

Is the positive relationship between species richness and shoot morphological plasticity mediated by ramet density or is there a direct link?

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Abstract Little is known about the consequences of phenotypic plasticity in co-existing species for plant community structure. However, it has been proposed that the potential of plants to exhibit plastic responses to light availability could be a key factor determining the capability of individuals to co-exist at small scales. Our previous research demonstrated that morphological plasticity to light was positively related to small-scale species richness in a temperate grassland. However, it remained unclear whether this relationship was solely due to a higher shoot density in plastic assemblages, or whether diversity was directly related to the morphological plasticity of the co-inhabitants. We used two data sets to clarify this relationship: experimentally acquired estimates of plasticity to light availability for 45 herbaceous plant species, and species richness and ramet density data from a 2-year permanent plot study in a semi-natural calcareous grassland. There was little ramet mortality observed in the permanent plot study indicating that the link between plasticity and richness does not operate through reduced mortality in more morphologically plastic assemblages. The local density of ramets explained most of variation in small-scale

richness, but there was also a significant direct density-independent effect of mean shoot plasticity on richness, showing that plasticity to light directly enhances the small-scale co-existence of species.

Keywords Grassland vegetation · Herbaceous species · Plant density · Plasticity · Species diversity

Introduction

Ecologists have dedicated considerable effort to understanding the principles according to which natural communities are assembled, given the species and functional traits present in the species pool (Vellend 2010; Bello et al. 2012; Götzenberger et al. 2012). However, the interdependence between species traits and community structure can also be approached from a different direction—by asking how community-level processes depend on the characteristics of species present in the assemblage. It is evident that the values of important species characteristics vary between sites (Díaz et al. 1998), resulting, among other things, in differing interaction patterns, mortality rates and resource-use economies (Wacker et al. 2009), and thus in different community parameters.

Many studies have shown that species functional traits can alter the structure and diversity of plant communities (Díaz et al. 1998; Bello et al. 2012): however, morphological plasticity—the ability to express a range of morphotypes as a function of environmental conditions—has received relatively little attention. As conveyed by Callaway et al. (2003): ‘we know a great deal about the plastic responses of plant phenotypes to the abiotic and biotic environment, but very little about the consequences of phenotypic plasticity for plant communities.’

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There are at least two good reasons to predict that high morphological plasticity could significantly enhance the survival of individuals in communities, thus leading to denser and more diverse stands. Firstly, high shoot plasticity may improve the ability of plants to adjust to high ramet density and thus reduce the degree of competitive asymmetry in crowded stands (Weiner et al. 1990; Schmitt and Wulff 1993; Sorrensen-Cothorn et al. 1993; Schwinning and Weiner 1998; Stoll et al. 2002; Lepik et al. 2005; Vermeulen et al. 2008). Avoidance of competition is thought to be a frequently employed strategy in potentially competitive situations (Novoplansky 2009; Semchenko et al. 2010). A common response of plastic plants to a neighbour is to reduce branching and keep away from it, thus decreasing the overall competitive effect (Callaway et al. 2003; Herben and Novoplansky 2010). As a result, plasticity represents an equalizing mechanism that reduces inherent differences in species performance, and thus promotes coexistence (Callaway et al. 2003; Wacker et al. 2009; Lankau 2011; Nagashima and Hikosaka 2011).

Secondly, plasticity enhances the ability of plants to adjust to changing environments, and mortality due to environmental fluctuations should consequently decrease with increasing plasticity (Jung et al. 2010). Therefore, in addition to reduced competitive exclusion, plant density and diversity should be higher in stands occupied by species with high shoot plasticity, because of lower mortality.

There is still at least one possible explanation for how plasticity of co-occurring individuals could affect assemblage species diversity other than through changes in ramet density (as described above). When species with high shoot plasticity are growing in a site, the plastic response of nearby individuals to increased shade can result in decreased vegetative sprouting and therefore reduced ramet number per genet (Skálová 2010). Reduced tillering in high-plasticity assemblages could result in higher species richness per area even if ramet density does not change (this may happen only if there are enough species available in a community species pool).

