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1 **Linking Darwin's naturalisation hypothesis and Elton's diversity-invasibility**  
2 **hypothesis in experimental grassland communities**

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19 **Abstract**

20 1. Darwin's naturalisation hypothesis posing that phylogenetic distance of alien species  
21 to native residents predicts invasion success, and Elton's diversity-invasibility  
22 hypothesis posing that diversity of native communities confers resistance to invasion,  
23 are both rooted in ideas of species coexistence. Because the two hypotheses are  
24 inherently linked, the mechanisms underlying them may interact in driving the  
25 invasion success. Even so, these have not been explicitly disentangled in one  
26 experimental study before.

27 2. To disentangle the potential links and interactions, we created greenhouse  
28 mesocosms with 90 native grassland communities of different diversities with 36  
29 herbaceous native species and introduced each of five herbaceous alien species as  
30 seeds and seedlings. Specifically, we tested how the alien-native (phylogenetic or  
31 functional) *distance* and the native *diversity* affected each other in their effects on  
32 germination, seedling survival, growth and reproduction of the aliens. To disentangle  
33 the underlying mechanisms of the interactions, we used phylogeny and four  
34 functional traits (plant height, specific leaf area, leaf size, seed mass) to calculate  
35 different measures of phylogenetic and functional *distance* and *diversity*.

36 3. Overall, our results supported both hypotheses. Multivariate functional distance  
37 based on four traits jointly had stronger positive effects than phylogenetic distance  
38 and the univariate ones based on each trait separately. Moreover, the aliens were  
39 more successful if they are more competitive by being taller and having larger leaves  
40 with a lower SLA than the native residents. Univariate functional diversity based on

41 each trait separately had stronger negative effects than phylogenetic and multivariate  
42 functional diversity. More importantly, we found that the effects of alien-native  
43 phylogenetic and multivariate functional distance strengthened as diversity increased.  
44 Our analyses with single traits also showed that the strength of the effects of both  
45 alien-native hierarchical functional *distances* (indicative of competitive inequalities)  
46 and absolute functional *distances* (indicative of niche differences) reinforced at higher  
47 *diversities* where competition is more severe.

48 4. *Synthesis*. Our study explicitly demonstrates for the first time how the mechanisms  
49 underlying the two classical invasion hypotheses interact in driving invasion success  
50 in grassland communities. This may help to explain some of the puzzling results of  
51 studies testing either of the two hypotheses.

## 52 **Keywords**

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

## 55 Introduction

56 A major quest in ecology is to understand the mechanisms driving the success of alien  
57 species in native communities. While numerous invasion hypotheses have been proposed, it  
58 is suggested that the mechanisms associated with some of them may be implicitly interlinked  
59 (Catford, Jansson & Nilsson 2009; Jeschke 2014). In essence, whether or not alien species  
60 invade native communities is a question of coexistence between alien species and native  
61 residents. Classical invasion hypotheses, which are often rooted in ideas of species  
62 coexistence (Levine & D'Antonio 1999; MacDougall, Gilbert & Levine 2009), have long  
63 focused on identifying the characteristics predisposing alien species to become invasive and  
64 the properties that render native communities invulnerable (Richardson & Pyšek 2006). Darwin  
65 (1859) posited that alien species will be more successful in a native community if they are  
66 phylogenetically distantly related to native residents (Darwin's naturalisation hypothesis),  
67 because phylogenetic distance may indicate niche differences favouring coexistence (Violle  
68 *et al.* 2011). Elton (1958) proposed that alien species will be less successful in more diverse  
69 native communities (Elton's diversity-invasibility hypothesis), where fewer unoccupied niches  
70 are available for newcomers (Herbold & Moyle 1986).

71 Numerous studies have tested Darwin's naturalisation hypothesis, but the results are  
72 mixed (Duncan & Williams 2002; Strauss, Webb & Salamin 2006; Diez *et al.* 2008; Jiang,  
73 Tan & Pu 2010; Li *et al.* 2015a; Feng & van Kleunen 2016; Yannelli *et al.* 2017). Potential  
74 explanations are that the studies differ in the spatial and phylogenetic scales considered  
75 (Thuiller *et al.* 2010) and stages of invasions (Li *et al.* 2015b; Cadotte *et al.* 2018), and are

76 based on observations rather than experiments. Furthermore, the mixed findings may also  
77 be because phylogenetic distance could indicate not only niche differences favouring  
78 coexistence but also competitive inequality (i.e. species' differences in competitive ability)  
79 driving competitive exclusion (Chesson 2000; Godoy, Kraft & Levine 2014). Here, we argue  
80 that the mixed results might also result from the potential confounding of phylogenetic  
81 distance with diversity of native communities. For instance, phylogenetic distance may have  
82 stronger effects as native diversity increases and thereby more niche space is occupied.  
83 However, very few studies have considered the potential confounding effects of native  
84 diversity when testing for Darwin's naturalisation hypothesis (but see Tan *et al.* 2015).

85         With a few exceptions (Robinson & Dickerson 1984), studies with experimentally  
86 constructed communities that tested for Elton's diversity-invasibility hypothesis often found  
87 evidence that diversity is a barrier to species invasions (e.g. Tilman 1997; Prieur-Richard *et*  
88 *al.* 2000; Kennedy *et al.* 2002). Despite these findings, an unresolved but critical question is  
89 to what degree the diversity effect is affected by phylogenetic distance between alien species  
90 and native residents. Some recent studies have implicitly recognized this by emphasizing  
91 that not only the diversity but also alien species' identity (which affects alien-native  
92 phylogenetic distance) determines invasion success (Crawley *et al.* 1999a; Hooper & Dukes  
93 2010; Byun, de Blois & Brisson 2013; Tan *et al.* 2015). However, a clear understanding of  
94 how the effect of diversity depends on alien-native phylogenetic distance is lacking.

