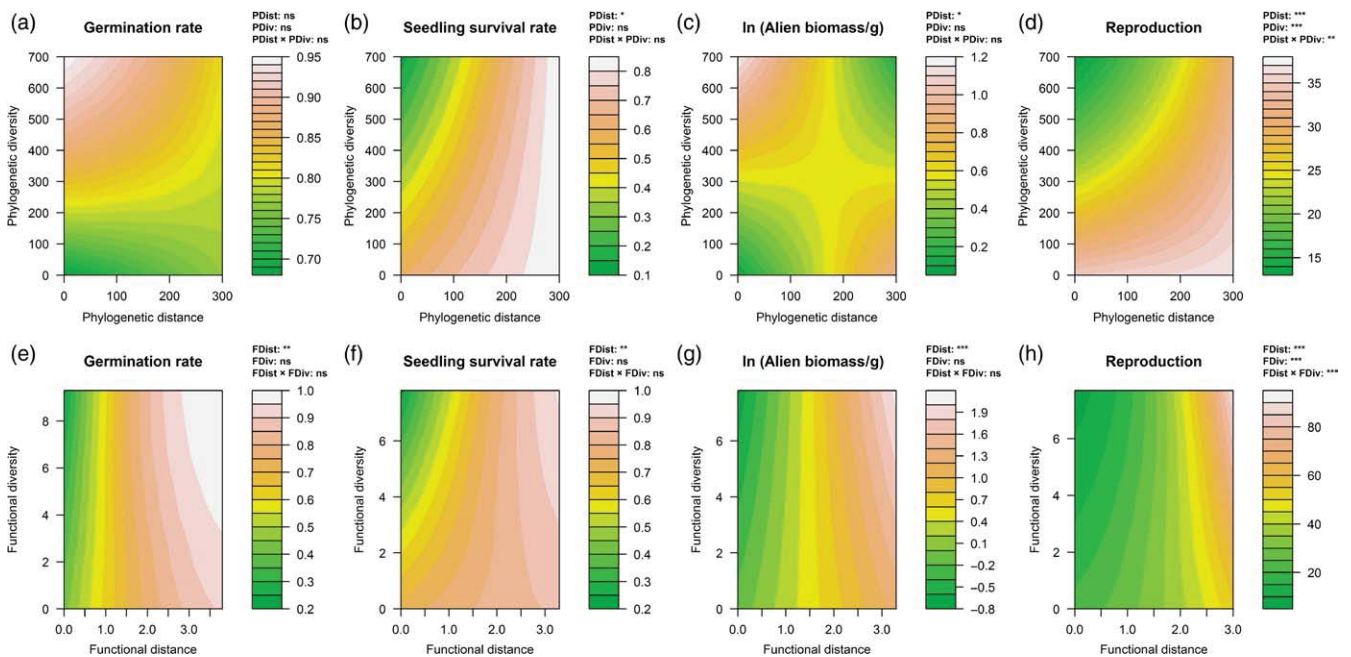


FIGURE 1 Contour plots illustrating the effects of: (a–d) phylogenetic distance between alien species and residents (PDist), phylogenetic diversity of native communities (PDiv), and their interaction (PDist × PDiv), and (e–h) multivariate functional distance between alien species and residents (FDist) and multivariate functional diversity of native communities (FDiv), based on all four functional traits (height, SLA, leaf size, and seed mass) jointly, and their interaction (FDist × FDiv), on germination rate, seedling survival rate, biomass, and reproduction (number of reproductive units) of alien species. For the statistical results, see Tables 1 and 2. Significance of the main effects (PDist, PDiv, FDist, and FDiv) and the interactions (PDiv × PDist, FDist × FDiv) is indicated as ns (i.e., non-significant, $p \geq 0.05$), * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$) in the upper right corner of each plot. The legend column on the right of each plot indicates values of the respective response variable [Colour figure can be viewed at wileyonlinelibrary.com]

analyses, we used as explanatory variables multivariate functional distance (FDist), multivariate functional diversity (FDiv) and their interaction. In a third set of analyses, to explore the effects of each single trait, we ran separate models in which univariate functional distance (hFDist or aFDist) and univariate functional diversity (FDiv)

based on the respective trait, and their interaction, were used as explanatory variables.