In a previous study (Lepik et al. 2005), we found a positive relationship between the mean shoot plasticity of locally co-occurring species and species richness using three data sets: experimentally assessed shoot morphological plasticity to light in 35 temperate grassland species, species richness and ramet density data from 17 herbaceous communities with very different richness and productivity (inter-community study), and species richness data from a 5-year 40 × 40-cm permanent plot experiment in a species-rich calcareous grassland (intra-community study). In both the inter-community and intra-community study we found strong positive relationships between species richness and the average shoot plasticity of those species involved that had been experimentally measured. In the inter-community

study we also collected data on mean ramet density (number of plant ramets per unit area) for the 17 communities involved. Using these data we detected a positive relationship between average plasticity and ramet density, indicating that higher richness in more plastic assemblages was largely due to a higher number of plant ramets occurring per unit area. Because we lacked data on local ramet density in the intra-community study, it remained unclear whether the same was true for small-scale variation in diversity, i.e. were assemblages of species that were on average more plastic more species rich simply because of a greater number of plant ramets occupying the 40 × 40-cm plots? Such an explanation seemed quite likely because a positive relationship between species richness per unit area and plant cover had been detected in an earlier study in the same grassland (Laelatu wooded meadow) (Eek and Zobel 2001).

So far all predictions about the plasticity-richness relationship have implicitly or explicitly assumed higher local richness per unit area because more symmetrical competition leads to reduced mortality, denser canopies and ultimately higher plant density (Weiner et al. 1990; Schmitt and Wulff 1993; Sorrensen-Cothorn et al. 1993; Schwinning and Weiner 1998; Stoll et al. 2002; Lepik et al. 2005). Thus, the detection of a density-independent relationship between plasticity and diversity would open entirely new perspectives and indicate the existence of an unidentified mechanism of coexistence, in which small-scale diversity is directly linked to the degree of plasticity of neighbouring taxa.

In this paper we report the results from a 2-year permanent plot study that we established in Laelatu wooded grassland to test whether the consistent positive relationship between small-scale richness and among-species average plasticity found by Lepik et al. (2005) is mediated solely by the number of plant shoots (ramets) per unit area, or whether there is a direct effect of shoot morphological plasticity on small-scale diversity.

Materials and methods

Assessment of species plasticity

Species morphological plasticity to light availability was assessed in a common garden experiment in Tartu, Estonia (58°23'N, 26°43'E). Seeds of 45 perennial herbaceous plant species were collected from a range of temperate grassland communities in Estonia. Twenty similar-sized seedlings of each species were planted, one seedling per pot, into 1.2-l pots filled with fine sand. Plants were distributed equally among four spectrally neutral shading treatments: 10, 25, 50 and 100 % of full daylight.

It is well known that plants respond differently to neutral shade and green canopy shade (Casal and Mazzella 1998; Stuefer and Huber 1998; Pigliucci and Schmitt 1999; Weinig 2000). Nevertheless, the only really consistent difference between the overall effect of neutral and canopy shade is the weaker effect of neutral shade on plant morphology [except on biomass (Stuefer and Huber 1998; Weinig 2000)]. Therefore, the use of neutral shade instead of ‘green’ shade probably causes systematically lower plasticity estimates to light availability and consequently increases the probability of type II error in statistical analyses, and is not likely to cause artefacts and biased statistical inferences.

After 10 weeks of growth, the roots and shoots of each plant were harvested separately. Plants were past the juvenile stage but only a few of the harvested individuals were flowering. Plant leaf number was counted and total leaf area was measured using a scanner, and the image-editing software Aldus PhotoStyler 2.0 (Aldus, Seattle, WA) and Pindala 1.0 (I. Kalamees; Eesti Loodusfoto, Tartu). Plants were dried at 75 °C for 24 h and weighed. For a detailed description of the experiment see Lepik et al. (2005) and Semchenko et al. (2012).

