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High shoot plasticity favours plant coexistence in herbaceous vegetation

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Abstract Several theoretical considerations imply that high shoot morphological plasticity could increase competition symmetry and favour plant coexistence. We tested whether mean plasticity across co-occurring species is a key trait for explaining ramet density and species richness in herbaceous vegetation. We used three data sets to test the hypotheses: (a) experimentally achieved estimates of plasticity to light availability for 35 herbaceous species; (b) richness, ramet density and canopy architecture data from 17 herbaceous communities; (c) species richness data from a 5-year permanent-plot study in a calcareous grassland. In herbaceous communities containing species with relatively higher shoot plasticity, ramet density was significantly higher. Consequently, relatively more species were growing per unit area—a greater proportion of the community species pool was represented on 1 m^2. In the permanent plot study species-richness was higher in those 40×40 cm quadrats where species with high shoot plasticity prevailed—there was a positive regression of richness on the mean plasticity of species. This relationship was highly significant in five consecutive years. Our results suggest that shoot plasticity to light availability is evidently one of the key traits in processes that alter the density of co-existing plants and, therefore, species diversity in herbaceous communities.

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Introduction

It is not clear which traits of interacting plants are important in determining the density of locally co-existing ramets of same or different species (Wilson et al. 2000; Rajaniemi 2003). Even in apparently homogenous stands the number of mature ramets per unit area may vary greatly between microsites, not to mention variation between community types—it is easy to observe 100-fold difference in herbaceous plant densities even within a compact geographical region (Zobel and Liira 1997). Often it is not possible to explain small-scale and large-scale differences in the density of co-existing plants through differences in resource availability, environment heterogeneity, plant size, and growth form alone. It may be assumed that part of this variance is attributable to some significant but so far not fully recognised plant trait which varies over different assemblies of locally co-existing species.

In mesic herbaceous communities, ramet density at the seasonal biomass maximum is usually a result of intense self-thinning, which means local competitive exclusion of plant modules (ramets, branches, leaves), individuals, and sometimes species. The self-thinning process often operates through asymmetric competition—larger individuals have a disproportionably strong competitive advantage over smaller individuals (Weiner 1990; Schwinning and Weiner 1998; Rajaniemi 2003; Rajaniemi et al. 2003). In plant communities, asymmetric competition usually occurs above ground (Weiner et al. 1990; Calhill 2003; but see Rajaniemi et al. 2003; Day et al. 2003). Larger (higher) plants are able to obtain a disproportionate share of the light resource and are likely to outcompete smaller ones by overgrowing and shading (Carson and Pickett 1990; Weiner 1990; Schwinning and Weiner 1998; Berntson and Wayne 2000; Zobel 2001; Day et al. 2003; Falster and Westoby 2003; Rajaniemi 2003).

It is reasonable to assume that high shoot plasticity can enhance the ability of plants to adjust to high ramet density and thus reduce the degree of competition asymmetry in crowded stands (Weiner et al. 1990; Schmitt and Wulff 1993; Sorrensen-Cothern et al. 1993; Schwinning and Weiner 1998; Stoll et al. 2002). The interaction of two plastic plants could lead to successful avoidance of competitive exclusion, through adjustments of their morphology to each other. This is demonstrated empirically for above- and below-ground plant organs (van Kleunen and Fisher 2001; Stoll et al. 2002; Callaway et al. 2003) as well as in mathematical models (Sorrensen-Cothern et al. 1993). Since, in vegetation, the outcome of direct competitive interaction largely depends on the morphology of co-occurring individuals, the interaction of two non-plastic plants should eventually lead to the elimination of one of them.

The role of plasticity in reducing competitive size asymmetry has been demonstrated in a series of experiments on transgenic plants. In crowded populations with experimentally reduced plasticity to red:far red ratio (“green” shade of plants), smaller individuals were rapidly suppressed by their larger neighbours, resulting in the development of large size inequalities (Ballaré et al. 1994; Ballaré 1999; Stoll et al. 2002, reviewed by Schwinning and Weiner 1998). According to the optimisation model (Sekimura et al. 2000), in crowded populations, shoots of plastic plant individuals are usually taller and thinner and with fewer branches than shoots of similar biomass in non-crowded populations (Weiner et al. 1990). Thus, in dense communities, high shoot plasticity to light availability could possibly retard competitive exclusion through lower light pre-emption by elongated shoots (Grime 1979; Sorrensen-Cothern et al. 1993; Gersani et al. 1998; Schwinning and Weiner 1998; Berntson and Wayne 2000; Stoll et al. 2002; Callaway et al. 2003).

Since plasticity to light enables plants to adapt with changing light climate, random mortality caused by environmental fluctuations should decrease with increasing mean shoot plasticity. Therefore, in addition to decreased competition asymmetry, and thus retarded competitive exclusion, ramet density should also be higher in stands occupied by species with high shoot plasticity, because of a lower neutral mortality.

In natural communities, small-scale species richness per unit area is a density-dependent measure. Species number per unit area is relatively higher in stands with high ramet density and vice versa (Goldberg and Miller 1990; Zobel and Liira 1997; Goldberg and Estabrook 1998; Eek and Zobel 2001). This means that, in addition to ramet density, small-scale species richness may also be predicted by competitive asymmetry of locally co-existing individuals (Rajaniemi 2003).