95         The use of functional traits may help disentangle the implicit linkage and potential  
96 interactions between the mechanisms underlying Darwin's and Elton's invasion hypotheses,

97 because traits are claimed to capture species' differences in niches and competitive ability  
98 (McGill *et al.* 2006; Violle & Jiang 2009; Kunstler *et al.* 2012; Godoy & Levine 2014; Kraft,  
99 Godoy & Levine 2015). Potentially important traits include plant height, specific leaf area, leaf  
100 size and seed mass, which are at the core of plant strategies relevant to growth, survival and  
101 reproduction (Westoby 1998; Díaz *et al.* 2016). Plant height corresponds with the ability to  
102 compete for light resources, leaf size is relevant for light interception and affects leaf energy  
103 and water balance, SLA reflects a trade-off between carbon gain and longevity, and seed  
104 mass reflects a trade-off between seedling survival and colonisation ability (Díaz *et al.* 2016).

105 To disentangle the implicit linkage and potential interactions between the mechanisms  
106 underlying Darwin's and Elton's invasion hypotheses, we sowed seeds and planted seedlings  
107 of five alien herbaceous species into pot-mesocosms with native grassland communities of  
108 different diversities assembled with 36 native herbaceous species to test the success of alien  
109 species at different life stages. We used a phylogeny of all 41 study species and measured  
110 four of their functional traits (height, specific leaf area, leaf size and seed mass) to quantify  
111 alien-native phylogenetic and functional distances, and phylogenetic and functional diversity  
112 of the native communities. We used these distance and diversity measures to test the  
113 following hypothesis: the effect of alien-native phylogenetic and functional distances on the  
114 success of alien species strengthens at higher native diversities where niche availability is  
115 supposed to be lower and thereby competition is more severe.

## 116 **Materials and Methods**

### 117 Study species

118 We selected five alien species and 36 native species from the herbaceous flora of  
119 Germany (see Appendix S1 for the complete list of study species). The five alien species  
120 were *Bidens frondosa* (Asteraceae), *Senecio inaequidens* (Asteraceae), *Ambrosia*  
121 *artemisiifolia* (Asteraceae), *Epilobium ciliatum* (Onagraceae) and *Veronica persica*  
122 (Plantaginaceae), which are all native to non-European countries and are now invasive or  
123 widely naturalised in Europe (Appendix S1). The selection of the alien species reflects the  
124 fact that compared to other families, Asteraceae has the most number of naturalized and  
125 invasive species (Kowarik 2002; Jarošik, Pyšek & Kadlec 2011; Pyšek et al. 2017). We  
126 selected 36 native species that naturally occur in grasslands in Germany (Kühn, Durka &  
127 Klotz 2004) from six families (six species per family) (Appendix S1): Rosaceae, Asteraceae,  
128 Caryophyllaceae, Poaceae, Lamiaceae and Plantaginaceae. We purchased seeds of the 36  
129 native species from a commercial seed company (Rieger-Hofmann GmbH, Blaufelden,  
130 Germany), which produces seeds for restoration purposes and for creation of meadows and  
131 pastures on agricultural land. We obtained seeds of the five alien species from botanical  
132 gardens in Germany.

### 133 Design of native communities

134 We used the pool of 36 native species to design 90 native communities, including 36  
135 monocultures, 36 three-species polycultures and 18 six-species polycultures. In three-



136 species and six-species polycultures, we created a gradient of phylogenetic diversity by  
137 drawing species from a single family, partly different families or all different families (for  
138 details, see Appendix S1). This way, our design of communities could cover much of  
139 phylogenetic space that the 36 native species could create. In this design, each of the 36  
140 native species is equally represented in each level of species richness (but see a seed-  
141 contamination issue below).

## 142 Experimental setup

143 On 8 February 2015, we sowed c. 500 seeds of each of the 36 native species separately  
144 into trays (46 cm \* 31 cm \* 6.5 cm) filled with a standard potting soil (Gebr. Patzer GmbH &  
145 Co. KG, Sinntal, Germany), and then put all the trays in growth chambers (16h daylight, 21°C  
146 day / 17°C night). Two weeks later, we did the same for each of the five alien species. They  
147 were sown later because we intended to first establish native communities and then  
148 introduced the aliens into the communities, to simulate how invasion occurs in nature. On 23  
149 February 2015, we filled 1020 pots ( $\varnothing$  = 18 cm; H = 14 cm) with a 2:1 mixture of sand and  
150 standard potting soil enriched with 6.25 g slow-release fertilizer (Osmocote Pro 3-4 Months,  
151 Everris GmbH, Nordhorn, Germany). Directly after this, we transplanted seedlings of the 36  
152 native species into pots to assemble 11 times the 90 native communities (Appendix S1): five  
153 for testing success of the five alien species during early establishment (i.e. germination and  
154 survival of emerged seedlings; *sowing experiment*), five for testing success of growth and  
155 reproduction (*growth experiment*) of the five alien species, and one as the control of native  
156 communities without alien species. In each of these 990 pots, we transplanted a total of six

157 native seedlings as illustrated in Fig. S1 of Appendix S1. In addition, we had six control pots,  
158 each transplanted with a single alien plant without native residents (see below), for each of  
159 the five alien species (30 control pots in total) (Fig. S1). Note that the alien and native control  
160 pots were only used to measure functional traits (see below).

