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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 have not been explicitly disentangled in one experimental study before.
2. To disentangle the potential links and interactions, we created greenhouse mesocosms with 90 native grassland communities of different diversities with 36 herbaceous native species and introduced each of five herbaceous alien species as seeds and seedlings. Specifically, we tested how the alien-native (phylogenetic or functional) *distance* and the native *diversity* affected each other in their effects on germination, seedling survival, growth and reproduction of the aliens. To disentangle the underlying mechanisms of the interactions, we used phylogeny and four functional traits (plant height, specific leaf area, leaf size, seed mass) to calculate different measures of phylogenetic and functional *distance* and *diversity*.
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 are 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. More importantly, we found that the effects of alien-native phylogenetic and multivariate functional distance strengthened 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) reinforced 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

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

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 invasible (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 et al. 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 (Duncan & Williams 2002; Strauss, Webb & Salamin 2006; Diez *et al.* 2008; Jiang, Tan & Pu 2010; Li *et al.* 2015a; Feng & van Kleunen 2016; Yannelli *et al.* 2017). Potential explanations are that the studies differ in the spatial and phylogenetic scales considered (Thuiller *et al.* 2010) and stages of invasions (Li *et al.* 2015b; Cadotte *et al.* 2018), and are based on observations rather than experiments. Furthermore, the mixed findings may also be because phylogenetic distance could indicate not only niche differences favouring coexistence but also competitive inequality (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 *et al.* 2015).

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. Tilman 1997; Prieur-Richard *et al.* 2000; Kennedy *et al.* 2002). 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 recent studies have implicitly recognized this by emphasizing that not only the diversity but also alien species' identity (which affects alien-native phylogenetic distance) determines invasion success (Crawley *et al.* 1999a; Hooper & Dukes 2010; Byun, de Blois & Brisson 2013; 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 disentangle the implicit linkage and potential interactions between the mechanisms underlying Darwin's and Elton's invasion hypotheses, because traits are claimed to capture species' differences in niches and competitive ability (McGill *et al.* 2006; Violle & Jiang 2009; Kunstler *et al.* 2012; Godoy & Levine 2014; Kraft, Godoy & Levine 2015). 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 (Westoby 1998; Díaz *et al.* 2016). Plant height corresponds with the ability to compete for light resources, leaf size is relevant for light interception and affects 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 five 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 diversity of the native communities. We used these distance and diversity measures to test the following hypothesis: the effect of alien-native phylogenetic and functional distances on the success of alien species strengthens at higher native diversities where niche availability is supposed to be lower and thereby competition is more severe.

Materials and Methods

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 most number of naturalized and invasive species (Kowarik 2002; Jarošik, Pyšek & Kadlec 2011; Pyšek et al. 2017). We selected 36 native 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.

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 much of 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).

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 (16h 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 intended to first establish native communities and then introduced the aliens into the communities, to simulate how invasion occurs in nature. On 23 February 2015, we filled 1020 pots (ø = 18 cm; H = 14 cm) with a 2:1 mixture of sand and standard potting soil enriched with 6.25 g slow-release fertilizer (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 times 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 Fig. 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) (Fig. S1). Note that the alien and native control pots 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 *F. 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.

Sowing experiment

About three weeks after transplanting (18 - 20 March 2015), for each of the five alien species we sowed one seed into each of 25 positions in each native community separately (90 native communities x 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 x 5 grid; see Fig. S1 in Appendix S1). We watered the pots regularly to keep the soil moist. We checked germination of each seed about every three 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 i) germination rate, i.e. the number of germinated seeds / 25, and ii) survival rate, i.e. 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).

Growth experiment and control pots

About two 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 (Fig. S1 in Appendix S1; 90 communities x 5 alien species, totalling 450 pots). The same procedure was done for each of the five alien species in the control pots (i.e. no native residents; 30 control pots in total), whereby we transplanted a single seedling of the respective alien species (Fig. 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 plant, we harvested aboveground biomass, and for the alien plants we also 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, and therefore we excluded it from the analyses of reproduction.

Distance and diversity measures

For the calculation of functional distance and diversity, 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 digitized 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 hours prior to weighing. In addition, we determined seed-mass values of each species on five samples of 100 randomly selected purchased seeds.

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 trait 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 *et al.* 2009), based on all four functional traits measured, using the "*vegan*" R package (Oksanen *et al.* 2017). Following the recommendations of Swenson (2014), we 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 3 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; Chesson 2013).

