



Plasticity in plant functional traits is shaped by variability in neighbourhood species composition

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1 **Plasticity in plant functional traits is shaped by variability in neighbourhood**
2 **species composition**

3

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15 Summary

- 16 • Plant functional traits can vary widely due to phenotypic plasticity to abiotic conditions.
17 Trait variation may also reflect responses to the identity of neighbours, though not all
18 species are equally responsive to their biotic surroundings. We hypothesized that
19 responses to neighbours are shaped by spatial community patterns and resulting
20 variability in neighbour composition. More precisely, we tested the theoretical prediction
21 that plasticity is most likely to evolve if alternative environments (in this case, different
22 neighbour species) are common and encountered at similar frequencies.
- 23 • We estimated the frequencies of encountering different neighbour species in the field for
24 27 grassland species and measured the aboveground morphological responses of each
25 species to conspecific *versus* heterospecific neighbours in a common garden.
- 26 • Responses to neighbour identity were dependent on how frequently the experimental
27 neighbours were encountered by the focal species in their home community, with the
28 greatest plasticity observed in species that encountered *both* neighbours (conspecific and
29 heterospecific) with high and even frequency.
- 30 • Biotic interactions with neighbouring species can impose selection on plasticity in
31 functional traits, which may feed back through trait divergence and niche differentiation
32 to influence species co-existence and community structure.

33

34 **Key words:** biotic environment, competition, functional traits, local adaptation, neighbour
35 recognition, phenotypic plasticity, selection, spatial patterns.

36

37 **Introduction**

38 Variation in plant traits is known to play an important role in plant community assembly and
39 ecosystem functioning (Lavorel & Garnier, 2002; de Bello *et al.*, 2010; Götzenberger *et al.*,
40 2012) but the causes and consequences of intraspecific trait variation are still poorly understood
41 (Albert *et al.*, 2010; Violle *et al.*, 2012). Besides genetic variation, plant traits can vary widely as
42 a result of phenotypic plasticity (Bradshaw, 1965). Plants are known to modify their morphology
43 in response to variation in abiotic factors such as light, water and nutrient availability, and
44 extensive research has revealed the molecular mechanisms involved, the adaptive value of
45 plasticity and the factors that promote or inhibit the evolution of plasticity (e.g. Pigliucci, 2001;
46 Alpert & Simms, 2002; Givnish, 2002). It has recently become evident that plants respond
47 plastically not only to their abiotic environment but also to the presence and identity of
48 neighbouring individuals. Plants can discriminate between roots belonging to themselves and a
49 physiologically independent individual, the same and different genotypes, and sibling and non-
50 sibling neighbours (Gruntman & Novoplansky, 2004; Dudley & File, 2007; Semchenko *et al.*,
51 2014). However, these studies produced variable results, with some species modulating their
52 responses to different neighbouring genotypes and others seemingly lacking the ability to do so
53 (File *et al.*, 2012; Lepik *et al.*, 2012). The factors underlying this variation remain unidentified.
54 Even less is known about the ability of plants to differentiate between neighbours belonging to
55 different species (Mahall & Callaway, 1992; Semchenko *et al.*, 2007).

56 Different neighbouring species can be viewed as alternative biotic environments, and the
57 factors favouring the evolution of an ability to respond to neighbour identity are likely to match
58 those favouring any other type of adaptive phenotypic plasticity. Firstly, local interactions with
59 immediate neighbours have to exert different selective pressures on plant functional traits
60 depending on the identities of interacting plants. Indeed, it has been shown that when the identity
61 of neighbours is stable in space and time, plant neighbourhoods of different species composition
62 (including conspecific *versus* heterospecific neighbourhoods) select for specific phenotypes and
63 lead to genetic differentiation and local adaptation (Turkington, 1989; Callaway *et al.*, 2005;
64 Lipowsky *et al.*, 2011). It is reasonable to predict that plants will experience selective pressure
65 for phenotypic plasticity to neighbour identity if spatial and temporal variability in neighbour
66 composition requires different morphology to be adopted for successful survival and
67 reproduction.

68 Theoretical models and limited empirical evidence suggest that plasticity is likely to
69 evolve if a focal species experiences environmental fluctuation in space or time comparable to
70 the size or generation time of an individual (Bradshaw, 1965; Baythavong, 2011) and the
71 alternative environments (in this case, different neighbour species) are common and occur at even
72 frequencies (Moran, 1992). Plasticity is expected to be greatest if each of two alternative
73 environments is experienced 50% of the time. Conversely, a fixed developmental strategy that
74 maximizes fitness in the predominating environment is likely to be favoured if one of two
75 alternative environments is rare (Alpert & Simms, 2002; Givnish, 2002). In plants, variability in
76 neighbour identity will strongly depend on species life history traits and community
77 characteristics. Neighbouring individuals may be predominantly conspecific due to limited seed
78 dispersal or spatial aggregation of vegetatively propagated offspring (Lovett Doust, 1981;
79 reviewed in Cheplick, 1992; Herben & Hara, 2003). Decreasing community species richness
80 increases the probability of encountering any particular neighbouring species, while low
81 community evenness makes dominant species the most likely neighbours (Oksanen, 1997; Perry
82 *et al.*, 2009).

83 In a previous study, we found that species competitive ability was significantly related to
84 the frequency of encountering conspecifics and heterospecifics in the field (Semchenko *et al.*,
85 2013). In this study, we use the same set of plant species from a range of temperate grassland
86 communities to determine whether the evenness of encounters with different neighbours could be
87 a condition for the evolution of morphological plasticity to neighbour identity. In particular, we
88 tested the hypothesis that morphological plasticity to neighbours of two given species identities is
89 most likely to evolve when both neighbours are common and are encountered at similar
90 frequencies. We also tested whether plasticity to neighbour identity is affected by species
91 abundance in the community, with dominant species either exhibiting or triggering greater
92 plasticity. Each focal species was grown in a common garden with either conspecifics or with
93 individuals of another species that is frequently encountered as a nearest neighbour in the field.
94 Conspecifics were included in the design as they are frequent neighbours in nature for many
95 species and play an important role in shaping competitive ability and the potential for co-
96 existence with other species (Turnbull *et al.*, 2007; Semchenko *et al.*, 2013). Plasticity to
97 neighbour identity was assessed based on five traits known to be important for plant function
98 (Weiher *et al.*, 1999; Poorter *et al.*, 2012). Using spatial data collected from the field, we

99 determined whether the degree of plasticity to neighbouring species was dependent on how
100 commonly and at how even frequencies these neighbours were encountered by each focal species
101 in its respective community.