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

#### 169 Sowing experiment

170       About three weeks after transplanting (18 - 20 March 2015), for each of the five alien  
171 species we sowed one seed into each of 25 positions in each native community separately  
172 (90 native communities x 5 alien species, totalling 450 pots). The sowing was carried out  
173 using a mould with 25 holes (2 cm apart and arranged in a 5 x 5 grid; see Fig. S1 in  
174 Appendix S1). We watered the pots regularly to keep the soil moist. We checked germination  
175 of each seed about every three days until very few new germination happened (16 April  
176 2015). On 13 May 2015, we scored survival of each emerged seedling. For each pot, we  
177 then calculated i) germination rate, i.e. the number of germinated seeds / 25, and ii) survival

178 rate, i.e. the number of surviving seedlings / the number of germinated seeds. As germination  
179 of *B. frondosa* was overall very poor (only 5 % of the pots showed some germination), we  
180 excluded *B. frondosa* from the respective analyses (i.e. for germination rate and seedling  
181 survival rate, see below).

## 182 Growth experiment and control pots

183 About two weeks after transplanting the native species (10 March 2015), we  
184 transplanted a single seedling of one of the five alien species in the centre of each of the 90  
185 native communities (Fig. S1 in Appendix S1; 90 communities x 5 alien species, totalling 450  
186 pots). The same procedure was done for each of the five alien species in the control pots (i.e.  
187 no native residents; 30 control pots in total), whereby we transplanted a single seedling of  
188 the respective alien species (Fig. S1). In each of the 90 control native communities, we did  
189 not transplant any alien plant. Two days after transplanting, we counted the number of leaves  
190 of each alien seedling to estimate its initial biomass using a regression equation established  
191 for each alien species (biomass = coefficient \* number of leaves + intercept) in a harvest of  
192 seedlings randomly selected from the germination trays on 15 March 2015 (for details, see  
193 Appendix S2). From 18 May to 4 June 2015, we harvested all alien plants in the *growth*  
194 *experiment* table by table. For each plant, we harvested aboveground biomass, and for the  
195 alien plants we also counted the total number of reproductive units (buds, flowers and fruits)  
196 as a measure of reproduction. *Epilobium ciliatum* did not produce any reproductive units  
197 during the experimental period, and therefore we excluded it from the analyses of  
198 reproduction.

199 Distance and diversity measures

200 For the calculation of functional distance and diversity, we measured vegetative height,  
201 and determined size and SLA of the largest healthy leaf (Pérez-Harguindeguy *et al.* 2013) for  
202 each plant in the 90 control native communities and the 30 alien control pots during the  
203 harvest (from 18 May to 4 June 2015). Leaves were digitized with a scanner (Expression  
204 10000XL, Epson, Suwa, Japan), and we determined their areas (i.e. leaf sizes) with ImageJ  
205 (Abràmoff, Magalhães & Ram 2004). We then calculated SLA by dividing the area of each  
206 leaf by its dry mass. All the biomass was dried at 70°C for 72 hours prior to weighing. In  
207 addition, we determined seed-mass values of each species on five samples of 100 randomly  
208 selected purchased seeds.

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

216 As functional trait measures, we calculated mean multivariate (Euclidean) functional  
217 distance between alien species and native residents (FDist), and multivariate functional  
218 diversity of native communities (FDiv, i.e. total branch length of the dendrogram connecting  
219 all individuals of native residents within a community) (Cianciaruso *et al.* 2009), based on all

220 four functional traits measured, using the “*vegan*” R package (Oksanen *et al.* 2017).  
221 Following the recommendations of Swenson (2014), we log-transformed all traits to make  
222 them normally distributed, and then scaled them. After that we did Principal Component  
223 Analysis (PCA) to get orthogonal trait axes, and used the resulting 3 PCA axes to do the  
224 FDist and FDiv calculations.

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

235 Measures of alien-native phylogenetic and functional distances overall varied  
236 independently of measures of diversity of native communities ( $|$  Pearson correlation  $(r) | <$   
237 0.50, see Figs S3-S5 in Appendix S4), which helps avoid collinearity problems in the data  
238 analyses (see below). We also calculated minimum values of PDist, FDist, hFDist and aFDist  
239 between alien species and native residents, but their effects (Appendix S5) were very similar  
240 to those of the mean values that we presented in the *Results*. Moreover, we also calculated

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

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

#### 254 Data analysis

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

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

267 To account for variation in initial size of alien plants, we included their estimated initial  
268 biomass (see above) as a covariate in the models for biomass and reproduction of the aliens.  
269 As random factors in all the models, we included identity of alien species and greenhouse  
270 table nested within greenhouse compartment. In addition, for all the models, we checked  
271 whether the variance inflation factor was  $<4$  for each explanatory variable to ensure there  
272 was no collinearity problem (Zuur et al. 2009). We used log-likelihood-ratio tests to assess  
273 the significance of each explanatory variable by comparing the full model to the model  
274 without the variable of interest (Zuur *et al.* 2009). We illustrated significant interaction effects  
275 in the respective models with contour plots using the “*effects*” R package (Fox & Hong 2009)  
276 and the ‘filled.contour’ function in R. All the analyses were performed in R 3.4.3 (R Core  
277 Team 2018).