To account for variation in initial size of alien plants, we included their estimated initial biomass as a covariate in the models for biomass and reproduction of the aliens. As random factors in all the models,

TABLE 2 Results of mixed-effects models testing the effects of multivariate functional distance between alien species and residents (FDist) and multivariate functional diversity of native communities (FDiv), based on all four functional traits (height, SLA, leaf size, and seed mass) jointly, and their interaction (FDist × FDiv) on germination rate, seedling survival rate, biomass, and reproduction of alien species. Up and down arrows next to significant ($p < 0.05$, in bold) p -values indicate positive and negative effects respectively

	df	Germination rate		Seedling survival rate		Biomass		Reproduction	
		χ^2	p	χ^2	p	χ^2	p	χ^2	p
Fixed									
Initial biomass	1	–	–	–	–	0.21	0.640	2.64	0.103
FDist	1	8.36	0.004↑	8.18	0.004↑	29.63	<0.001↑	1,215.12	<0.001↑
FDiv	1	1.68	0.193	2.12	0.144	0.18	0.668	34.19	<0.001↓
FDist × FDiv	1	0.95	0.329	1.74	0.185	1.53	0.214	76.61	<0.001
Random									
		Variance		Variance		Variance		Variance	
Alien identity		0.89		0.00		1.42		0.59	
Compartment		0.00		0.00		0.00		0.10	
Table		0.01		0.00		0.00		0.16	