102

103 **Materials and methods**

104 **(a) Study sites and species**

105 Seven study sites in Estonia were selected to represent a range of different semi-natural
106 grasslands. The sites differed in species richness (ranging between 8 and 88 species per site) and
107 composition, soil fertility, pH, and management history. Site 1 (58°35'N, 23°34'E) and Site 2
108 (58°39'N, 23°31'E) are species-rich, calcareous grasslands, both managed by grazing or mowing
109 for at least 200 years. Site 3 (58°25'N, 26°31'E) and Site 4 (58°07'N, 27°04'E) are mesophytic
110 meadows, the former probably ploughed and forested in the past and the latter probably forested
111 in the past. Site 5 (58°31'N, 23°40'E) is an islet, Site 6 (58°26'N, 26°31'E) a riverside flood-
112 meadow and Site 7 (58°44'N, 23°39'E) a coastal meadow, all periodically disturbed by ice and
113 water. Plant community composition was estimated for each site by sampling along randomly
114 placed 10m long transects and recording the species identity of the shoots with rooting points
115 closest to metal poles inserted every 33cm. Different numbers of plants were sampled depending
116 upon the species richness within each site: 913 plants at Site 1; 677 at Site 2; 596 at Site 3; 565 at
117 Site 4; 330 at Site 5; 351 at Site 6; and 242 at Site 7. We selected 27 focal species (Table1)
118 aiming to provide a representative sample of the studied communities; the abundances of the
119 focal species ranged from rare (less than 1%) to dominant (up to 34%) based on shoot counts. The
120 species identity of the nearest neighbour was recorded in the field for one hundred individuals of
121 each focal species. The seeds of focal and potential neighbour species were collected at each
122 study site from a large number of plants to obtain a representative sample of genotypes for each
123 species. The seeds were air-dried, stored at 4°C, and used the following year in a pot experiment.

124

125

126 **(b) Common garden experiment**

127 Individual plants of each focal species were subjected to treatments that manipulated a)
128 neighbour identity (surrounded by either conspecifics or heterospecifics), and b) neighbour
129 density (0, 1, 2, 3, 4, 6 or 8 neighbours). Each neighbour identity by density combination was

130 replicated twice. In the heterospecific treatment, each focal species was grown together with a
131 species that it frequently encountered in the field as its nearest neighbour. If the most frequent
132 neighbour species could not be used due to low seed viability or germination, the next most
133 frequent neighbour was used. For 8 focal species, we used the most frequent heterospecific
134 neighbour; for 6 focal species the chosen neighbour species was within 99-70% of the frequency
135 of the most common neighbour; for 9 focal species the chosen neighbour species had a
136 corresponding frequency in the range 69-30%; and for 4 focal species, the chosen neighbour
137 species had a corresponding frequency in the range 29-20%. Encounters with conspecifics and
138 the chosen heterospecific neighbour together accounted for 14-96% of all recorded nearest
139 neighbour encounters (low values were for species with high neighbour diversity and high values
140 were for species with high levels of conspecific aggregation). Due to poor germination and
141 seedling mortality, a total of 731 pots were measured at the end of the experiment instead of the
142 planned 756 pots ($27 \text{ focal species} \times 2 \text{ neighbour identities} \times 7 \text{ neighbour densities} \times 2$
143 replicates).

144 Pots contained a mixture of commercial soil, sand, lime powder and natural soil inoculum
145 prepared separately for species from each study site to match the N content and pH of soil from
146 the corresponding site. No fertiliser or herbicide was applied during the experiment. Three pot
147 sizes were used to account for differences in productivity and average plant size in different study
148 communities: 3.5 litre pots for Sites 2 and 7; 5 l pots for Sites 1, 3 and 4; 7.5 l pots for Sites 5 and
149 6. The distance between the focal plant (planted in the centre) and its neighbours was 5.7 cm in
150 the 3.5 l pots, 6.8 cm in the 5 l pots and 7.8 cm in the 7.5 l pots (equivalent to $2/3$ of the pot
151 radius in each case). Pots were placed randomly in an outdoor paved area, and their positions
152 were re-randomized twice during the experiment. Pots received natural precipitation but were
153 watered daily in dry and sunny weather. Weeds were regularly removed. Plants were harvested
154 after 11-14 weeks of growth. The experiment was carried out in Tartu, Estonia ($58^{\circ}22'N$,
155 $26^{\circ}41'E$).

156

157 **(c) Plant measurements**

158 Before harvesting, the maximum vegetative height of the focal plants was measured as the
159 highest point reached by stem leaves (or rosette leaves in the absence of a leafed stem) at the end
160 of the experiment. Next, plants were cut at the rooting point and were immediately placed in air-

161 tight polyethylene bags, with the cut ends of the stems submerged in water at the bottom of the
162 bags. The plants were stored upright in the dark at 4°C for at least 24 h before leaf water content
163 measurements were conducted, as suggested by Garnier *et al.* (2001). Two newly produced but
164 fully expanded leaf blades were selected from each focal plant, dried with tissue paper, and
165 weighed immediately to determine their fresh mass. More leaves were weighed for species with
166 small leaves (four leaves for *Carex ornithopoda*, *Juncus gerardii*, *Veronica chamaedrys*; five
167 leaves for *Antennaria dioica*; ten leaves for *Lotus corniculatus*; 25 leaves for *Galium verum*).
168 Leaf water content was calculated by dividing the difference between fresh and dry mass by the
169 fresh mass of the leaf blades. To calculate specific leaf area (SLA), the fresh leaves used for the
170 water content measurements were scanned (Epson perfection V700 PHOTO, Long Beach, CA,
171 USA) and leaf area calculated using program WinRhizo 2008a (Regent Instruments Inc., Quebec,
172 Canada). SLA was calculated as the ratio of leaf area and leaf dry mass. All remaining leaves of
173 the focal plants were also scanned if they could be scanned without overlap on a single A4 format
174 sheet. If part of the leaves could not be fitted on this area, total leaf area was calculated as the
175 ratio of scanned leaf area and the dry mass of scanned leaves multiplied by the total leaf dry
176 mass. The exception was *Peucedanum palustre* for which, due to the particularly large size of
177 individual leaves, multiple A4-sized scans were performed to obtain total leaf area. The dry mass
178 of the supportive structures was found by summing the dry mass of stems (including stolons),
179 leaf petioles and leaf sheaths (in the case of graminoids). All above-ground parts of each focal
180 plant and its neighbours were oven-dried at 70° C for 48 h and weighed separately as necessary
181 for calculations. As plants were grown in soil for a prolonged time period, it was not possible to
182 disentangle entire root systems and obtain root biomass data. Root density data obtained for a
183 subset of species showed a strong correlation with aboveground biomass (Semchenko *et al.*,
184 2013). Trait data are available at Dryad Digital repository (doi:10.5061/dryad.83g9k).

185

186 **(d) Statistical analysis**

187 *Plasticity estimation from the pot experiment*

188 For each of the focal species, linear models were constructed with one of the five measured traits
189 (dry mass of supportive structures, maximum vegetative height, total leaf area, specific leaf area,
190 leaf water content) as a response variable and neighbour identity (fixed factor with two levels:
191 heterospecific or conspecific), neighbour density and the interaction term between the two as

192 predictor variables. Prior to analysis, all trait values were ln-transformed. An overall plasticity
 193 estimate for each focal species was calculated as the average of five absolute values of
 194 coefficients for the interaction term between neighbour identity and density ($\Delta\beta$, i.e. $\beta_{\text{het}} - \beta_{\text{con}}$ in
 195 Table S1), which can be expressed as:

$$196 \text{ Mean plasticity} = (|\beta_{1\text{het}} - \beta_{1\text{con}}| + |\beta_{2\text{het}} - \beta_{2\text{con}}| + |\beta_{3\text{het}} - \beta_{3\text{con}}| + |\beta_{4\text{het}} - \beta_{4\text{con}}| + |\beta_{5\text{het}} - \beta_{5\text{con}}|)/5,$$

197 where β denotes a slope of ln(trait) vs neighbour density relationship, numbers 1 to 5 denote the
 198 five measured traits, and *con* and *het* denote conspecific and heterospecific treatments,
 199 respectively. In addition, *biomass plasticity* (change in focal biomass in response to neighbour
 200 identity) was calculated as above but using total above-ground biomass instead of the five
 201 morphological traits.