The degree of plasticity to light availability was defined as the slope of the reaction norm of a trait value along the experimental illumination gradient. Such an estimate of plasticity is comparable across different traits and species, provided that the trait value is log transformed and the allometric effect of biomass is considered and removed. Thus, we used a generalized linear model with log mean leaf area as the dependent variable and two continuous independent variables: experimentally manipulated light availability, and plant above-ground biomass with its statistically significant modifications to account for size-dependent variation in the trait value (log, log–log, square root, square, inverse, etc.; suitable modifications were selected using a backward stepwise model-building method). Because the allometric effect of biomass was included in the model, the plasticity estimate of a certain trait could be considered as size independent. As a result, the plasticity estimate should reflect mostly the presumably adaptive (also described as ‘active’ or ‘true’) plasticity of the trait and not phenotypic responses to resource availability or plant developmental stage [also referred to as ‘inevitable’ or ‘passive’ plasticity (Sultan 1995; McConnaughay and Coleman 1999)]. Plasticity estimates were calculated using Statistica 6.0 software (StatSoft, Tulsa, OK). For a detailed description of the calculations see Lepik et al. (2005).

Permanent plot study

Small-scale species richness data were collected in a mesic calcareous wooded grassland in western Estonia (Laelatu

wooded meadow 58°35′N, 26°34′E) during a 2-year permanent plot study. The meadow has a scattered tree layer, with *Quercus robur*, *Fraxinus excelsior*, *Corylus avellana* and *Betula* spp. the most abundant species. The average coverage of the tree canopy is ca 50 %. The meadow has been annually mown for hay in early July for more than 200 years. The perennial-dominated (98 % of species are perennials) herbaceous community is very species rich at the small scale—up to 25 species have been recorded in a 0.01-m² quadrat and 68 in a 1-m² quadrat (Kull and Zobel 1991). This study was conducted in a less species rich part of the meadow (the average of 40–50 species m⁻²).

The study had a quasi-randomized design. Eighty circular permanent subplots (10-cm diameter, ca. 0.008 m²) were centred on the corners of twenty 40 × 40-cm permanent plots. Plots were located randomly in a 500-m² area. Preliminary observations had shown notable local variation of ramet density as well as small-scale species richness inside the study area (unpublished data). The number of vascular plant species and the taxonomic identity of each ramet growing in a subplot were recorded for all 80 permanent subplots four times a year in both 2004 and 2005. Sampling was conducted between mid-May and late July in both years. The quasi-randomized design was chosen because we wanted to characterize the sampling localities using environmental data (soil depth, amount of plant litter, illumination conditions, etc.) that could not be acquired non-destructively or with little disturbance of the subplots. Thus, the four subplots served as replicate vegetation samples for an environment measured in the 20 randomly chosen permanent plot locations. The relationship between local environmental conditions and vegetation structure will be discussed in another paper.

In our previous study (Lepik et al. 2005), we used a combined plasticity estimate that included both plasticity in the number of shoot modules and plasticity of leaf area, because these characteristics showed the strongest relationships with species richness in the permanent plots. In this study, we use only the degree of leaf area plasticity because the addition of module number plasticity into an overall plasticity estimate did not improve the relationships under study.

We calculated the average degree of leaf area plasticity in a subplot as the weighted (by ramet count) average mean leaf area plasticity for all species growing in the plot for which we had a plasticity estimate from Lepik et al. (2005). Average plasticity was only estimated for a subplot when we had data for at least two species in the plot. Subplots with no plasticity estimates were excluded from the analyses (on average of 2 % of subplots across the eight sampling dates were excluded).

The species used in the garden experiment of Lepik et al. (2005) were selected randomly from those that occur

in these grasslands, so we argue that they are a representative sample of the total pool of species in the plots under observation. The only selection criterion was that all growth-form groups occurring in temperate mesic grasslands be included: graminoids (including ferns), rosette-forming forbs, erosulate forbs, legumes. The final list of 45 species (initially seeds of more than 100 species were collected) was determined by availability of viable seeds, the ability of species to survive in experimental conditions and space in the shading tents.

The comparison of mean Ellenberg ecological indicator values for light, water and nutrients among the group of species selected for plasticity estimation, and across all species recorded in the permanent plots in 2 years, showed that none of the differences were significant (ANOVA; Statistica 6.0).

Statistical analysis

Seasonal changes in the number of plant ramets per subplot and species richness per subplot were studied using repeated-measures ANOVA (Statistica 6.0 software; StatSoft).