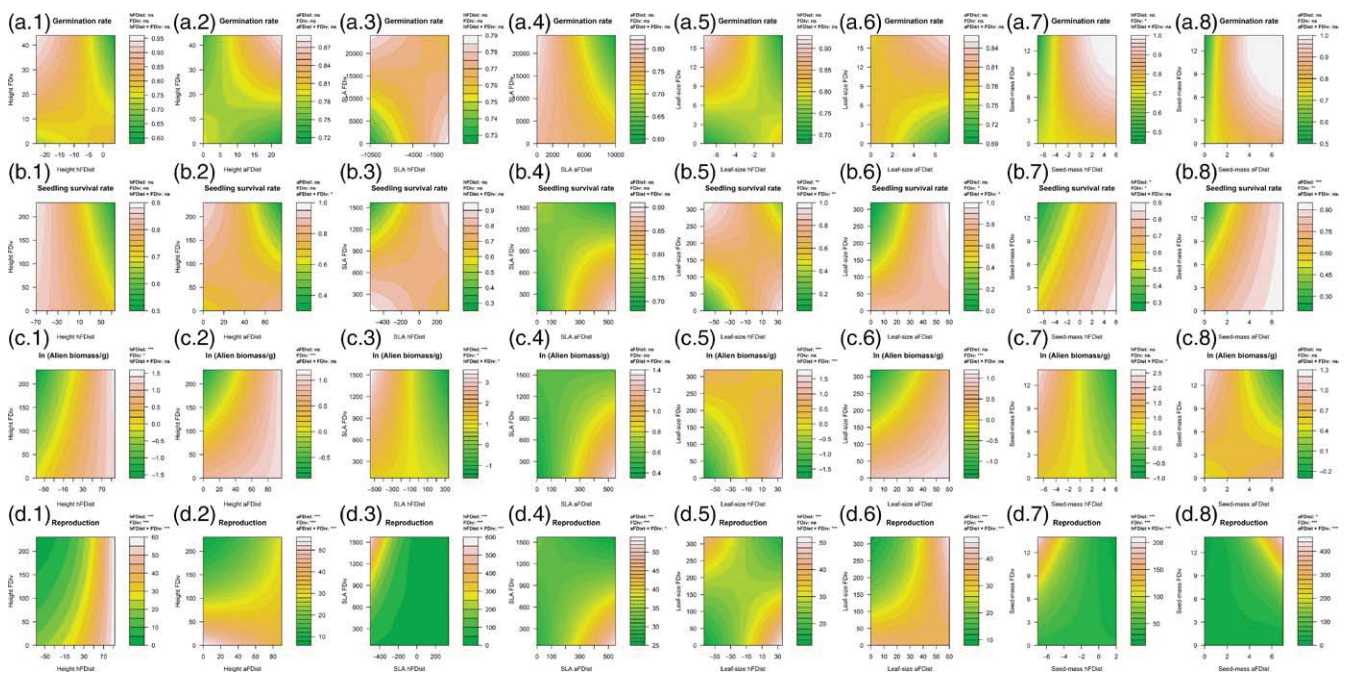


FIGURE 2 Contour plots illustrating the effects of either univariate hierarchical functional distance (hFDist) or univariate absolute functional distance (aFDist) between alien species and residents, univariate functional diversity of native communities (FDiv), based on each single functional trait (height, SLA, leaf size and seed mass) separately, and their interaction (hFDist or aFDist × FDiv), on (a.1–a.8) germination rate, (b.1–b.8) seedling survival rate, (c.1–c.8) biomass, and (d.1–d.8) reproduction (number of reproductive units) of alien species. For the statistical results, see Table 3. Significance of the main effects (hFDist, aFDist, and FDiv) and the interactions (hFDist × FDiv, aFDist × FDiv) is indicated as ns (i.e., non-significant, $p \geq 0.05$), * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$) in the upper right corner of each plot. The legend column on the right of each plot indicates values of the respective response variable [Colour figure can be viewed at wileyonlinelibrary.com]

we included identity of alien species and greenhouse table nested within the greenhouse compartment. In addition, for all the models, we checked whether the variance inflation factor was < 4 for each explanatory variable to ensure there was no collinearity problem (Zuur,

leno, Walker, Saveliev, & Smith, 2009). We used log-likelihood-ratio tests to assess the significance of each explanatory variable by comparing the full model to the model without the variable of interest (Zuur et al., 2009). We illustrated significant interaction effects in the

TABLE 3 Results of separate mixed-effects models testing the effects of either univariate hierarchical functional distance (hFDist) or univariate absolute functional distance (aFDist) between alien species and residents and univariate functional diversity of native communities (FDiv), based on each single functional trait (height, SLA, leaf size, and seed mass) separately, and their interaction (hFDist/aFDist × FDiv), on germination rate, seedling survival rate, biomass, and reproduction of alien species. Up and down arrows next to significant ($p < 0.05$, in bold) and marginally significant ($0.05 \leq p < 0.1$, in italic) p -values indicate positive and negative effects respectively.