278 **Results**

279 Phylogenetic and multivariate functional distances and diversities

280 Seedling survival, biomass and reproduction of the aliens increased with increasing  
281 alien-native phylogenetic distance (Table 1, Fig. 1b-d), and reproduction decreased with  
282 increasing phylogenetic diversity of the native communities (Table 1, Fig. 1d). However, the  
283 positive effect of phylogenetic distance on reproduction became weaker with decreasing  
284 phylogenetic diversity (significant PDiv × PDist interaction in Table 1, Fig. 1d). The analyses  
285 using multivariate functional distance and diversity showed a similar pattern as the analyses  
286 using the phylogenetic measures (Table 2, Fig. 2e-h). The only difference was that  
287 germination of the aliens also increased with increasing multivariate functional distance, in  
288 addition to seedling survival, biomass and reproduction (Table 2, Fig. 2e-h).

289 Univariate functional distances and diversities

290 Germination of the aliens was neither affected by alien-native hierarchical functional  
291 distance (hFDist) nor by absolute functional distance (aFDist) of any trait (Table 3, Figs 2a.1-  
292 a.8). However, germination increased with increasing seed-mass functional diversity (FDiv)  
293 of the native communities (Table 3, Figs 2a.7 and a.8), but it was not affected by FDiv of the  
294 other functional traits (Table 3, Figs 2a.1-a.6). Subsequent survival of the emerged seedlings  
295 was on average positively affected by both hFDist and aFDist of leaf size and seed mass  
296 (Table 3, Figs 2b.5-8), but it was not affected by both hFDist and aFDist of the other two traits  
297 (Table 3, Figs 2b.1-4). Moreover, seedling survival was on average negatively affected by  
298 FDiv of leaf size and seed mass (Table 3, Figs 2b.6-b.8), but it was not affected by FDiv of  
299 the other two traits (Table 3, Figs 2b.1-b.4). However, the overall positive effect of leaf-size  
300 hFDist on seedling survival turned into a negative effect for large leaf-size FDiv values, as  
301 indicated by a significant hFDist × FDiv interaction (Table 3, Fig. 2b.5). Moreover, the positive  
302 effect of leaf-size aFDist on seedling survival was only marginally significant, but it became  
303 stronger with increasing values of leaf-size FDiv (Table 3, Fig. 2b.6). Furthermore, although



304 the overall effect of height aFDist on seedling survival was not significant, it changed from  
305 weakly positive to negative with increasing height FDiv (Table 3; Fig. 2b.2).

306 Biomass and reproduction of the aliens largely showed similar patterns, although the  
307 significances of the effects sometimes varied (Table 3, Figs 2c.1-c.8 and 2d.1-d.8). Biomass  
308 and reproduction increased with increasing hFDist of height and leaf size (Table 3, Figs 2c.1  
309 and c.5, Figs 2d.1 and d.5). On the other hand, biomass and reproduction decreased with  
310 increasing hFDist of SLA (Table 3, Figs 2c.3 and d.3), and for reproduction also with  
311 increasing hFDist of seed mass (Table 3, Fig. 2d.7). Biomass and reproduction both  
312 increased with increasing leaf-size aFDist (Table 3, Figs 2c.6 and 2d.6), and reproduction  
313 also increased with increasing aFDist of height, SLA and seed mass (Table 3, Figs 2d.2, d.4  
314 and d.8). Moreover, biomass and reproduction decreased with increasing FDiv of height, SLA  
315 and leaf size (Table 3, Figs 2c.1-c.3 and 2c.6, and Figs 2d.1-d.4 and 2d.6), and for  
316 reproduction also with increasing FDiv of seed mass (Table 3, Figs 2d.7 and d.8).

317 The strength and even the direction of effects of alien-native distances of many of the  
318 functional traits on biomass and reproduction of the aliens frequently depended on native  
319 diversities of the respective traits, as shown by many significant hFDist × FDiv and aFDist ×  
320 FDiv interactions (Table 3). The positive effect of height hFDist on reproduction increased  
321 with increasing height FDiv (Table 3, Fig. 3c.1). However, the overall positive effects of leaf-  
322 size hFDist on both biomass and reproduction turned into negative effects with increasing  
323 leaf-size FDiv (Table 3, Figs 2c.5 and 2d.5). The negative effects of hFDist of SLA and seed  
324 mass on biomass and reproduction became stronger as FDiv in the respective traits  
325 increased (Table 3, Figs 2c.3, 2c.7, 2d.3 and 2d.7). So, with the exception of leaf size, the  
326 effects (positive or negative, depending on traits) of functional trait hFDist on biomass and  
327 reproduction of the aliens became stronger with increasing FDiv of the respective functional  
328 trait. Similarly, with the exception of SLA, the positive effects of functional trait aFDist on  
329 reproduction became stronger with increasing FDiv of the respective functional trait (Table 3,  
330 Figs 2d.2, d.4, d.6 and d.8).

331 **Discussion**

332 In this study, we used phylogenetic and different functional trait measures of alien-native  
333 distance and native diversity to assess the links between Darwin's naturalisation hypothesis  
334 and Elton's diversity-invasibility hypothesis in experimental grassland communities. In  
335 support of Darwin's hypothesis, we found that alien-native distance increased performance of  
336 the aliens. In support of Elton's hypothesis, we found that diversity of the native communities  
337 reduced performance of the aliens. More importantly, in line with our hypothesis, we showed  
338 that the effects of alien-native phylogenetic and multivariate functional distance strengthened  
339 as native diversity increased. The same pattern was shown by our analyses with single traits,  
340 with both hierarchical trait distances (indicative of competitive inequalities) and absolute trait  
341 distances (indicative of niche differences) between alien and native species reinforcing at  
342 higher native diversities where competition is more severe.