Measures of alien-native phylogenetic and functional distances overall varied independently of measures of diversity of native communities (| Pearson correlation (r) | < 0.50, see Figs 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 *Results*. Moreover, we also calculated

MPD (mean phylogenetic distance)/MFD (mean functional distance), and MNTD (mean nearest taxon distance)/MNTD (mean nearest functional distance), as phylogenetic and functional diversity measures, but the results were generally similar (see Appendix S6). Especially, as MPD/MFD are extremely correlated with PDiv/FDiv ($r>0.93$), the results based on the two were very similar (for the 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).

Data analysis

We used linear or generalized 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 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 (see above) as a covariate in the models for biomass and reproduction of the aliens. As random factors in all the models, we included identity of alien species and greenhouse table nested within 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 et al. 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 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).

Results

Phylogenetic and multivariate functional distances and diversities

Seedling survival, biomass and reproduction of the aliens increased with increasing alien-native phylogenetic distance (Table 1, Fig. 1b-d), and reproduction decreased with increasing phylogenetic diversity of the native communities (Table 1, Fig. 1d). However, the positive effect of phylogenetic distance on reproduction became weaker with decreasing phylogenetic diversity (significant PDiv × PDist interaction in Table 1, Fig. 1d). The analyses using multivariate functional distance and diversity showed a similar pattern as the analyses using the phylogenetic measures (Table 2, Fig. 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, Fig. 2e-h).

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, Figs 2a.1-a.8). However, germination increased with increasing seed-mass functional diversity (FDiv) of the native communities (Table 3, Figs 2a.7 and a.8), but it was not affected by FDiv of the other functional traits (Table 3, Figs 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, Figs 2b.5-8), but it was not affected by both hFDist and aFDist of the other two traits (Table 3, Figs 2b.1-4). Moreover, seedling survival was on average negatively affected by FDiv of leaf size and seed mass (Table 3, Figs 2b.6-b.8), but it was not affected by FDiv of the other two traits (Table 3, Figs 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 × FDiv interaction (Table 3, Fig. 2b.5). Moreover, 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, Fig. 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; Fig. 2b.2).

Biomass and reproduction of the aliens largely showed similar patterns, although the significances of the effects sometimes varied (Table 3, Figs 2c.1-c.8 and 2d.1-d.8). Biomass and reproduction increased with increasing hFDist of height and leaf size (Table 3, Figs 2c.1 and c.5, Figs 2d.1 and d.5). On the other hand, biomass and reproduction decreased with increasing hFDist of SLA (Table 3, Figs 2c.3 and d.3), and for reproduction also with increasing hFDist of seed mass (Table 3, Fig. 2d.7). Biomass and reproduction both increased with increasing leaf-size aFDist (Table 3, Figs 2c.6 and 2d.6), and reproduction also increased with increasing aFDist of height, SLA and seed mass (Table 3, Figs 2d.2, d.4 and d.8). Moreover, biomass and reproduction decreased with increasing FDiv of height, SLA and leaf size (Table 3, Figs 2c.1-c.3 and 2c.6, and Figs 2d.1-d.4 and 2d.6), and for reproduction also with increasing FDiv of seed mass (Table 3, Figs 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 × FDiv and aFDist × FDiv interactions (Table 3). The positive effect of height hFDist on reproduction increased with increasing height FDiv (Table 3, Fig. 3c.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, Figs 2c.5 and 2d.5). The negative effects of hFDist of SLA and seed mass on biomass and reproduction became stronger as FDiv in the respective traits increased (Table 3, Figs 2c.3, 2c.7, 2d.3 and 2d.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, Figs 2d.2, d.4, d.6 and d.8).

Discussion

In this study, we used phylogenetic and different functional trait 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 strengthened as native diversity increased. The same pattern was 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 reinforcing at higher native diversities where competition is more severe.

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 target invasive species. This is in line with some previous studies which also found supportive evidence for the hypothesis (Strauss, Webb & Salamin 2006; Jiang, Tan & Pu 2010; Feng & van Kleunen 2016), but others showed that the effects of alien-native distances were dependent on whether phylogenetic distance indicates niche preadaptation or competitive interactions, and on stages of invasion (Duncan & Williams 2002; Diez *et al.* 2008; Li *et al.* 2015a; Li *et al.* 2015b). 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 is generally strong phylogenetic signal in all the four traits, SLA and leaf size that also had strong effects tend to have relatively weaker phylogenetic signal (Appendix S7). Moreover, it is also possible that other important traits not covered here (e.g. leaf N) may have made multivariate functional distance a better predictor than phylogenetic distance.