	df	Germination rate		Seedling survival rate		Biomass		Reproduction	
		χ^2	p	χ^2	p	χ^2	p	χ^2	p
Height									
hFDist	1	0.02	0.893	1.15	0.283	11.80	<0.001 ↑	354.03	<0.001 ↑
FDiv	1	0.03	0.873	0.61	0.436	4.65	0.031 ↓	294.30	<0.001 ↓
hFDist × FDiv	1	0.50	0.482	0.29	0.591	2.76	0.096	201.94	<0.001
aFDist	1	0.08	0.784	0.29	0.587	2.47	0.116	30.66	<0.001 ↑
FDiv	1	0.04	0.849	0.12	0.727	15.03	<0.001 ↓	1,058.23	<0.001 ↓
aFDist × FDiv	1	0.14	0.705	5.01	0.025	2.54	0.111	149.37	<0.001
SLA									
hFDist	1	0.06	0.807	0.04	0.838	12.10	<0.001 ↓	1,171.26	<0.001 ↓
FDiv	1	0.00	0.969	0.06	0.813	4.77	0.029 ↓	451.84	<0.001 ↓
hFDist × FDiv	1	0.01	0.922	1.48	0.224	6.15	0.013	446.68	<0.001
aFDist	1	0.08	0.784	0.66	0.418	2.35	0.125	41.94	<0.001 ↑
FDiv	1	0.00	0.982	0.07	0.786	0.17	0.681	17.77	<0.001 ↓
aFDist × FDiv	1	0.03	0.857	0.10	0.748	0.15	0.701	5.52	0.019
Leaf size									
hFDist	1	0.25	0.619	6.61	0.009 ↑	18.30	<0.001 ↑	64.65	<0.001 ↑
FDiv	1	0.18	0.670	0.61	0.434	0.41	0.521	0.06	0.802
hFDist × FDiv	1	0.32	0.569	7.86	0.005	10.94	<0.001	150.26	<0.001
aFDist	1	0.27	0.601	3.64	0.057↑	3.42	0.064	111.00	<0.001 ↑
FDiv	1	0.19	0.663	4.08	0.043 ↓	13.72	<0.001 ↓	44.22	<0.001 ↓
aFDist × FDiv	1	0.08	0.774	5.31	0.021	2.51	0.113	37.34	<0.001
Seed mass									
hFDist	1	0.19	0.663	6.01	0.014 ↑	1.34	0.247	29.74	<0.001 ↓
FDiv	1	4.02	0.045 ↑	4.09	0.043 ↓	0.00	0.984	90.96	<0.001 ↓
hFDist × FDiv	1	1.61	0.205	0.04	0.834	4.97	0.026	137.02	<0.001
aFDist	1	1.43	0.233	13.94	<0.001 ↑	0.78	0.377	6.46	0.011 ↑
FDiv	1	2.74	0.098	9.33	0.002 ↓	0.11	0.735	120.90	<0.001 ↓
aFDist × FDiv	1	2.81	0.094	0.53	0.467	2.40	0.121	231.87	<0.001

respective models with contour plots using the “effects” R package (Fox & Hong, 2009) and the “filled.contour” function in R. All the analyses were performed in R 3.4.3 (R Core Team, 2018).

3 RESULTS

3.1 Phylogenetic and multivariate functional distances and diversities

Seedling survival, biomass, and reproduction of the aliens increased with increasing alien–native phylogenetic distance (Table 1, Figure 1b–d), and reproduction decreased with increasing phylogenetic diversity of the native communities (Table 1, Figure 1d). However, the positive

effect of phylogenetic distance on reproduction became weaker with decreasing phylogenetic diversity (significant PDiv × PDist interaction in Table 1, Figure 1d). The analyses using multivariate functional distance and diversity showed a similar pattern as the analyses using the phylogenetic measures (Table 2, Figure 2e–h). The only difference was that germination of the aliens also increased with increasing multivariate functional distance, in addition to seedling survival, biomass, and reproduction (Table 2, Figure 2e–h).

3.2 Univariate functional distances and diversities

Germination of the aliens was neither affected by alien–native hierarchical functional distance (hFDist) nor by absolute functional

distance (aFDist) of any trait (Table 3, Figure 2a.1–a.8). However, germination increased with increasing seed-mass functional diversity (FDiv) of the native communities (Table 3, Figure 2a.7 and a.8), but it was not affected by FDiv of the other functional traits (Table 3, Figure 2a.1–a.6). Subsequent survival of the emerged seedlings was on average positively affected by both hFDist and aFDist of leaf size and seed mass (Table 3, Figure 2b.5–b.8), but it was not affected by hFDist and aFDist of the other two traits (Table 3, Figure 2b.1–b.4). Moreover, seedling survival was on average negatively affected by FDiv of leaf size and seed mass (Table 3, Figure 2b.6–b.8), but it was not affected by FDiv of the other two traits (Table 3, Figure 2b.1–b.4). However, the overall positive effect of leaf-size hFDist on seedling survival turned into a negative effect for large leaf-size FDiv values, as indicated by a significant hFDist \times FDiv interaction (Table 3, Figure 2b.5). The positive effect of leaf-size aFDist on seedling survival was only marginally significant, but it became stronger with increasing values of leaf-size FDiv (Table 3, Figure 2b.6). Furthermore, although the overall effect of height aFDist on seedling survival was not significant, it changed from weakly positive to negative with increasing height FDiv (Table 3; Figure 2b.2).

