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

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## Summary

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

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

**Introduction**

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

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

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

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

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

**Materials and methods**

**(a) Study sites and species**

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

**(b) Common garden experiment**

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

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

Pots contained a mixture of commercial soil, sand, lime powder and natural soil inoculum prepared separately for species from each study site to match the N content and pH of soil from the corresponding site. No fertiliser or herbicide was applied during the experiment. Three pot sizes were used to account for differences in productivity and average plant size in different study 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 6. The distance between the focal plant (planted in the centre) and its neighbours was 5.7 cm in 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 radius in each case). Pots were placed randomly in an outdoor paved area, and their positions were re-randomized twice during the experiment. Pots received natural precipitation but were watered daily in dry and sunny weather. Weeds were regularly removed. Plants were harvested after 11-14 weeks of growth. The experiment was carried out in Tartu, Estonia (58°22'N, 26°41'E).

### (c) Plant measurements

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

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

#### **(d) Statistical analysis**

##### *Plasticity estimation from the pot experiment*

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



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

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

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

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

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

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

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

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

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

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

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

#### *Alternative explanatory variables*

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

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

## Results

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

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

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

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

## Discussion

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

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

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

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

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

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

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

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# Author contributions

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

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## Supporting Information

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

**Table 1.** List of focal and neighbour species and the sites where their spatial patterns were 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

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

**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  $-(p_{\text{con}} \times \ln(p_{\text{con}}) + p_{\text{het}} \times \ln(p_{\text{het}}))$ , where  $p_{\text{con}}$  and  $p_{\text{het}}$  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.

**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. S5 for a graph with highlighted study sites.

**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.

**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.

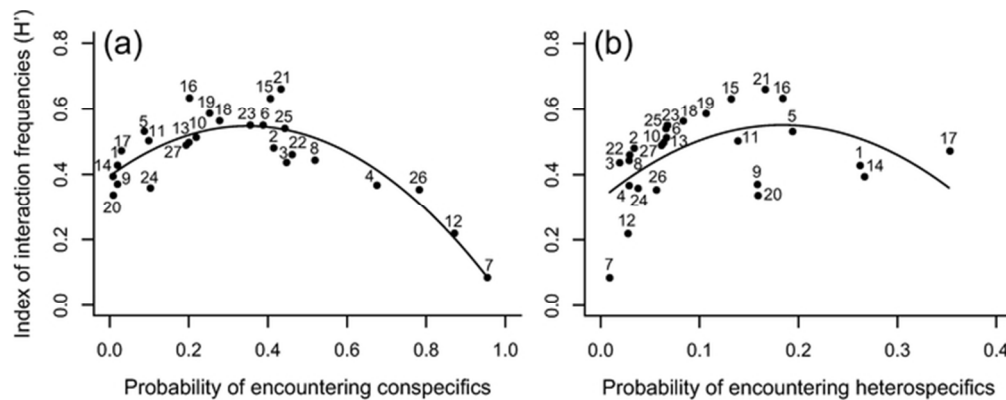


Fig. 1. Relationship between the index of interaction frequencies ( $H'$ ) and (a) probability of encountering conspecific neighbours ( $F_{2,24} = 40.3$ ,  $P < 0.0001$ ,  $R^2 = 0.77$ ), (b) probability of encountering the species used as the neighbour in the heterospecific treatment ( $F_{2,24} = 4.6$ ,  $P = 0.021$ ,  $R^2 = 0.28$ ). 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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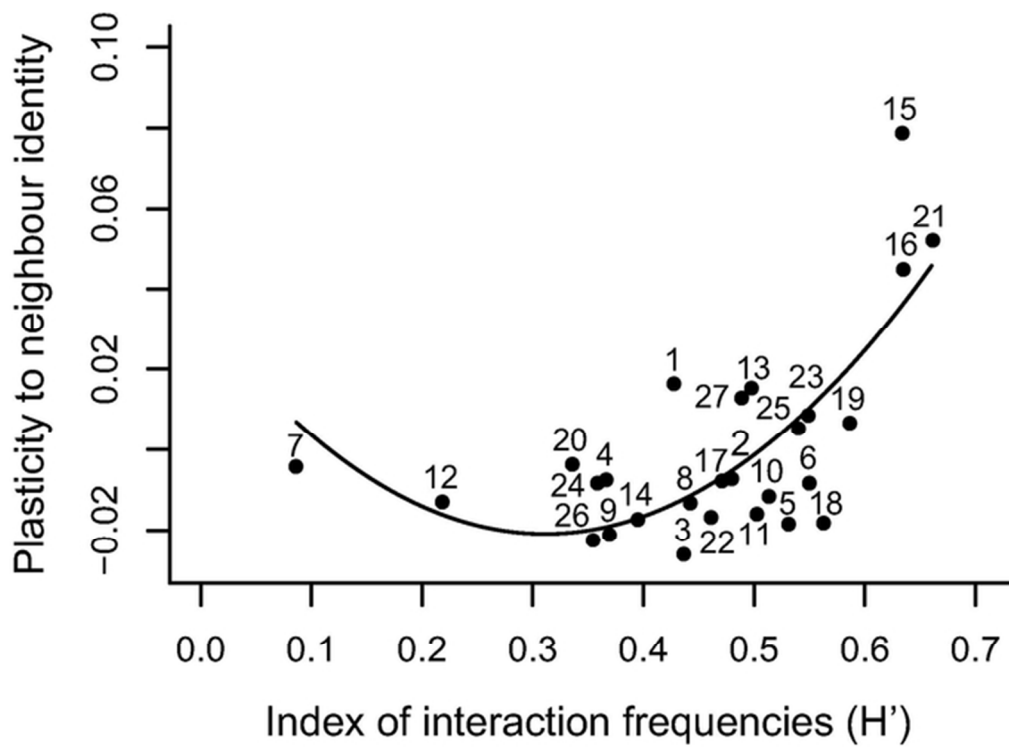