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 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 finding indicates 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. Feng & van Kleunen 2016; Conti *et al.* 2018), 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 (Kraft, Godoy & Levine 2015; Feng & van Kleunen 2016; 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 utilizing light resources, while the distance of SLA or seed mass may indicate some temporal alien-native niche differences (e.g. utilizing 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 this space. Finally, note that, although phylogeny and traits offer a useful tool to infer alien-native competitive and niche differences, to more rigorously quantify these differences, one needs to parameterize competition models with population dynamics data (Godoy, Kraft & Levine 2014; Godoy & Levine 2014).

Elton’s diversity-invasibility hypothesis

Performance of our selected aliens plants decreased as diversity of the native communities increased, thus supporting what posed by Elton’s diversity-invasibility hypothesis and in line with previous studies testing for the hypothesis (e.g. Tilman 1997; Crawley *et al.* 1999b; Prieur-Richard *et al.* 2000; Kennedy *et al.* 2002). These effects were in general much stronger for biomass and reproduction than for germination and seedling survival. Moreover, the causes explaining the positive effect of seed-mass functional diversity on germination are less clear. Yet, these results might imply that diversity-driven biotic resistance acts mainly against later life stages of alien species, as suggested by previous studies (Theoharides & Dukes 2007; Sun et al. 2015).

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 *et al.* 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 reason for this is 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 (Kunstler *et al.* 2012; Kraft, Godoy & Levine 2015).

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, Gilbert & Levine 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 same pattern is 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. 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 characterized 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, i.e. 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 (Fig. S4 in Appendix S4). This finding emphasizes 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.

Conclusion

Our study is to the best of our knowledge the first one that explicitly demonstrates 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 focused particularly 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 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 emphasizes the importance of integrating different ideas and hypotheses to gain a more complete understanding of invasion mechanisms (Catford, Jansson & Nilsson 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 coexistence theory.

Acknowledgements

We thank Otmar Ficht, Claudia Martin, Dominika Kundel, Denise Wagner, Lena Horstmeyer, Katya Stift-Mamonova, Yannik Büchi, Sigurd Holstein, Nicholas Sauer, Yanjie Liu, Yan Li, Mialy Razanajatovo, Noëlie Maurel, Eva Malecore, Alice Garnier and Fieya Bors for practical assistance. YHF is grateful to the China Scholarship Council (CSC) for support and TDF thanks the ENS de Lyon for financial support.

Authors' contributions

YHF, TDF and MvK designed the experiment. YHF and TDF performed the experiment. YHF analyzed data. YHF drafted the manuscript, which TDF and MvK substantially improved.

Data Accessibility

The data associated with this paper will be archived in the Dryad repository.

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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.

			Germination rate		Seedling survival rate		Biomass		Reproduction	
		df	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**
			Variance		Variance		Variance		Variance	
Random	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	

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.

			Germination rate		**Seedling survival rate**		**Biomass**		**Reproduction**	
		df	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**↑	1215.12	**<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**
			Variance		Variance		Variance		Variance	
Random	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	

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 ($0.05 \le p < 0.1$, in italic) p values indicate positive and negative effects, respectively.

			Germination rate		Seedling survival rate		Biomass		Reproduction	
		df	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**↓	1058.23	**<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**↓	1171.26	**<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**

Fig. 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, 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 column right to each plot indicates values of the respective response variable.