202 203 *Index of interaction frequencies (H') based on field data*

204 To describe the frequency and evenness of neighbour encounters for each focal species in its
 205 respective community, we used Shannon's diversity index calculated for the subset of two
 206 species:

$$207 H' = - (p_{\text{con}} \times \ln(p_{\text{con}}) + p_{\text{het}} \times \ln(p_{\text{het}})),$$

208 where p_{con} and p_{het} denote the proportions of total nearest neighbour encounters in the field that
 209 represented the conspecific or the species used in the pot experiment as the heterospecific
 210 neighbour, respectively. The index was unimodally related to the empirical probabilities of
 211 conspecific as well as heterospecific neighbour encounters across the 27 focal species (Fig. 1).
 212 The index reaches its highest value when neighbours of *both* identities are encountered at even
 213 and intermediate frequencies, satisfying a condition necessary for the evolution of plasticity to
 214 alternative environments (Moran, 1992).

215 216 *Relationship between plasticity and the index of interaction frequencies (H')*

217 *Mean plasticity* was used as a response variable, while H' and its second order polynomial
 218 (to test for non-linearity) were used as predictor variables. Resource competition with neighbours
 219 may result in changes to morphology that reflect focal plant size rather than changes in plant
 220 development (see examples in Fig. S1). Accounting for biomass effects when estimating
 221 plasticity has been widely used to assess active plastic responses that involve adjustments of the
 222 allometric relationship between a trait and biomass but exclude responses caused by ontogenetic

223 drift (i.e. shift along the same trait-biomass trajectory, McConnaughay & Coleman, 1999;
224 Weiner, 2004). To account for focal plant size effects, *biomass plasticity* was added to the model
225 as a covariate. In addition, the difference in mean neighbour mass was included as a covariate to
226 test whether plasticity to neighbour identity was mediated by differences in neighbour size (see
227 examples in Fig. S2). The difference in neighbour size was calculated as the absolute value of the
228 difference between mean ln-transformed aboveground mass of neighbours in the conspecific and
229 heterospecific treatments (mean across all neighbour densities). Study site and pot size were
230 initially included in the models as random factors but were excluded from the final model as
231 these did not significantly improve the fit of the model and produced nearly identical fixed effect
232 estimates. To visualise the relationship between plasticity and H' while accounting for the effect
233 of focal plant size, residuals from a model with mean morphological plasticity as a response
234 variable and biomass plasticity as an explanatory variable were used. To test whether our findings
235 were sensitive to the precise method used to account for plant size effects, we also calculated
236 plasticity as the difference between slopes of the allometric relationships between a
237 morphological trait and focal plant biomass in the con- and heterospecific treatments (see
238 examples in Fig. S3). This approach resulted in a very similar relationship between plasticity and
239 H' as that found using biomass plasticity as a covariate (Fig S4).

240 Since analysis of interspecific datasets may be confounded by phylogenetic dependence
241 of study species (known as “phylogenetic signal”), two models were compared (Revell, 2010).
242 First, we fitted a Pagel’s λ model using generalized least squares with a correlation structure that
243 accounts for phylogenetic dependencies between species based on the observed λ (function *gls* in
244 *nlme* package and *corPagel* in package *ape*, program R 3.2.0, R Development Core Team 2015).
245 Second, a *gls* model assuming phylogenetic independence was fitted to the same data ($\lambda = 0$). The
246 fit of the two models was compared using likelihood ratio tests. A phylogeny containing our
247 study species was obtained from Durka & Michalski (2012).

248

249 *Alternative explanatory variables*

250 In addition to H' , conspecific and heterospecific encounter frequencies, species abundances and
251 the spatial association of focal species with their heterospecific neighbours and overall neighbour
252 diversity were also tested as alternative explanatory variables for variation in plasticity. Species
253 abundances within each study site were calculated as the proportion of total randomly sampled

254 shoot counts belonging to that species. Spatial association between each focal species and the
255 heterospecific used in the pot experiment was calculated as the difference between the observed
256 frequency of encountering the heterospecific as the nearest neighbour (p_{het}) and its abundance
257 based on random sampling. Neighbour diversity index was calculated as the Shannon diversity
258 index using field data on all neighbouring species (as opposed to the two neighbour species used
259 for the calculation of H'). Spatial field data are available in Table S2.

260

261 **Results**

262 There was a significant non-linear relationship between mean plasticity to neighbour identity,
263 averaged across five measured traits, and the index of interaction frequencies (H') based on field
264 data (Figs. 2, S4-5; Table 2). No significant phylogenetic signal was detected for the relationship
265 between plasticity and H' – applying a correlation structure based on phylogenetic dependencies
266 between the focal species did not improve model fit (Table 2). Within the range of data values,
267 the relationship was overall positive in nature: the greater the index describing the commonness
268 and evenness of interactions with the two neighbours (H'), the greater the observed plasticity to
269 neighbour identity (Fig. 2). The species with the highest degree of plasticity (*L. flos-cuculi*, *M.*
270 *lupulina* and *R. acetosa* in Fig. 2, also *P. officinarum*, *C. jacea* and *T. repens* in Fig. S4)
271 originated from different study sites, indicating that plasticity to neighbour identity was not
272 restricted to a particular grassland or taxonomic group (Fig. S5). While H' described 56% of
273 variation in the mean plasticity after accounting for biomass effects (Fig. 2), the frequencies of
274 conspecific and heterospecific encounters separately described considerably less variation (8%
275 and 17%, respectively; Fig. 3). The degree of plasticity to neighbour identity showed no
276 significant relationship with the difference in neighbour mass between conspecific and
277 heterospecific treatments (Table 2; Fig. S6) or the neighbour diversity index based on all
278 neighbouring species encountered in the field ($F_{2,24} = 0.28$; $P = 0.758$; $R^2 = 0.02$; Fig. S7).

279 When examining responses to neighbour identity in each measured trait separately,
280 similar positive relationships with the index of interaction frequency were observed for each of the
281 measured traits (Fig. S8). The relationships were strongest for plasticity in allocation to
282 supportive structures ($F_{2,24} = 7.7$; $P = 0.003$; $R^2 = 0.39$) and leaf area ($F_{2,24} = 5.1$; $P = 0.014$; $R^2 =$
283 0.30). The index of interaction frequency explained less variation in plasticity in SLA ($F_{2,24} = 2.8$;
284 $P = 0.082$; $R^2 = 0.19$), leaf water content ($F_{2,24} = 1.6$; $P = 0.214$; $R^2 = 0.12$) and vegetative height

285 ($F_{2,24} = 1.1$; $P = 0.337$; $R^2 = 0.09$). There were significant positive correlations between plasticity
286 in leaf area and vegetative height ($r = 0.50$; $P = 0.008$; Fig. S9), and between plasticity in
287 allocation to supportive structures and SLA ($r = 0.59$; $P = 0.001$; Fig. S9).