We used two parallel statistical models to study the relationships among species richness, average shoot plasticity and ramet density. The first one (mixed model) allowed us to use a proper nested design with random effects (plot, subplot); the second approach (path analysis) allowed us to evaluate a structural equation model where interdependence of the two independent variables (average plasticity, ramet density) was considered.

The effect of ramet density and mean leaf area plasticity on subplot richness across the eight sampling dates was studied using a repeated-measures mixed general linear model (procedure MIXED, type 3 sums of squares, model fitted using REML methodology, SAS 9.2 software). The number of species per subplot was included as the dependent variable, while log ramet density and the average degree of leaf area plasticity were included as continuous independent variables. To account for spatial effects, subplot nested within plot (four subplots in each of 20 plots) was also included in the model as a random effect.

For studying the relationships among species average plasticity, ramet density and species diversity on subplot, we performed a path analysis (i.e. a structural equation model with only observed variables) using a maximum likelihood method. Path analysis was performed with the `sem()` function of the `lavaan` package (Rosseeel 2012) in R version 3.1.0 (R Core Team 2014). Because the results from the mixed general linear model showed that sampling time was not statistically significant, we used only data from the last sampling date of the first year. Path coefficients were

estimated using maximum likelihood, and the model fit was tested with a χ^2 goodness-of-fit test, a Bollen–Stine bootstrap test with 1,000 bootstrap draws, a root mean square error of approximation (RMSEA) test, and the comparative fit index (CFI). A non-significant χ^2 , Bollen–Stine and RMSEA test, as well as CFI values above 0.90, indicate a good fit of the model to the data (Kline 2011).

Results

An average of 24.3 ramets (minimum two, maximum 63) from 8.9 species (minimum one, maximum 18) were recorded in the 0.008-m² subplots over the 2 years (eight dates; four sampling dates per year). The number of plant ramets per subplot showed a slight but consistent increase over the growing season (from 20.6 in mid-May to 25.5 in late July; *t*-test; $p < 0.0001$); a similar seasonal increase was also observed in subplot richness (from 7.9 species in mid-May to 9.1 in late July; *t*-test; $p = 0.0004$).

On average, plasticity estimates could be assigned to 4.3 species per subplot, representing an average of 52 % of the species (minimum 13 %, maximum 100 %) and 43 % of recorded ramets (minimum 5 %, maximum 100 %) in a subplot.

Both average leaf area plasticity and ramet density were significant determinants of species richness (Table 1; Online Resource 1). This indicated that average shoot plasticity per assemblage (ca. 20 adjacent ramets) had a direct density-independent positive effect on local richness (Figs. 1, 2).

The path analysis determined using data the last sampling date in the first year resulted in a just-identified model (SEM): $n = 73$; $\chi^2 = 0$, $df = 0$, $p(\chi^2) = 1$, p (Bollen–Stine bootstrap) = 0.56; RMSEA = 0, $p = 1$; CFI = 1. Although the model structure was not supported, our main interest was in the magnitude of the path coefficients between plasticity, richness and ramet density (see Fig. 3). Species mean leaf area plasticity and ramet density together accounted for half of the observed variation in species richness ($R^2 = 0.5$), while a direct link between plasticity and ramet density was not statistically significant (Fig. 3).