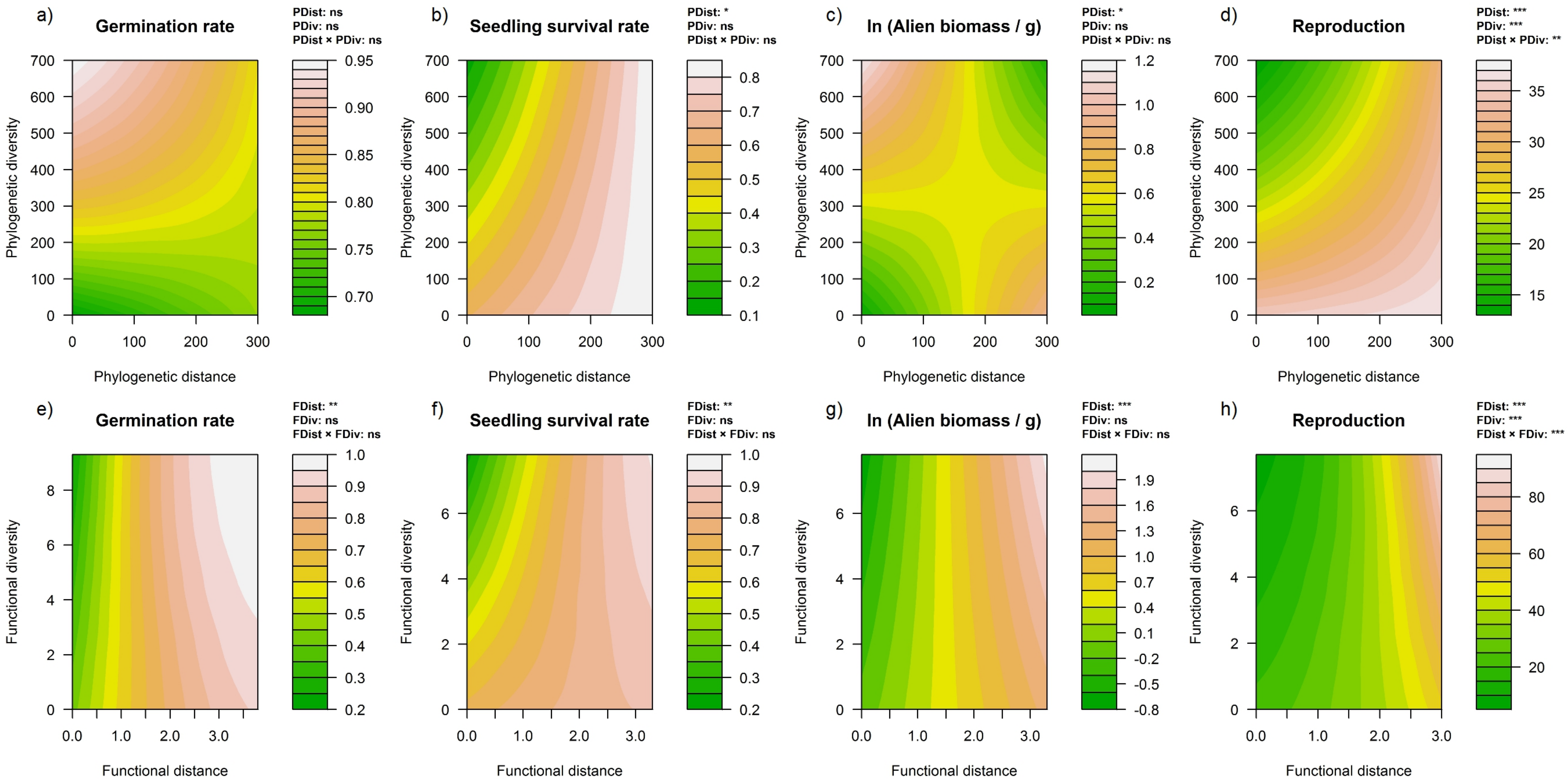
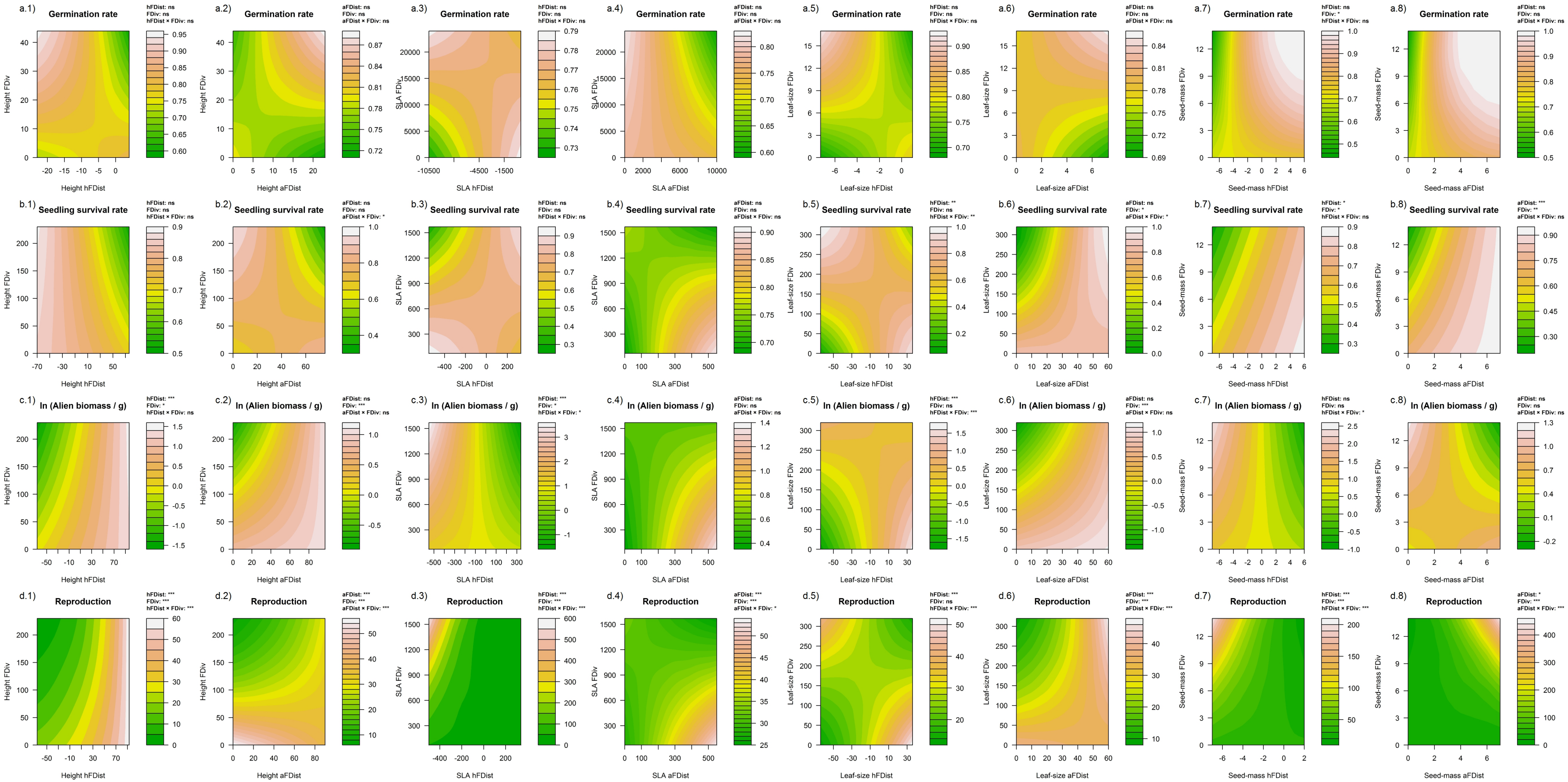