288 The relative abundance of a focal species in its home community did not affect the degree
289 of plasticity it exhibited (non-significant linear relationship: $F_{1,25} = 0.83$; $P = 0.371$; $R^2 = 0.03$),
290 while more abundant heterospecific neighbours elicited a greater plastic response in focal plants
291 (significant linear relationship: $F_{1,25} = 8.6$; $P = 0.007$; $R^2 = 0.26$; Fig. 4). Plasticity was not
292 significantly affected by the degree of spatial association with neighbour species in the field
293 (non-significant linear relationship: $F_{1,25} = 2.4$; $P = 0.132$; $R^2 = 0.09$; Fig. 4). There was no
294 significant correlation between H' and the abundance of the neighbour species ($r = 0.22$; $P =$
295 0.275).

296

297 Discussion

298 We found that a significant proportion of interspecific variation in plasticity to neighbour identity
299 could be explained by how frequently different neighbours are encountered by a focal species in
300 its natural environment. The degree of plasticity to neighbour identity was highest for focal
301 species that encountered both conspecific and heterospecific neighbours with high and
302 comparable frequency in their home community. If interactions with one or both of the
303 neighbours were infrequent in the field, low levels of plasticity were detected, in accordance with
304 theoretical predictions (Moran, 1992; Alpert & Simms, 2002). The relationship between plasticity
305 and the index of interaction frequency remained significant when phylogenetic dependencies
306 between the studied species were taken into account. Also, this index explained considerably
307 more variance in plasticity than the frequencies of conspecific and heterospecific encounters
308 separately, suggesting it was the relative frequency of interactions with *both* neighbours that was
309 responsible for the observed relationship.

310 In this study, we treated the ability to respond to neighbour identity as a form of
311 phenotypic plasticity and empirically demonstrated a crucial condition favouring the evolution of
312 plasticity – alternative environments (in this study, neighbourhoods composed of different
313 species) should be common and encountered with similar frequency (Moran 1992; Alpert &
314 Simms 2002). We also found that plants exhibited a greater plastic response to neighbour identity
315 when the focal species was coupled with a heterospecific neighbour that was overall more

316 abundant in the field. This suggests that plants may experience a stronger selective pressure to
317 respond plastically to species that dominate their home communities. Though this study was not
318 designed to study neighbour recognition, these findings are relevant to a growing field of research
319 into the ability of plants to differentiate between neighbours of different identities. Wide variation
320 in recognition ability has been reported, raising controversy and criticism (File *et al.* 2012; Lepik
321 *et al.* 2012). The frequencies of interactions with different genotypes may be an important factor
322 underlying observed variability.

323 Our study was not designed to establish environmental factors that triggered plasticity to
324 neighbour identity. It has been shown that competitive ability can be strongly influenced by plant
325 size (Keddy *et al.*, 2002; Wang *et al.*, 2010), with larger individuals exerting a stronger negative
326 impact on the growth of their neighbours. We found that differences in neighbour mass could not
327 explain variation in morphological plasticity to the species identity of neighbours, suggesting that
328 size-mediated resource competition was not the mechanism underlying the differential response
329 to neighbours. This is to be expected as plasticity was estimated as a change in plant morphology
330 and biomass allocation that could not be explained by changes in total biomass. It is likely that
331 differential response to neighbours was triggered by differences in the spatial or temporal pattern
332 of their resource acquisition (e.g. Marcuvitz & Turkington, 2000; Weinig, 2000). In addition,
333 non-nutritious cues such as volatiles and root exudates have been shown by previous studies to
334 mediate neighbour recognition (reviewed in Schenk, 2006; Pierik *et al.*, 2013; Semchenko *et al.*,
335 2014).

336 Depending on the identity and strategy of the neighbours, plastic responses in plant
337 functional traits in response to neighbour identity may result in trait divergence between
338 neighbouring plants and, possibly, improved co-existence if this leads to niche differentiation
339 (Zuppinge-Dingley *et al.*, 2014; Lipowsky *et al.*, 2015). In our study, we only measured traits of
340 focal plants and used a single population from each species. Future research should examine the
341 adaptive value of plasticity to neighbour identity and its consequences for niche differentiation
342 and species co-existence. Nonetheless, our findings highlight the importance of plant-plant
343 interactions for intraspecific trait variation, which should be considered in studies attempting to
344 predict community and ecosystem processes based on species traits (Burns & Strauss, 2012; Zhu
345 *et al.*, 2015).

346 Although we found a strong positive relationship between plasticity to neighbour identity
347 and the relative frequency of interactions with different neighbours, other factors besides
348 environmental variability are known to be important for the evolution of plasticity. Some focal
349 species may not benefit from morphological plasticity to neighbour identity if the same
350 phenotype is equally effective in competition with both neighbour species. Greater plasticity is
351 likely to be expressed if plants experience neighbours with contrasting growth forms (e.g.
352 differences in plant height, vertical distribution of leaf area and roots) or life histories (e.g.
353 phenology). The evolution of phenotypic plasticity may also be constrained by factors such as
354 deficient sensory capabilities, the maintenance costs of the genetic and cellular machinery
355 required for a plastic response, the lag-time between environmental and phenotypic change or a
356 lack of genetic variability (DeWitt *et al.*, 1998; Pigliucci, 2001). Furthermore, competition with
357 neighbours of different identities may have triggered physiological adjustments or changes in
358 belowground traits, which were not measured in this study.

359 Studies on invasive plant species and biodiversity manipulation experiments show
360 potential for fast local adaptation to abiotic and biotic components of the ecosystem (Callaway *et al.*
361 *al.*, 2005; Lankau, 2012; Ravenscroft *et al.*, 2014; Zuppinger-Dingley *et al.*, 2014). Our study
362 shows a similar pattern in natural grassland systems where variability in species composition of
363 immediate neighbours results in an enhanced ability to modify morphology in response to
364 neighbour identity. The relationship between neighbourhood interactions and plasticity can be
365 viewed in the framework of eco-evolutionary dynamics (Lankau, 2012; reviewed in Strauss,
366 2014), where ecological interactions with neighbours drive an evolutionary change in plasticity,
367 which in turn may have consequences for ecological interactions and spatial patterns. This study
368 demonstrates a significant link between community patterns and plasticity, but further research is
369 necessary to demonstrate the cause and effect underlying this relationship and to identify how
370 differences in plasticity feed back to ecological interactions and affect species co-existence.
371 Future studies employing multiple populations of the same species and communities of different
372 age are also needed to shed light on the resolution and speed of local adaptation to neighbour
373 diversity.

374

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382 **Author contributions**

383 M.S. planned and designed the study, M.A., K.Z., A.L., and M.S. performed fieldwork and
384 experiments, M.A. and M.S. analysed the data and wrote the first draft of the manuscript, and
385 M.A., K.Z., A.L., and M.S. contributed substantially to revisions.

386

387 **References**

388

389 **Albert CH, Thuiller W, Yoccoz NG, Soudant A, Boucher F, Saccone P, Lavorel S. 2010.**

390 Intraspecific functional variability: extent, structure and sources of variation. *Journal of*
391 *Ecology* **98**: 604-613.