Biomass and reproduction of the aliens largely showed similar patterns, although the significances of the effects sometimes varied (Table 3, Figure 2c.1–c.8 and d.1–d.8). Biomass and reproduction increased with increasing hFDist of height and leaf size (Table 3, Figure 2c.1, c.5, d.1, and d.5). On the other hand, biomass and reproduction decreased with increasing hFDist of SLA (Table 3, Figure 2c.3 and d.3), and for reproduction also with increasing hFDist of seed mass (Table 3, Figure 2d.7). Biomass and reproduction both increased with increasing leaf-size aFDist (Table 3, Figure 2c.6 and d.6), and reproduction also increased with increasing aFDist of height, SLA and seed mass (Table 3, Figure 2d.2, d.4, and d.8). Moreover, biomass and reproduction decreased with increasing FDiv of height, SLA and leaf size (Table 3, Figure 2c.1–c.3, c.6, d.1–d.4, and d.6), and for reproduction also with increasing FDiv of seed mass (Table 3, Figure 2d.7 and d.8).

The strength and even the direction of effects of alien–native distances of many of the functional traits on biomass and reproduction of the aliens frequently depended on native diversities of the respective traits, as shown by many significant hFDist \times FDiv and aFDist \times FDiv interactions (Table 3). The positive effect of height hFDist on reproduction increased with increasing height FDiv (Table 3, Figure 2c.1). However, the overall positive effects of leaf-size hFDist on both biomass and reproduction turned into negative effects with increasing leaf-size FDiv (Table 3, Figure 2c.5 and d.5). The negative effects of hFDist of SLA and seed mass on biomass and reproduction became stronger when FDiv in the respective traits increased (Table 3, Figure 2c.3, 2c.7, d.3, and d.7). So, with the exception of leaf size, the effects (positive or negative, depending on traits) of functional trait hFDist on biomass and reproduction of the aliens became stronger with increasing FDiv of the respective functional trait. Similarly, with the exception of SLA, the positive effects of functional trait aFDist on reproduction became stronger with increasing FDiv of the respective functional trait (Table 3, Figure 2d.2, d.4, d.6, and d.8).

4 DISCUSSION

In this study, we used phylogenetic and functional measures of alien–native distance and native diversity to assess the links between Darwin's naturalisation hypothesis and Elton's diversity–invasibility hypothesis in experimental grassland communities. In support of Darwin's hypothesis, we found that alien–native distance increased performance of the aliens. In support of Elton's hypothesis, we found that diversity of the native communities reduced performance of the aliens. More importantly, in line with our hypothesis, we showed that the effects of alien–native phylogenetic and multivariate functional distance became stronger when native diversity increased. The similar patterns were shown by our analyses with single traits, with both hierarchical trait distances (indicative of competitive inequalities) and absolute trait distances (indicative of niche differences) between alien and native species having stronger effects at higher native diversities, where competition is more severe.