343 Darwin's naturalisation hypothesis

344 In support of the predictions of Darwin's naturalisation hypothesis, increasing values of  
345 the different measures of alien-native distance resulted in enhanced performance (from  
346 germination to reproduction) of our target invasive species. This is in line with some previous  
347 studies which also found supportive evidence for the hypothesis (Strauss, Webb & Salamin  
348 2006; Jiang, Tan & Pu 2010; Feng & van Kleunen 2016), but others showed that the effects  
349 of alien-native distances were dependent on whether phylogenetic distance indicates niche  
350 preadaptation or competitive interactions, and on stages of invasion (Duncan & Williams  
351 2002; Diez *et al.* 2008; Li *et al.* 2015a; Li *et al.* 2015b). Moreover, in our study, the effects of  
352 multivariate functional distance were much stronger than those of phylogenetic distance,  
353 which suggests that multiple traits-based functional distance is better than phylogenetic  
354 distance in capturing niche differences that favour coexistence between the aliens and the  
355 native residents. This may be explained by the fact that, although there is generally strong  
356 phylogenetic signal in all the four traits, SLA and leaf size that also had strong effects tend to  
357 have relatively weaker phylogenetic signal (Appendix S7). Moreover, it is also possible that

358 other important traits not covered here (e.g. leaf N) may have made multivariate functional  
359 distance a better predictor than phylogenetic distance.

360 Our analyses with univariate measures of hierarchical and absolute functional distances  
361 provided more insights into the underlying mechanisms, as hierarchical trait distances may  
362 indicate alien-native competitive inequalities and absolute trait distances may indicate alien-  
363 native niche differences. Interestingly, seedling survival increased but reproduction  
364 decreased as alien-native univariate hierarchical functional distance based on seed mass  
365 increased. Seed mass differences themselves are not expressed in the experiment, but seed  
366 mass is likely to be positively associated with seedling size. Possibly, our finding indicates  
367 that the large seedlings of large-seeded species are more likely to survive, but that this is at  
368 a cost of reproduction (Díaz *et al.* 2016), at least during the period that our experiment lasted.  
369 In line with several other studies (e.g. Feng & van Kleunen 2016; Conti *et al.* 2018), our  
370 results showed that the effects of univariate hierarchical functional distance based on plant  
371 height or leaf size on the performance of the alien species were positive, whereas those  
372 based on SLA were negative. This shows that alien plants are more successful if they are  
373 taller and have larger leaves with a lower SLA than the native residents. Although a high SLA  
374 is usually associated with a fast relative growth rate (e.g. Poorter & Remkes 1990), several  
375 recent studies found that a greater SLA tends to be associated with greater competitive  
376 disadvantage (Kraft, Godoy & Levine 2015; Feng & van Kleunen 2016; Kunstler *et al.* 2016).  
377 In short, our findings thus confirm that these univariate hierarchical functional distances are  
378 indeed able to capture alien-native competitive inequalities.

379 The performance of the alien species in our study increased as alien-native univariate  
380 absolute functional distance based on each single trait separately increased. This may imply  
381 that these univariate functional distance measures are also able to capture alien-native niche  
382 differences. For example, the univariate functional distance of height or leaf size may capture  
383 alien-native niche differences in utilizing light resources, while the distance of SLA or seed  
384 mass may indicate some temporal alien-native niche differences (e.g. utilizing resources in

385 different times) because both SLA and seed mass could affect plant growth rate. However,  
386 the multivariate functional distance based on all four traits jointly had greater explanatory  
387 power than the univariate ones (Appendix S5). This suggests that the multivariate distance  
388 may better reflect alien-native niche differences than the univariate ones, because the former  
389 may capture the multidimensional niche space while the latter may only capture one aspect  
390 of this space. Finally, note that, although phylogeny and traits offer a useful tool to infer alien-  
391 native competitive and niche differences, to more rigorously quantify these differences, one  
392 needs to parameterize competition models with population dynamics data (Godoy, Kraft &  
393 Levine 2014; Godoy & Levine 2014).

#### 394 Elton's diversity-invasibility hypothesis

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

404 Phylogenetic diversity and multivariate functional diversity tended to have stronger  
405 effects on the alien species than species richness *per se* (Appendix S5), which may be  
406 because the former can better capture niche availability of native communities than the latter  
407 (Hooper & Dukes 2010; Srivastava *et al.* 2012). Interestingly, our results showed that  
408 univariate functional diversity measures (especially the ones for plant height) had greater  
409 explanatory power than phylogenetic diversity and multivariate functional diversity (Appendix  
410 S5). The reason for this is not clear, but we speculate that this may be because multivariate  
411 functional diversity mainly indicates the occupancy of niche space. However, diversity

412 measures based on single traits (e.g. height) may also reflect the occupancy of competitive  
413 space (i.e. how competitive a community is), if some traits are more related to competitive  
414 inequalities than to niche differences (Kunstler *et al.* 2012; Kraft, Godoy & Levine 2015).