392 **Alpert P, Simms EL. 2002.** The relative advantages of plasticity and fixity in different

393 environments: when is it good for a plant to adjust? *Evolutionary Ecology* **16**: 285–297.

394 **Baythavong BS. 2011.** Linking the spatial scale of environmental variation and the evolution of

395 phenotypic plasticity: selection favors adaptive plasticity in fine-grained environments.

396 *American Naturalist* **178**: 75–87.

397 **Bradshaw, A.D. (1965).** Evolutionary significance of phenotypic plasticity in plants. *Advances*

398 *in Genetics* **13**: 115–155.

399 **Burns JH, Strauss SY. 2012.** Effects of competition on phylogenetic signal and phenotypic

400 plasticity in plant functional traits. *Ecology* **93**: S126-S137.

401 **Callaway RM, Ridenour WM, Laboski T, Weir T, Vivanco JM. 2005.** Natural selection for

402 resistance to the allelopathic effects of invasive plants. *Journal of Ecology* **93**: 576–583.

403 **Cheplick GP. 1992.** Sibling competition in plants. *Journal of Ecology* **80**: 567–575.

404 **de Bello F, Lavorel S, Diaz S, Harrington R, Cornelissen JHC, Bardgett RD, Berg MP,**

405 **Cipriotti P, Feld CK, Hering D, et al. 2010.** Towards an assessment of multiple

- 406 ecosystem processes and services via functional traits. *Biodiversity and Conservation*
407 **19**(10): 2873-2893.
- 408 **deWitt TJ, Sih A, Wilson DS. 1998.** Costs and limits of phenotypic plasticity. *Trends in Ecology*
409 *and Evolution* **13**: 77–81.
- 410 **Dudley SA, File AL. 2007.** Kin recognition in an annual plant. *Biology Letters* **3**: 435–438.
- 411 **Durka W, Michalski SG. 2012.** Daphne: a dated phylogeny of a large European flora for
412 phylogenetically informed ecological analyses. *Ecology* **93**: 2297.
- 413 **File AL, Murphy GP, Dudley SA. 2012.** Fitness consequences of plants growing with siblings:
414 reconciling kin selection, niche partitioning and competitive ability. *Proceedings of the*
415 *Royal Society. B, Biological Sciences* **279**: 209–218.
- 416 **Garnier E, Shipley B, Roumet C, Laurent G. 2001.** A standardized protocol for the
417 determination of specific leaf area and leaf dry matter content. *Functional Ecology* **15**:
418 688–695.
- 419 **Givnish TJ. 2002.** Ecological constraints on the evolution of plasticity in plants. *Evolutionary*
420 *Ecology* **16**: 213–242.
- 421 **Gruntman M, Novoplansky A. 2004.** Physiologically mediated self/non-self discrimination in
422 roots. *Proceedings of the National Academy of Sciences of the United States of America*
423 **101**: 3863–3867.
- 424 **Götzenberger L, de Bello F, Brathen KA, Davison J, Dubuis A, Guisan A, Leps J, Lindborg**
425 **R, Moora M, Pärtel M, Pellissier L, Pottier J, Vittoz P, Zobel K, Zobel M. 2012.**
426 Ecological assembly rules in plant communities—approaches, patterns and prospects.
427 *Biological Reviews* **87**: 111-127.
- 428 **Herben T, Hara T. 2003.** Spatial pattern formation in plant communities. In *Morphogenesis and*
429 *Pattern Formation in Biological Systems—Experiments and Models* (eds Sekimura, T., Noji,
430 S., Ueno, N. & Maini, P.K.), pp. 223–235. Springer Verlag, Tokyo.
- 431 **Keddy P, Nielsen K, Weiher E, Lawson R. 2002.** Relative competitive performance of 63
432 species of terrestrial herbaceous plants. *J. Veg. Science*, **13**: 5–16.
- 433 **Lankau RA. 2012.** Coevolution between invasive and native plants driven by chemical
434 competition and soil biota. *Proceedings of the National Academy of Sciences of the United*
435 *States of America* **109**: 11240-11245.

- 436 **Lavorel S, Garnier E. 2002.** Predicting changes in community composition and ecosystem
437 functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**: 545-556.
- 438 **Lepik A, Abakumova M, Zobel K, Semchenko M. 2012.** Kin recognition is density-dependent
439 and uncommon among temperate grassland plants. *Functional Ecology* **26**: 1214–1220.
- 440 **Lipowsky A, Schmid B, Roscher C. 2011.** Selection for monoculture and mixture genotypes in
441 a biodiversity experiment. *Basic and Applied Ecology* **12**: 360–371.
- 442 **Lipowsky A, Roscher C, Schumacher J, Michalski SG, Gubsch M, Buchmann N, Schulze E-
443 D, Schmid B. 2015.** Plasticity of functional traits of forb species in response to
444 biodiversity. *Perspectives in Plant Ecology, Evolution and Systematics* **17**: 66-77.
- 445 **Lovett Doust L. 1981.** Population dynamics and local specialization in a clonal perennial
446 (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. *Journal of Ecology*
447 **69**: 743–755.
- 448 **Mahall BE, Callaway RM 1992.** Root communication mechanisms and intracommunity
449 distributions of two Mojave desert shrubs. *Ecology* **73**: 2145–2151.
- 450 **Marcuvitz S, Turkington R. 2000.** Differential effects of light quality, provided by different
451 grass neighbours, on the growth and morphology of *Trifolium repens* L. (white clover).
452 *Oecologia* **125**: 293–300.
- 453 **McConnaughay KDM, Coleman JS. 1999.** Biomass allocation in plants: ontogeny or
454 optimality? A test along three resource gradients. *Ecology* **80**: 2581–2593.
- 455 **McPhee CS, Aarssen LW. 2001.** The separation of above- and below-ground competition in
456 plants - A review and critique of methodology. *Plant Ecology* **152**: 119-136.
- 457 **Moore PD, Chapman SB. 1986.** *Methods in Plant Ecology*. Blackwell Scientific Publications,
458 Oxford.
- 459 **Moran NA. 1992.** The evolutionary maintenance of alternative phenotypes. *American Naturalist*
460 **139**: 971–989.
- 461 **Oksanen J. 1997.** Plant neighbour diversity. *Journal of Vegetation Science* **8**: 255–258.
- 462 **Perry GLW, Enright NJ, Miller BP, Lamont BB. 2009.** Nearest-neighbour interactions in
463 species-rich shrublands: the roles of abundance, spatial patterns and resources. *Oikos* **118**:
464 161–174.
- 465 **Pierik R, Mommer L, Voeselek LACJ. 2013.** Molecular mechanisms of plant competition:
466 neighbour detection and response strategies. *Functional Ecology* **27**: 841–853.