4.1 Darwin's naturalisation hypothesis

In support of the predictions of Darwin's naturalisation hypothesis, increasing values of the different measures of alien–native distance resulted in enhanced performance (from germination to reproduction) of our five target invasive species. This is in line with some previous studies which also found evidence in support of the hypothesis (Feng & van Kleunen, 2016; Jiang et al., 2010; Strauss et al., 2006), but others showed that the effects of alien–native distances were dependent on whether phylogenetic distance indicates niche preadaptation or competitive interactions, and on the stages of invasion (Diez et al., 2008; Duncan & Williams, 2002; Li, Cadotte, et al., 2015; Li, Guo, et al., 2015). Moreover, in our study, the effects of multivariate functional distance were much stronger than those of phylogenetic distance, which suggests that multiple traits-based functional distance is better than phylogenetic distance in capturing niche differences that favour coexistence between the aliens and the native residents. This may be explained by the fact that, although there was generally a strong phylogenetic signal in all the four traits, SLA and leaf size tended to have a relatively weaker phylogenetic signal (Appendix S7), but functional distances based on each of these two traits had strong effects on the performance of the alien species.

Our analyses with univariate measures of hierarchical and absolute functional distances provided more insights into the underlying mechanisms, as hierarchical trait distances may indicate alien–native competitive inequalities and absolute trait distances may indicate alien–native niche differences. Interestingly, seedling survival increased but reproduction decreased as the alien–native univariate hierarchical functional distance based on seed mass increased. Seed-mass differences themselves are not expressed in the experiment, but seed mass is likely to be positively associated with seedling size. Possibly, our findings indicate that the large seedlings of large-seeded species are more likely to survive, but that this is at a cost of reproduction (Díaz et al., 2016), at least during the period that our experiment lasted. In line with several other studies (e.g., Conti et al., 2018; Feng

& van Kleunen, 2016), our results showed that the effects of univariate hierarchical functional distance based on plant height or leaf size on the performance of the alien species were positive, whereas those based on SLA were negative. This shows that alien plants are more successful if they are taller and have larger leaves with a lower SLA than the native residents. Although a high SLA is usually associated with a fast relative growth rate (e.g., Poorter & Remkes, 1990), several recent studies found that a greater SLA tends to be associated with greater competitive disadvantage (Feng & van Kleunen, 2016; Kraft et al., 2015; Kunstler et al., 2016). In short, our findings thus confirm that these univariate hierarchical functional distances are indeed able to capture alien–native competitive inequalities.

The performance of the alien species in our study increased as alien–native univariate absolute functional distance based on each single trait separately increased. This may imply that these univariate functional distance measures are also able to capture alien–native niche differences. For example, the univariate functional distance of height or leaf size may capture alien–native niche differences in utilising light resources, while the distance of SLA or seed mass may indicate some temporal alien–native niche differences (e.g., utilising resources in different times) because both SLA and seed mass could affect plant growth rate. However, the multivariate functional distance based on all four traits jointly had greater explanatory power than the univariate ones (Appendix S5). This suggests that the multivariate distance may better reflect alien–native niche differences than the univariate ones, because the former may capture the multidimensional niche space while the latter may only capture one aspect of the space. Finally, one should note that, although phylogeny and traits offer a useful tool to infer alien–native competitive and niche differences, a more rigorous quantification of these differences requires parameterisation of competition models with data of population dynamics (Godoy & Levine, 2014; Godoy et al., 2014).

4.2 Elton's diversity–invasibility hypothesis

Performance of our selected alien plants decreased as diversity of the native communities increased, thus supporting what Elton's diversity–invasibility hypothesis posed, and in line with previous studies testing this hypothesis (e.g., Crawley et al., 1999; Kennedy et al., 2002; Prieur-Richard et al., 2000; Tilman, 1997). These effects were in general much stronger for biomass and reproduction than for germination and seedling survival. The effect of seed-mass functional diversity on germination was even positive instead of negative. The causes for this are not clear. Yet, this might imply that diversity-driven biotic resistance acts mainly against later life stages of alien species, as suggested by previous studies (Sun, Müller-Schärer, Maron, & Schaffner, 2015; Theoharides & Dukes, 2007).