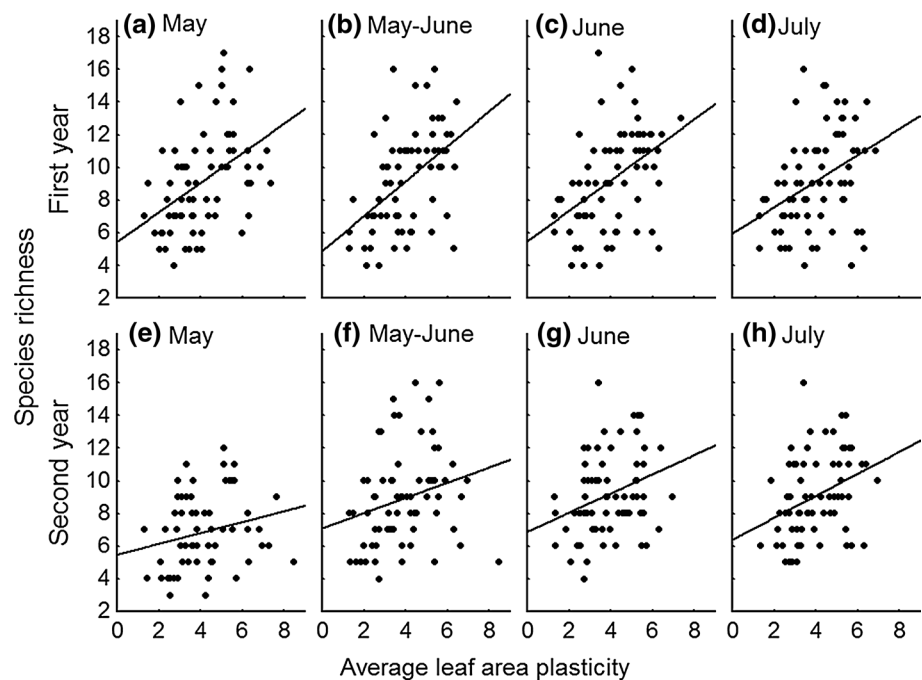
Practically no mortality of plant ramets was observed during the two sampling seasons—in both years, the number of ramets and recorded species richness increased from mid-May till the end of July. The wilting of some spring ephemerals (mostly *Anemone* spp.) in late June and early July did not outweigh the emergence of new ramets during the growing season. Because ramets were not individually marked, it is possible that some turnover of ramets remained unnoticed. In any case, we could not detect any self-thinning outside the active growing season.

Table 1 Results of a mixed general linear model comprising predictors of small-scale species richness in 2 sampling years (four sampling dates in each year)

Fixed effects	Numerator <i>df</i>	Denominator <i>df</i>	<i>F</i> -value	<i>p</i> -value
Log ramet density	1	598	380.3	<0.0001
Leaf area plasticity	1	598	13.90	0.0002
Sampling date	3	598	1.92	0.1250
Sampling year	1	598	2.52	0.1128
Random effects	Estimate	SE	Z-value	<i>p</i> -value
Plot	1.068	0.494	2.16	0.0152
Subplot (plot)	1.336	0.278	4.81	<0.0001
Residual	1.377	0.084	16.38	<0.0001

Significant *p*-values are in *italic*. See Figs. 1 and 2 for illustration of the main effects of interest

Fig. 1 The relationship between average shoot plasticity and species richness in **a–d** the first and **e–h** the second year of sampling. See Table 1 for significance values. *Regression lines* fitted separately for each sampling dates are shown for illustration



Discussion

Predictions concerning the plasticity–richness relationship have assumed that plasticity enhances local richness because it increases the symmetry of competition, which leads to reduced mortality and denser canopies (Weiner et al. 1990; Schmitt and Wulff 1993; Sorrensen-Cothorn et al. 1993; Schwinning and Weiner 1998; Stoll et al. 2002; Lepik et al. 2005). Our results show that this is not necessarily the case. We found that while most variation in small-scale diversity can be explained by local ramet density, there is a clear and significant density-independent effect of shoot plasticity on species richness. The average shoot plasticity of co-occurring plants had a small, but

consistent positive effect on species richness after accounting for the effect of ramet density. The strong positive relationship between ramet density and richness per unit area has previously been described at this site (Eek and Zobel 2001); by contrast, our finding that plasticity enhances the diversity of small-scale plant assemblages independently of plant density is certainly new and needs further investigation for a fuller understanding. Higher competitive symmetry and reduced mortality in more plastic stands (Weiner et al. 1990; Schmitt and Wulff 1993; Sorrensen-Cothorn et al. 1993; Schwinning and Weiner 1998; Stoll et al. 2002; Lepik et al. 2005) appear to be insufficient explanations for the full extent of the plasticity–richness relationship observed in the Laelatu meadow.