- 467 **Pigliucci M. 2001.** *Phenotypic Plasticity: Beyond Nature and Nurture*. Johns Hopkins University
468 Press, Baltimore, Maryland.
- 469 **Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012.** Biomass allocation to
470 leaves, stems and roots: meta-analyses of interspecific variation and environmental control.
471 *New Phytologist* **193**: 30-50.
- 472 **Ravenscroft CH, Fridley JD, Grime JP. 2014.** Intraspecific functional differentiation suggests
473 local adaptation to long-term climate change in a calcareous grassland. *Journal of Ecology*
474 **102**(1): 65-73.
- 475 **R Core Team 2015.** *R 3.2.0: A language and environment for statistical computing*. R
476 Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- 477 **Revell LJ. 2010.** Phylogenetic signal and linear regression on species data. *Methods in Ecology*
478 *Evolution* **1**: 319–329.
- 479 **Schenk HJ. 2006.** Root competition: beyond resource depletion. *Journal of Ecology* **94**(4): 725-
480 739.
- 481 **Semchenko M, Abakumova M, Lepik A, Zobel K. 2013.** Plants are least suppressed by their
482 frequent neighbours: the relationship between competitive ability and spatial aggregation
483 patterns. *Journal of Ecology* **101**: 1313–1321.
- 484 **Semchenko M, John EA, Hutchings M.J. 2007.** Effects of physical connection and genetic
485 identity of neighbouring ramets on root-placement patterns in two clonal species. *New*
486 *Phytologist* **176**: 644–654.
- 487 **Semchenko M, Saar S, Lepik A. 2014.** Plant root exudates mediate neighbour recognition and
488 trigger complex behavioural changes. *New Phytologist* **204**: 361-637.
- 489 **Strauss SY. 2014.** Ecological and evolutionary responses in complex communities: implications
490 for invasions and eco-evolutionary feedbacks. *Oikos* **123**: 257-266.
- 491 **Turkington R. 1989.** The growth, distribution and neighbour relationships of *Trifolium repens* in
492 a permanent pasture. V. The coevolution of competitors. *Journal of Ecology* **77**: 717–733.
- 493 **Turnbull LA, Coomes DA, Purves DW, Rees M. 2007.** How spatial structure alters population
494 and community dynamics in a natural plant community. *Journal of Ecology* **95**: 79–89.
- 495 **Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A.**
496 **(1964–80)** *Flora Europaea*, Vol. 1–5. Cambridge University Press, Cambridge.

- 497 **Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J. 2012.**
498 The return of the variance: intraspecific variability in community ecology. *Trends in*
499 *Ecology and Evolution* **27**: 244-252.
- 500 **Wang P, Stieglitz T, Zhou DW, Cahill JF. 2010.** Are competitive effect and response two sides
501 of the same coin, or fundamentally different? *Functional Ecology* **24**: 196–207.
- 502 **Weihner E, van der Werf A, Thompson K, Roderick M, Garnier E, Eriksson O. 1999.**
503 Challenging Theophrastus: A common core list of plant traits for functional ecology.
504 *Journal of Vegetation Science* **10**: 609-620.
- 505 **Weiner J. 2004.** Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology,*
506 *Evolution and Systematics* **6**: 207–215.
- 507 **Weinig C. 2000.** Differing selection in alternative competitive environments: shade-avoidance
508 responses and germination timing. *Evolution* **54**: 124–136.
- 509 **Zhu J, van der Werf W, Anten NPR, Vos J, Evers JB. 2015.** The contribution of phenotypic
510 plasticity to complementary light capture in plant mixtures. *New Phytologist* (in press). doi:
511 10.1111/nph.13416
- 512 **Zuppinger-Dingley D, Schmid B, Petermann JS, Yadav V, De Deyn GB, Flynn DFB. 2014.**
513 Selection for niche differentiation in plant communities increases biodiversity effects.
514 *Nature* **515**: 108-111.

515

516 **Supporting Information**

- 517 **Table S1.** Results of linear models for 27 focal species showing response to neighbour identity in
518 five aboveground traits.
- 519 **Figure S1.** Examples of low and high plasticity to neighbour identity.
- 520 **Figure S2.** Examples of trait dependence on neighbour mass.
- 521 **Figure S3.** Examples of allometric relationships between focal plant traits and biomass.
- 522 **Figure S4.** Relationship between the index of interaction frequencies (H') and plasticity
523 measured as the difference in trait-biomass allometry.
- 524 **Figure S5.** Relationship between plasticity and the index of interaction frequencies (H') at each
525 study site.
- 526 **Figure S6.** Relationship between **plasticity and** the difference in mean neighbour mass.
- 527 **Figure S7.** Relationship between plasticity and an index of neighbour diversity.

528 **Figure S8.** Relationship between plasticity and the index of interaction frequencies (H') for each
529 measured trait.

530 **Figure S9.** Correlations between plasticities in five aboveground traits.

531

532 **Table 1.** List of focal and neighbour species and the sites where their spatial patterns were
 533 studied (see Methods for site descriptions).

No	Focal species	Family	Neighbour species	Family	Site
1	<i>Achillea millefolium</i>	Asteraceae	<i>Festuca rubra</i>	Poaceae	3
2	<i>Antennaria dioica</i>	Asteraceae	<i>Lotus corniculatus</i>	Fabaceae	2
3	<i>Briza media</i>	Poaceae	<i>Festuca rubra</i>	Poaceae	1
4	<i>Carex ornithopoda</i>	Cyperaceae	<i>Trifolium pratense</i>	Fabaceae	1
5	<i>Carlina vulgaris</i>	Asteraceae	<i>Sesleria caerulea</i>	Poaceae	2
6	<i>Centaurea jacea</i>	Asteraceae	<i>Anthoxanthum odoratum</i>	Poaceae	3
7	<i>Deschampsia cespitosa</i>	Poaceae	<i>Peucedanum palustre</i>	Apiaceae	6
8	<i>Festuca rubra</i>	Poaceae	<i>Poa angustifolia</i>	Poaceae	4
9	<i>Filipendula vulgaris</i>	Rosaceae	<i>Sesleria caerulea</i>	Poaceae	2
10	<i>Galium verum</i>	Rubiaceae	<i>Filipendula vulgaris</i>	Rosaceae	2
11	<i>Inula salicina</i>	Asteraceae	<i>Sesleria caerulea</i>	Poaceae	1
12	<i>Juncus gerardii</i>	Juncaceae	<i>Agrostis stolonifera</i>	Poaceae	7
13	<i>Leontodon hispidus</i>	Asteraceae	<i>Sesleria caerulea</i>	Poaceae	1
14	<i>Lotus corniculatus</i>	Fabaceae	<i>Sesleria caerulea</i>	Poaceae	2
15	<i>Lychnis flos-cuculi</i>	Caryophyllaceae	<i>Deschampsia cespitosa</i>	Poaceae	6
16	<i>Medicago lupulina</i>	Fabaceae	<i>Festuca rubra</i>	Poaceae	3
17	<i>Peucedanum palustre</i>	Apiaceae	<i>Deschampsia cespitosa</i>	Poaceae	6
18	<i>Phleum pratense</i>	Poaceae	<i>Anthoxanthum odoratum</i>	Poaceae	3
19	<i>Pilosella officinarum</i>	Asteraceae	<i>Sesleria caerulea</i>	Poaceae	2
20	<i>Pimpinella saxifraga</i>	Apiaceae	<i>Sesleria caerulea</i>	Poaceae	2
21	<i>Rumex acetosa</i>	Polygonaceae	<i>Festuca rubra</i>	Poaceae	4
22	<i>Sesleria caerulea</i>	Poaceae	<i>Pilosella officinarum</i>	Asteraceae	2
23	<i>Succisa pratensis</i>	Caprifoliaceae	<i>Carex flacca</i>	Cyperaceae	1
24	<i>Trifolium montanum</i>	Fabaceae	<i>Festuca rubra</i>	Poaceae	1
25	<i>Trifolium repens</i>	Fabaceae	<i>Poa pratensis</i>	Poaceae	3
26	<i>Urtica dioica</i>	Urticaceae	<i>Artemisia vulgaris</i>	Asteraceae	5
27	<i>Veronica chamaedrys</i>	Plantaginaceae	<i>Rumex acetosa</i>	Polygonaceae	4