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

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

426       The same pattern is reflected in our results from univariate functional distances, with  
427 much stronger effect of these distances in more diverse communities. For instance, our  
428 results showed that the effects of univariate hierarchical functional distances of height, SLA  
429 and seed mass on biomass and reproduction overall became much stronger when univariate  
430 functional diversity of the respective trait increased. Note, however, that the effect of  
431 hierarchical functional distance in height was generally positive whereas those in SLA and  
432 seed mass were generally negative. This is because a greater competitive ability is  
433 characterized by greater height, and smaller SLA and seed mass. However, the effect of leaf-  
434 size hierarchical functional distance showed a different pattern in its interactions with leaf-  
435 size functional diversity, i.e. the effect tended to change from positive to negative as the  
436 diversity increased. We suspect this may at least partly result from the inherent strong  
437 correlation ( $r=-0.55$ ) between the distance and the diversity (Fig. S4 in Appendix S4). This  
438 finding emphasizes that the effects of alien-native distance and native diversity may in many

439 studies be confounded. Moreover, we also found a much stronger effect of univariate  
440 absolute functional distance measures of height, leaf size and seed mass on reproduction  
441 when univariate functional diversity of the respective traits was greater. These interactions  
442 are very similar to the interaction between the effects of phylogenetic distance and  
443 phylogenetic diversity on reproduction, which again indicates the stronger competition  
444 between alien species and native residents in more diverse communities.

#### 445 *Conclusion*

446 Our study is to the best of our knowledge the first one that explicitly demonstrates how  
447 two classical invasion hypotheses, one proposed by Darwin (1859) and one by Elton (1958),  
448 are linked in explaining the success of alien species in experimental grassland communities.  
449 While we focused particularly on how the effect of alien-native distance changes with native  
450 diversity, these interactions are of course bidirectional. In other words, the effect of native  
451 diversity also depends on alien-native distance. In general, our results indicate that the effect  
452 of one becomes stronger when the other makes the competition between the alien and  
453 native residents more severe. This finding may help explain some of the puzzling results of  
454 studies that tested the two hypotheses separately. It also emphasizes the importance of  
455 integrating different ideas and hypotheses to gain a more complete understanding of  
456 invasion mechanisms (Catford, Jansson & Nilsson 2009; Jeschke 2014). Finally, future  
457 studies should rigorously quantify species' differences in niches and competitive ability to  
458 more thoroughly understand causes and consequences of species invasions in the  
459 framework of modern coexistence theory.

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466 **Authors' contributions**

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

469 **Data Accessibility**

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

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641

642 **Table 1** Results of mixed-effects models testing the effects of phylogenetic distance between alien species and residents (PDist), phylogenetic  
 643 diversity of native communities (PDiv), and their interaction (PDist × PDiv) on germination rate, seedling survival rate, biomass and reproduction of  
 644 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	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p
<b>Fixed</b>	Initial biomass	1	---	---	---	---	0.00	0.938	20.25	<b>&lt;0.001</b>
	PDist	1	0.16	0.687	3.84	<b>0.049</b> ↑	4.69	<b>0.030</b> ↑	10.17	<b>&lt;0.001</b> ↑
	PDiv	1	2.62	0.104	2.68	0.101	1.30	0.252	216.52	<b>&lt;0.001</b> ↓
	PDist × PDiv	1	0.17	0.679	0.37	0.540	1.16	0.281	9.29	<b>0.002</b>
		Variance		Variance		Variance		Variance		
<b>Random</b>	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	

645

646

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

		Germination rate		Seedling survival rate		Biomass		Reproduction		
		df	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p
<b>Fixed</b>	Initial biomass	1	---	---	---	---	0.21	0.640	2.64	0.103
	FDist	1	8.36	<b>0.004</b> ↑	8.18	<b>0.004</b> ↑	29.63	<b>&lt;0.001</b> ↑	1215.12	<b>&lt;0.001</b> ↑
	FDiv	1	1.68	0.193	2.12	0.144	0.18	0.668	34.19	<b>&lt;0.001</b> ↓
	FDist × FDiv	1	0.95	0.329	1.74	0.185	1.53	0.214	76.61	<b>&lt;0.001</b>
<b>Random</b>			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	