a)
Germination rate
PDist: ns
PDiv: ns
PDist × PDiv: ns
Phylogenetic diversity
Phylogenetic distance
b)
Seedling survival rate
PDist: *
PDiv: ns
PDist × PDiv: ns
Phylogenetic diversity
Phylogenetic distance
c)
ln (Alien biomass / g)
PDist: *
PDiv: ns
PDist × PDiv: ns
Phylogenetic diversity
Phylogenetic distance
d)
Reproduction
PDist: ***
PDiv: ***
PDist × PDiv: **
Phylogenetic diversity
Phylogenetic distance
e)
Germination rate
FDist: **
FDiv: ns
FDist × FDiv: ns
Functional diversity
Functional distance
f)
Seedling survival rate
FDist: **
FDiv: ns
FDist × FDiv: ns
Functional diversity
Functional distance
g)
ln (Alien biomass / g)
FDist: ***
FDiv: ns
FDist × FDiv: ns
Functional diversity
Functional distance
h)
Reproduction
FDist: ***
FDiv: ***
FDist × FDiv: ***
Functional diversity
Functional distance

Fig. 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 / 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, 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 column right to each plot indicates values of the respective response variable.



a.1) Germination rate
a.2) Germination rate
a.3) Germination rate
a.4) Germination rate
a.5) Germination rate
a.6) Germination rate
a.7) Germination rate
a.8) Germination rate
b.1) Seedling survival rate
b.2) Seedling survival rate
b.3) Seedling survival rate
b.4) Seedling survival rate
b.5) Seedling survival rate
b.6) Seedling survival rate
b.7) Seedling survival rate
b.8) Seedling survival rate
c.1) ln (Alien biomass / g)
c.2) ln (Alien biomass / g)
c.3) ln (Alien biomass / g)
c.4) ln (Alien biomass / g)
c.5) ln (Alien biomass / g)
c.6) ln (Alien biomass / g)
c.7) ln (Alien biomass / g)
c.8) ln (Alien biomass / g)
d.1) Reproduction
d.2) Reproduction
d.3) Reproduction
d.4) Reproduction
d.5) Reproduction
d.6) Reproduction
d.7) Reproduction
d.8) Reproduction
Height FDiv
SLA FDiv
Leaf-size FDiv
Seed-mass FDiv
Height hFDist
Height aFDist
SLA hFDist
SLA aFDist
Leaf-size hFDist
Leaf-size aFDist
Seed-mass hFDist
Seed-mass aFDist