534
 535 **Table 2.** The results of models assessing the relationship between plasticity to neighbour identity
 536 (conspecific *versus* heterospecific) and the index of interaction frequencies (H'). The differences
 537 in focal and neighbour mass between conspecific and heterospecific treatments were included as
 538 covariates. Model coefficients (\pm SE) and their significance (** - $P < 0.01$; *** - $P < 0.001$) are
 539 presented. Two models were fitted for each relationship: a) a model assuming phylogenetic
 540 independence ($\lambda = 0$; No phyl. signal); and b) a model with a correlation structure that takes into
 541 account phylogenetic dependencies between species based on the observed Pagel's λ (With phyl.
 542 signal). Akaike information criteria (AIC), likelihood ratio (LR) and the statistical significance of
 543 the test are shown.

	No phyl. signal	With phyl. signal	LR	P
H'	-0.34 (0.12)**	-0.34 (0.11)**		
$H' \times H'$	0.54 (0.14)**	0.52 (0.13)***		
Dif. focal mass	0.38 (0.06)***	0.38 (0.05)***		
Dif. neighbour mass	-0.001 (0.003)	-0.001 (0.002)		
AIC	-135.2	-133.2	0.002	0.968

544 **Fig. 1.** Relationship between the index of interaction frequencies (H') and (a) probability of
545 encountering conspecific neighbours ($F_{2,24} = 40.3$, $P < 0.0001$, $R^2 = 0.77$), (b) probability of
546 encountering the species used as the neighbour in the heterospecific treatment ($F_{2,24} = 4.6$, $P =$
547 0.021 , $R^2 = 0.28$). The index was calculated as $-(p_{\text{con}} \times \ln(p_{\text{con}}) + p_{\text{het}} \times \ln(p_{\text{het}}))$, where p_{con} and
548 p_{het} denote the probabilities of encountering conspecifics and the species used in the
549 heterospecific treatment as the nearest neighbours in the field, respectively. Numbers on the
550 graph represent different focal species in Table 1.

551 **Fig. 2.** Relationship between the degree of plasticity to neighbour species identity (conspecific
552 *versus* heterospecific) and the index of interaction frequencies H' ($F_{2,24} = 15.3$, $P < 0.0001$, $R^2 =$
553 0.56). The index is more positive as encounters with both neighbour types become more common
554 and even in frequency. Plasticity was calculated based on five aboveground traits and is
555 represented by residual plasticity after accounting for differences in focal plant biomass (see
556 Methods for further details). Numbers on the graph represent different focal species in Table 1.
557 See Fig. S5 for a graph with highlighted study sites.

558 **Fig. 3.** Relationship between the degree of plasticity to neighbour species identity (conspecific
559 *versus* heterospecific) and (a) probability of encountering conspecific neighbours (polynomial
560 model: $F_{2,24} = 1.1$, $P = 0.351$, $R^2 = 0.08$), (b) probability of encountering the species used as the
561 neighbour in the heterospecific treatment (polynomial model: $F_{2,24} = 2.5$, $P = 0.108$, $R^2 = 0.17$).
562 Plasticity was calculated based on five aboveground traits and is represented by residuals after
563 accounting for differences in focal plant biomass (see Methods for further details). Numbers on
564 the graph represent different focal species in Table 1.

565 **Fig. 4.** Relationship between the degree of plasticity to neighbour species identity (conspecific
566 *versus* heterospecific) and (a) focal species abundance (linear relationship: $F_{1,25} = 0.83$; $P =$
567 0.371 ; $R^2 = 0.03$), (b) neighbour species abundance (linear relationship: $F_{1,25} = 8.6$; $P = 0.007$; R^2
568 $= 0.26$), and (c) association of focal species with the species used as the heterospecific neighbour
569 (calculated as the difference between the observed and expected frequencies of encountering the
570 neighbour species; linear relationship: $F_{1,25} = 2.4$; $P = 0.132$; $R^2 = 0.09$). Plasticity was calculated
571 based on five aboveground traits and is represented by residuals after accounting for differences
572 in focal plant biomass (see Methods for further details). Numbers on the graph represent different
573 focal species in Table 1.

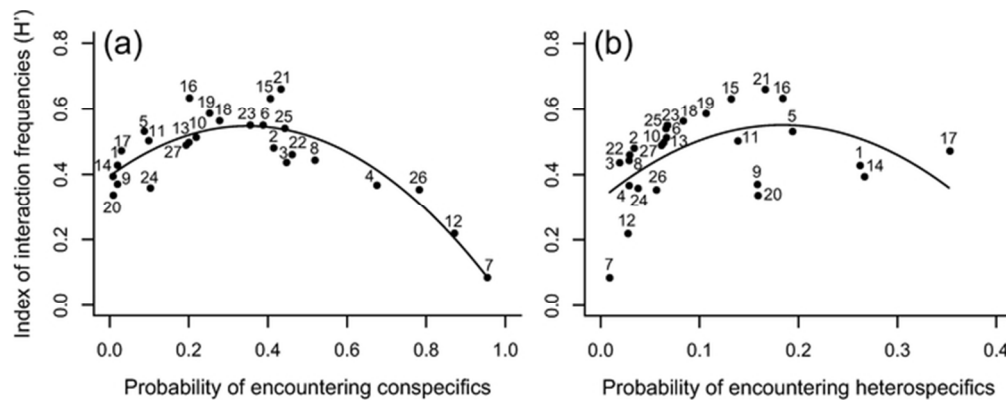


Fig. 1. Relationship between the index of interaction frequencies (H') and (a) probability of encountering conspecific neighbours ($F_{2,24} = 40.3$, $P < 0.0001$, $R^2 = 0.77$), (b) probability of encountering the species used as the neighbour in the heterospecific treatment ($F_{2,24} = 4.6$, $P = 0.021$, $R^2 = 0.28$). The index was calculated as $-(p_{con} \times \ln(p_{con}) + p_{het} \times \ln(p_{het}))$, where p_{con} and p_{het} denote the probabilities of encountering conspecifics and the species used in the heterospecific treatment as the nearest neighbours in the field, respectively. Numbers on the graph represent different focal species in Table 1.