Fig. 2. Relationship between the degree of plasticity to neighbour species identity (conspecific versus heterospecific) and the index of interaction frequencies  $H'$  ( $F_{2,24} = 15.3$ ,  $P < 0.0001$ ,  $R^2 = 0.56$ ). The index is more positive as encounters with both neighbour types become more 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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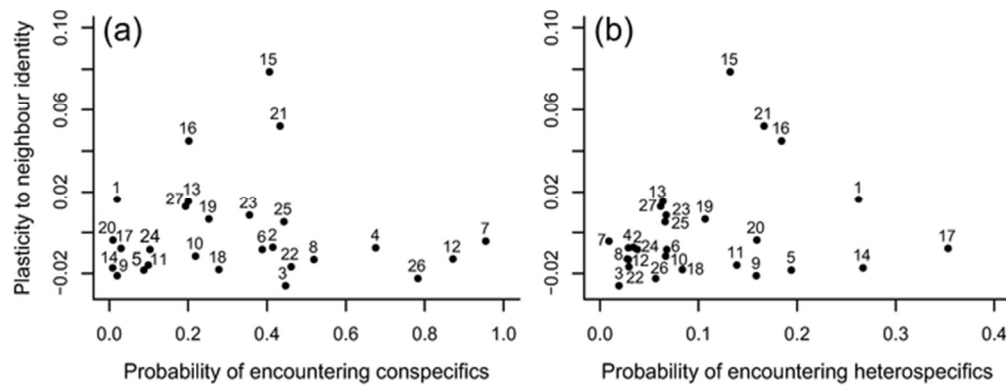


Fig. 3. Relationship between the degree of plasticity to neighbour species identity (conspecific versus heterospecific) and (a) probability of encountering conspecific neighbours (polynomial model:  $F_{2,24} = 1.1$ ,  $P = 0.351$ ,  $R^2 = 0.08$ ), (b) probability of encountering the species used as 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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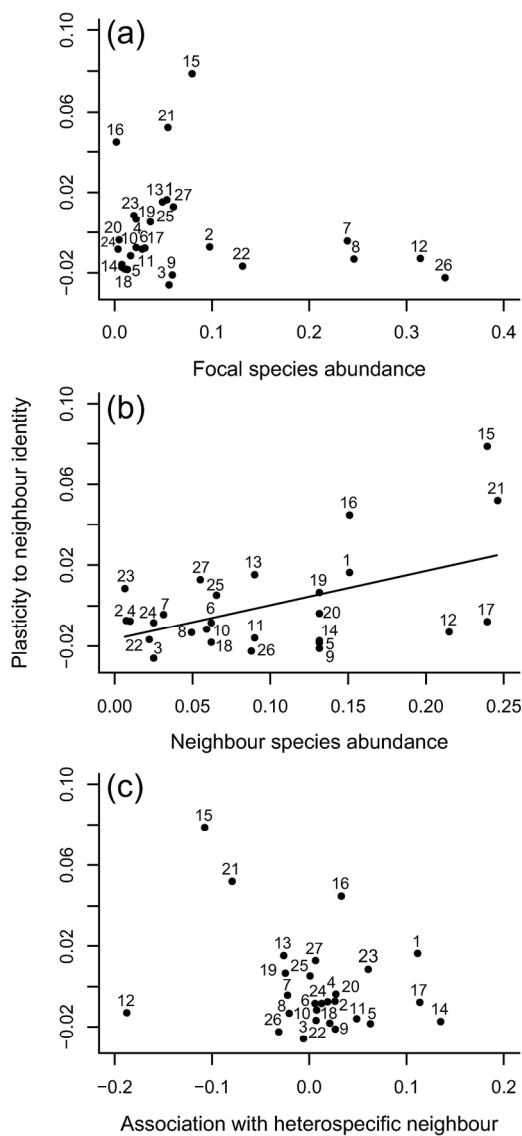


Fig. 4. Relationship between the degree of plasticity to neighbour species identity (conspecific versus heterospecific) and (a) focal species abundance (linear relationship:  $F_{1,25} = 0.83$ ;  $P = 0.371$ ;  $R^2 = 0.03$ ), (b) neighbour species abundance (linear relationship:  $F_{1,25} = 8.6$ ;  $P = 0.007$ ;  $R^2 = 0.26$ ), 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)