651

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

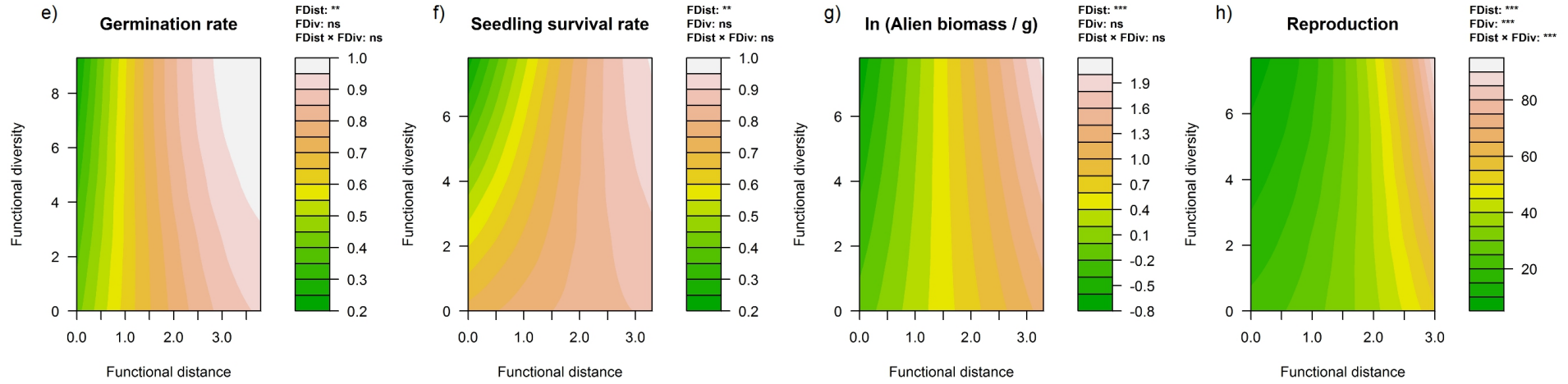
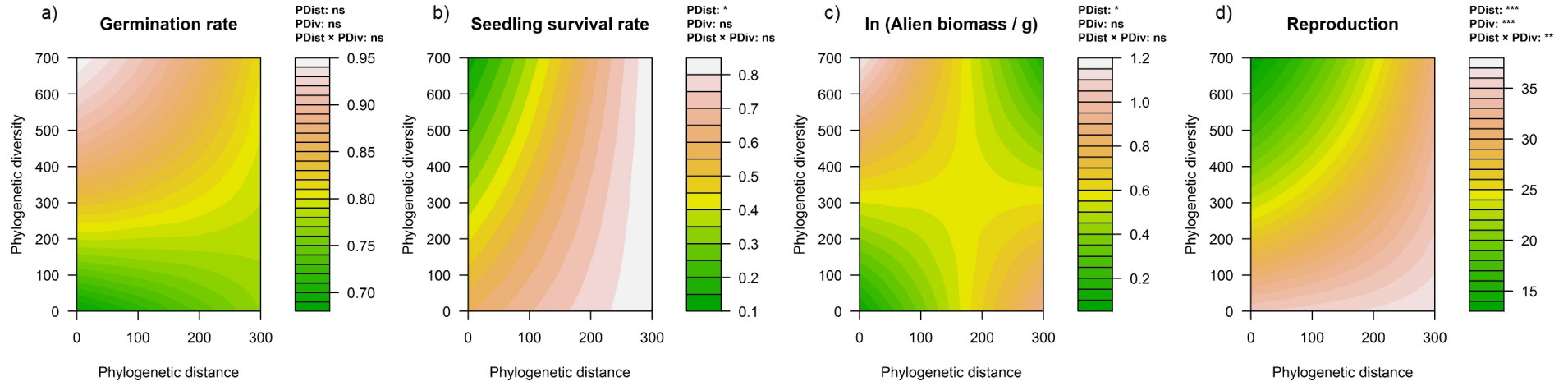
657

		Germination rate		Seedling survival rate		Biomass		Reproduction		
		df	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p
Height	hFDist	1	0.02	0.893	1.15	0.283	11.80	<b>&lt;0.001</b> ↑	354.03	<b>&lt;0.001</b> ↑
	FDiv	1	0.03	0.873	0.61	0.436	4.65	<b>0.031</b> ↓	294.30	<b>&lt;0.001</b> ↓
	hFDist × FDiv	1	0.50	0.482	0.29	0.591	2.76	0.096	201.94	<b>&lt;0.001</b>
	aFDist	1	0.08	0.784	0.29	0.587	2.47	0.116	30.66	<b>&lt;0.001</b> ↑
	FDiv	1	0.04	0.849	0.12	0.727	15.03	<b>&lt;0.001</b> ↓	1058.23	<b>&lt;0.001</b> ↓
	aFDist × FDiv	1	0.14	0.705	5.01	<b>0.025</b>	2.54	0.111	149.37	<b>&lt;0.001</b>
SLA	hFDist	1	0.06	0.807	0.04	0.838	12.10	<b>&lt;0.001</b> ↓	1171.26	<b>&lt;0.001</b> ↓
	FDiv	1	0.00	0.969	0.06	0.813	4.77	<b>0.029</b> ↓	451.84	<b>&lt;0.001</b> ↓
	hFDist × FDiv	1	0.01	0.922	1.48	0.224	6.15	<b>0.013</b>	446.68	<b>&lt;0.001</b>
	aFDist	1	0.08	0.784	0.66	0.418	2.35	0.125	41.94	<b>&lt;0.001</b> ↑
	FDiv	1	0.00	0.982	0.07	0.786	0.17	0.681	17.77	<b>&lt;0.001</b> ↓
	aFDist × FDiv	1	0.03	0.857	0.10	0.748	0.15	0.701	5.52	<b>0.019</b>
Leaf size	hFDist	1	0.25	0.619	6.61	<b>0.009</b> ↑	18.30	<b>&lt;0.001</b> ↑	64.65	<b>&lt;0.001</b> ↑
	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	<b>0.005</b>	10.94	<b>&lt;0.001</b>	150.26	<b>&lt;0.001</b>