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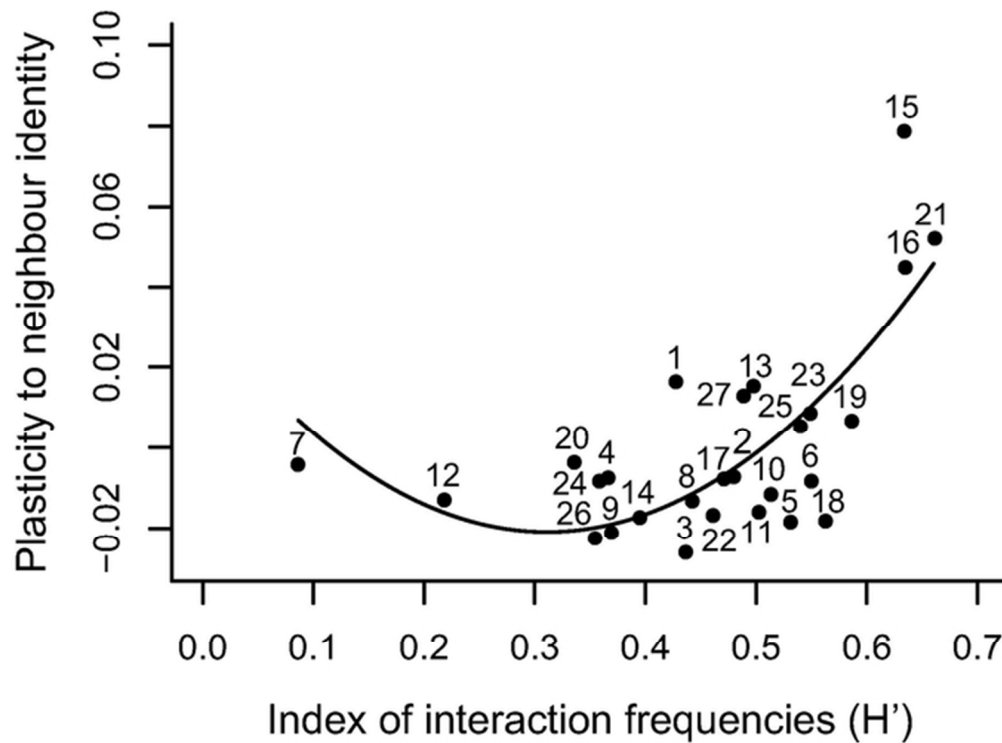


Fig. 2. Relationship between the degree of plasticity to neighbour species identity (conspecific versus heterospecific) and the index of interaction frequencies H' ($F_{2,24} = 15.3$, $P < 0.0001$, $R^2 = 0.56$). The index is more positive as encounters with both neighbour types become more common and even in frequency. Plasticity was calculated based on five aboveground traits and is represented by residual plasticity after accounting for differences in focal plant biomass (see Methods for further details). Numbers on the graph represent different focal species in Table 1. See Fig. S9 for a graph with highlighted study sites.

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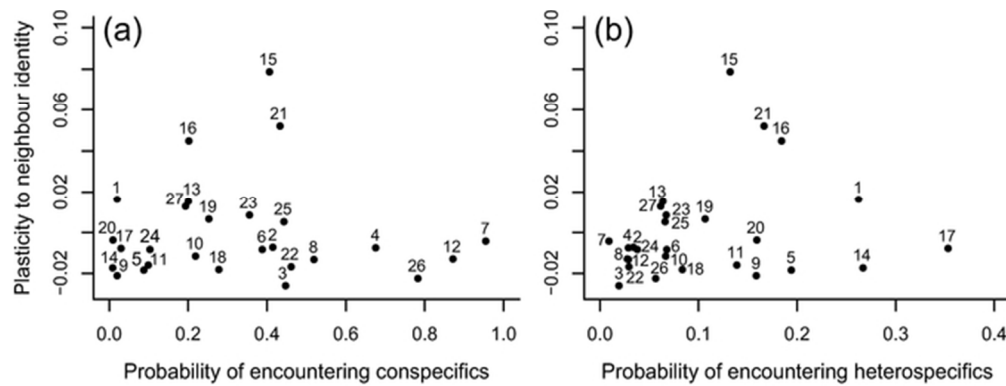


Fig. 3. Relationship between the degree of plasticity to neighbour species identity (conspecific versus heterospecific) and (a) probability of encountering conspecific neighbours (polynomial model: $F_{2,24} = 1.1$, $P = 0.351$, $R^2 = 0.08$), (b) probability of encountering the species used as the neighbour in the heterospecific treatment (polynomial model: $F_{2,24} = 2.5$, $P = 0.108$, $R^2 = 0.17$). Plasticity was calculated based on five aboveground traits and is represented by residuals after accounting for differences in focal plant biomass (see Methods for further details). Numbers on the graph represent different focal species in Table 1.

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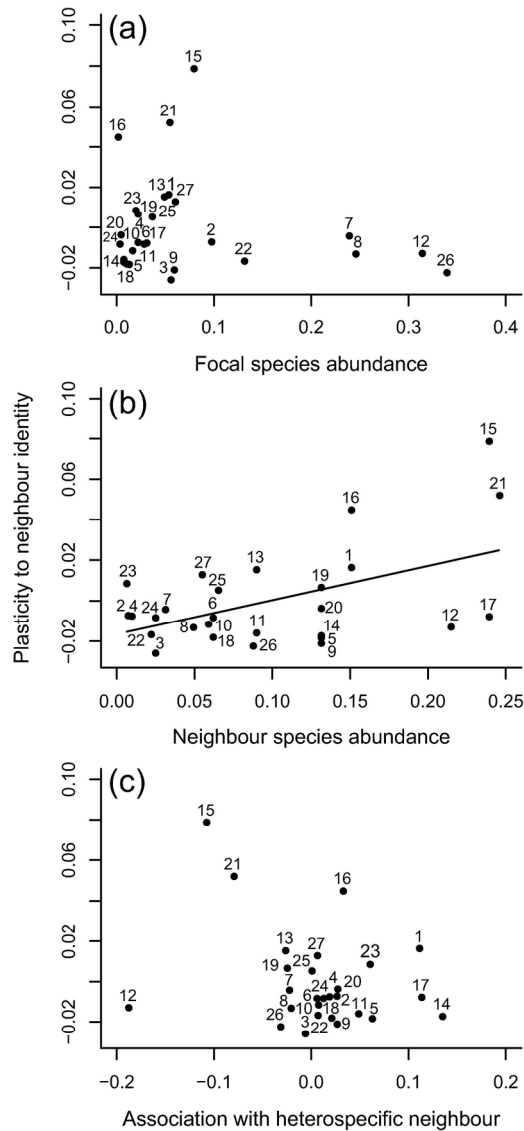


Fig. 4. Relationship between the degree of plasticity to neighbour species identity (conspecific versus heterospecific) and (a) focal species abundance (linear relationship: $F_{1,25} = 0.83$; $P = 0.371$; $R^2 = 0.03$), (b) neighbour species abundance (linear relationship: $F_{1,25} = 8.6$; $P = 0.007$; $R^2 = 0.26$), and (c) association of focal species with the species used as the heterospecific neighbour (calculated as the difference between the observed and expected frequencies of encountering the neighbour species; linear relationship: $F_{1,25} = 2.4$; $P = 0.132$; $R^2 = 0.09$). Plasticity was calculated based on five aboveground traits and is represented by residuals after accounting for differences in focal plant biomass (see Methods for further details). Numbers on the graph represent different focal species in Table 1.

173x195mm (300 x 300 DPI)