Phylogenetic diversity and multivariate functional diversity tended to have stronger effects on the alien species than species richness per se (Appendix S5), which may be because the former can better capture niche availability of native communities than the latter (Hooper & Dukes, 2010; Srivastava, Cadotte, MacDonald, Marushia, & Mirotnick, 2012). Interestingly, our results showed

that univariate functional diversity measures (especially the ones for plant height) had greater explanatory power than phylogenetic diversity and multivariate functional diversity (Appendix S5). The reasons for this are not clear, but we speculate that this may be because multivariate functional diversity mainly indicates the occupancy of niche space. However, diversity measures based on single traits (e.g., height) may also reflect the occupancy of competitive space (i.e., how competitive a community is), if some traits are more related to competitive inequalities than to niche differences (Kraft et al., 2015; Kunstler et al., 2012).

4.3 Interactions between the mechanisms underlying Darwin's and Elton's invasion hypotheses

As the mechanisms underlying Darwin's and Elton's invasion hypotheses are both rooted in ideas of species coexistence (Levine & D'Antonio, 1999; MacDougall et al., 2009), the two hypotheses are inherently connected. Indeed, our results showed that the strength and even direction of the effects of alien–native distance on the success of alien species frequently depended on native diversity. For instance, the strong positive effect of phylogenetic distance on reproduction was only manifested when phylogenetic diversity was high. We argue that this may be because competition between alien species and native residents was generally stronger in more diverse communities where the occupancy of niches is higher. As a result, the effect of phylogenetic distance is more pronounced in more diverse communities but becomes negligible in less diverse communities.

The similar patterns were reflected in our results from univariate functional distances, with much stronger effect of these distances in more diverse communities. For instance, our results showed that the effects of univariate hierarchical functional distances of height, SLA, and seed mass on biomass and reproduction overall became much stronger when univariate functional diversity of the respective trait increased. One should note, however, that the effect of hierarchical functional distance in height was generally positive whereas those in SLA and seed mass were generally negative. This is because a greater competitive ability is characterised by greater height, and smaller SLA and seed mass. However, the effect of leaf-size hierarchical functional distance showed a different pattern in its interactions with leaf-size functional diversity, that is, the effect tended to change from positive to negative as the diversity increased. We suspect this may at least partly result from the inherent strong correlation ($r = -0.55$) between the distance and the diversity measure of leaf size (Figure S4 in Appendix S4). This finding emphasises that the effects of alien–native distance and native diversity may in many studies be confounded. Moreover, we also found a much stronger effect of univariate absolute functional distance measures of height, leaf size, and seed mass on reproduction when univariate functional diversity of the respective traits was greater. These interactions are very similar to the interaction between the effects of phylogenetic distance and phylogenetic diversity on reproduction, which again indicates the stronger competition between alien species and native residents in more diverse communities.

5 CONCLUSIONS

To the best of our knowledge, our study is the first one explicitly demonstrating how two classical invasion hypotheses, one proposed by Darwin (1859) and one by Elton (1958), are linked in explaining the success of alien species in experimental grassland communities. While we particularly focused on how the effect of alien–native distance changes with native diversity, these interactions are of course bidirectional. In other words, the effect of native diversity also depends on alien–native distance. In general, our results indicate that the effect of one (distance or diversity) becomes stronger when the other makes the competition between the alien and native residents more severe. This finding may help explain some of the puzzling results of studies that tested the two hypotheses separately. It also emphasises the importance of integrating different ideas and hypotheses to gain a more complete understanding of invasion mechanisms (Catford et al., 2009; Jeschke, 2014). Finally, future studies should rigorously quantify species' differences in niches and competitive ability to more thoroughly understand causes and consequences of species invasions in the framework of modern co-existence theory.

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AUTHORS' CONTRIBUTIONS

Y.H.F., T.D.F., and M.v.K. designed the experiment; Y.H.F. and T.D.F. performed the experiment; Y.H.F. analysed data; Y.H.F. drafted the manuscript, which T.D.F. and M.v.K. substantially improved.

ORCID

Yanhao Feng  <http://orcid.org/0000-0003-0460-4883>

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