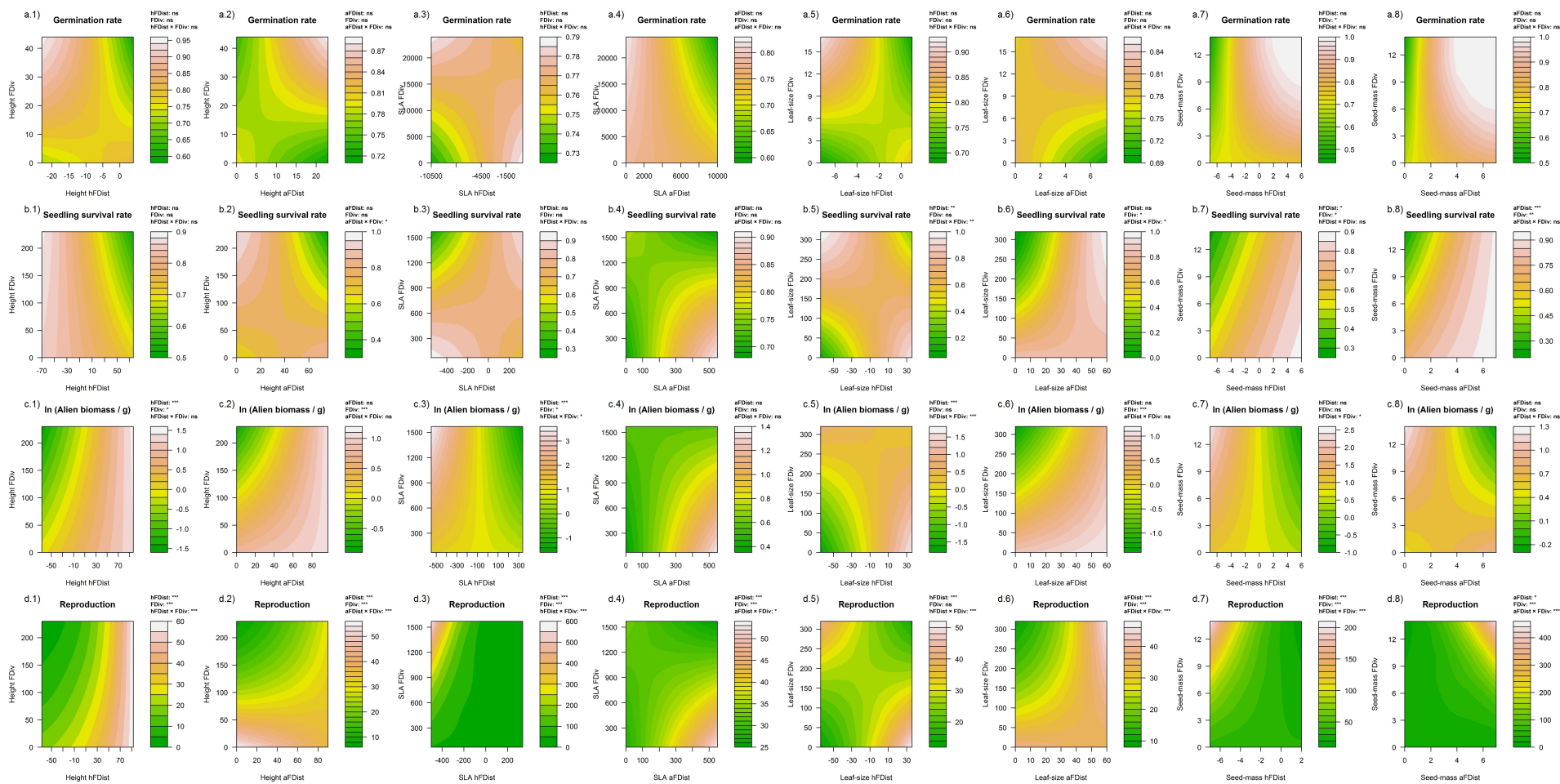
	aFDist	1	0.27	0.601	3.64	0.057↑	3.42	0.064	111.00	<0.001↑
	FDiv	1	0.19	0.663	4.08	<b>0.043</b> ↓	13.72	<0.001↓	44.22	<0.001↓
	aFDist × FDiv	1	0.08	0.774	5.31	<b>0.021</b>	2.51	0.113	37.34	<0.001
	hFDist	1	0.19	0.663	6.01	<b>0.014</b> ↑	1.34	0.247	29.74	<0.001↓
	FDiv	1	4.02	<b>0.045</b> ↑	4.09	<b>0.043</b> ↓	0.00	0.984	90.96	<0.001↓
	hFDist × FDiv	1	1.61	0.205	0.04	0.834	4.97	<b>0.026</b>	137.02	<0.001
Seed mass	aFDist	1	1.43	0.233	13.94	<0.001↑	0.78	0.377	6.46	<b>0.011</b> ↑
	FDiv	1	2.74	0.098	9.33	<b>0.002</b> ↓	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



659 **Fig. 1** Contour plots illustrating the effects of: a-d) phylogenetic distance between alien species and residents (PDist), phylogenetic diversity of  
660 native communities (PDiv), and their interaction (PDist × PDiv), and e-h) multivariate functional distance between alien species and residents  
661 (FDist) and multivariate functional diversity of native communities (FDiv), based on all four functional traits (height, SLA, leaf size and seed mass)  
662 jointly, and their interaction (FDist × FDiv), on germination rate, seedling survival rate, biomass and reproduction (number of reproductive units) of  
663 alien species. For the statistical results, see Tables 1 and 2. Significance of the main effects (PDist, PDiv, FDist, FDiv) and the interactions (PDiv ×  
664 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.  
665 The column right to each plot indicates values of the respective response variable.



668 **Fig. 2** Contour plots illustrating the effects of either univariate hierarchical functional distance (hFDist) or univariate absolute functional distance  
669 (aFDist) between alien species and residents, univariate functional diversity of native communities (FDiv), based on each single functional trait  
670 (height, SLA, leaf size and seed mass) separately, and their interaction (hFDist / aFDist  $\times$  FDiv), on a.1-a.8) germination rate, b.1-b.8) seedling  
671 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.  
672 Significance of the main effects (hFDist, aFDist, FDiv) and the interactions (hFDist  $\times$  FDiv, aFDist  $\times$  FDiv) is indicated as ns (i.e. non-significant,  
673  $P \geq 0.05$ ), \* ( $P < 0.05$ ), \*\* ( $P < 0.01$ ), \*\*\* ( $P < 0.001$ ) in the upper right corner of each plot. The column right to each plot indicates values of the  
674 respective response variable.



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