Fig. 2 The relationship between ramet density and species richness in **a–d** the first and **e–h** the second year of sampling. See Table 1 for significance values. Regression lines fitted separately for each sampling dates are shown for illustration

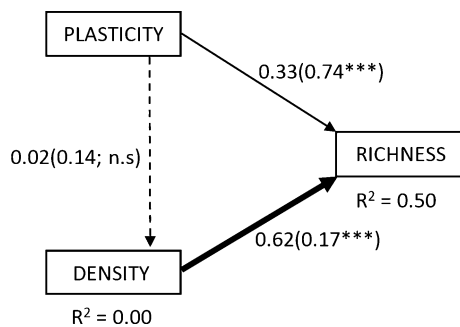
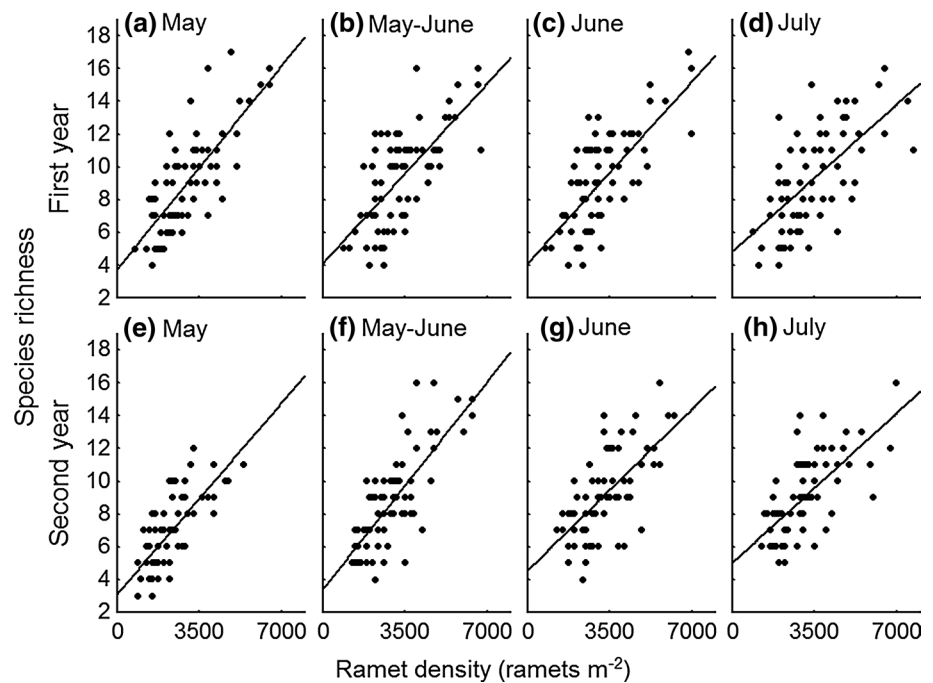


Fig. 3 Path diagram of the relationships among species mean leaf area plasticity (*PLASTICITY*), ramet density (*DENSITY*) and species richness (*RICHNESS*). Arrows show significant positive relationships and dashed arrow shows the tested, but non-significant relationship. Standardized path coefficients are displayed (with the corresponding unstandardized coefficients in parentheses; *** $p < 0.001$, not significant $p > 0.05$), together with the coefficient of determination for all variables; $n = 73$ (seven observations removed because of missing values)

One mechanism to explain the high density-independent richness (per ramet number) observed in plots with high average plasticity is the nature of the shade-avoidance syndrome exhibited by species in this community. Plants growing in shade often produce taller stems, slender vertical leaves, longer petioles, increased specific leaf area and exhibit reduced branching, resulting in fewer stems than individuals growing in illuminated areas (Schwinning and Weiner 1998; Maddonni et al. 2002; Franklin 2008; Leyser 2009; Keuskamp et al. 2010; Skálová 2010; Pierik et al. 2012). The plastic reaction to neighbouring shade can

therefore result in decreased vegetative sprouting and consequently lower ramet number per genet (Skálová 2010). At the scale of the local assemblage, this may result in higher species richness per number of ramets (if the community species pool is sufficiently large). In this scenario ramet density would decline without a loss of species diversity per unit area, because exclusions of genets does not occur.

Further work is needed to clarify the mechanisms that operate to allow higher species diversity to exist in more morphologically plastic plant assemblages at the small scale.

Author contribution statement M. L. and K. Z. conceived, designed and performed the experiments, analysed the data and wrote the manuscript.

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