According to the above, we hypothesize that:

1. Local shoot density is higher in communities with a higher concentration of morphologically plastic species.
2. Small-scale diversity is positively related to mean shoot morphological plasticity of locally coexisting species.

We shall use experimentally achieved estimates of morphological plasticity for 35 species, data from a 5-year permanent-plot study, and also richness and ramet density data from 17 communities to test these two working hypotheses, both at a small- and large-scale. We shall make an attempt to test the predictive value of an autecologically measured plant attribute—phenotypic plasticity—for plant performance in community-level processes. In other words, we shall study whether a plant trait, measured in a series of garden experiments, explains vegetation structure in multi-species stands.

Material and methods

Garden experiment (autecological study)

Species’ morphological plasticity to light availability was assessed in a garden experiment in 2001 and 2002. Seeds of 35 species (random choice from amongst all species growing in the study-areas; Westoby 2002; S1) were collected from different areas of Estonia in the summers of 2000 and 2001. Seeds were stratified at 2°C for 2 months before germination. The seeds were sown on perlite in a greenhouse in May. After about 2 weeks, 20 equal-sized seedlings of each species were planted into 1.2 l plastic pots (diameter 7 cm, height 31 cm) filled with fine sand. The planted seedlings were randomly distributed among four neutral shading treatments: 100, 50, 25 and 10% of full daylight, with five replicate plants in each. Shade treatment was provided using tents made of aluminium-coated shade cloths (spectrum neutral; Ludvig Svensson, Kinna, Sweden).

Though the effect of neutral and “green” canopy shade on plant growth is mediated through different mechanisms, and several studies show certain differences in responses to different shade types (Casal and Mazzella 1998; Neff and Chory 1998; Stuefer and Huber 1998; Dononhue and Schmitt 1999; Pigliucci and Schmitt 1999; Genoud and Métraux 1999; Weinig 2000), we believe that the garden experiment is appropriate for characterizing species’ basic autecological responses to changing light climate in a comparative study. Frequently, the effect of different light receptors is reciprocal and highly correlated to each other (Casal and Mazzella 1998; Neff and Chory 1998; Genoud and Métraux 1999; Pigliucci and Schmitt 1999; Schmitt et al. 1999). The only really consistent difference between the neutral and (simulated) canopy shade is that the effect of neutral shade on plant morphology is weaker (except on biomass; Stuefer and Huber 1998; Dorn et al. 2000; Weinig 2000). Therefore, the use of neutral shade instead of “green” shade probably causes systematically lower plasticities to light availability and consequently increases the probability of Type II error in statistical analyses, but can hardly cause artefacts and biased statistical inferences.

The plants were fertilized using water-soluble fertilizer twice a week (N, 0.78 mg; P, 0.39 mg; K, 1.95 mg; and microelements, per plant). Water stress was avoided by combining constant bottom watering (height of water-table 15 cm) and daily automatic top watering. The plants were harvested after about 10 weeks of growth. Leaf area was measured using scanner (ScanJet5p), Aldus Photo Styler 2.0, and Pindala 1.0 software. In counting plant leaves, the definition of "leaf" was species-specific (a more or less independent module, carrying photosynthetically active tissue). Plant dry biomass was measured after 24 h at 75°C.

Data from 17 herbaceous communities (inter-community study)

We used ramet density and species richness data from different Estonian communities to test our hypotheses at a large-scale. Seventeen study areas with contrasting productivity and diversity were selected from communities investigated in 1994 and 1995 by Zobel and Liira (Tables 1 and 2 in Zobel and Liira 1997). We chose communities in which more than 10% of the species found in the community species pool were grown in the garden experiment (Table 1, S1). The selected study areas were either mesic semi-natural grasslands (more or less regularly mown or grazed) or forest field layer communities, in both cases clearly dominated by perennials. In the studied 17 communities mean ramet density varied from 285 ramets m^{-2} to 16,546 ramets m^{-2} and mean dry standing biomass (without moss and litter) from 0.046 kg m^{-2} to 0.812 kg m^{-2}. Mean vascular plant species richness varied between 9.3 species m^{-2} and 61.3 species m^{-2}.

Community species pool was assessed as the number of species found in the whole community (see Zobel and Liira 1997 for more detailed description of the procedure). Spatial variability of canopy height was estimated using point quadrat analysis. A 3-mm diameter metal pin was inserted through the herbaceous canopy in randomly chosen locations within a 10×10 m seemingly homogenous plot. The heights at which the pin made contacts with the green foliage and stems of plants were recorded. The height measurements were taken with an accuracy of 0.5 cm. Pin insertion was recorded only when the pin touched a green plant at least once. The coefficient of variation of mean canopy height—*CV(canopy height)*—was calculated as the standard deviation of mean heights of contacts on a pin, divided by the overall mean of heights of contacts across all pins.

In each community the following community characteristics were estimated as means over three replicates: *Log(ramet biomass)* (mean size of one plant ramet), *Log(ramet density)* (number of plant ramets per unit area); and several species diversity measures: *relative richness per* 1 m^{-2} (proportion of community pool found in 1 m^2) and *relative richness per 500 ramets* (proportion of community pool found among 500 adjacent ramets). It was obvious that in the statistical analyses only relative richness measures—the ones describing proportions of total community species pools, represented in a local plant assembly—could be used as dependent variables. This is due to the fact that most of the variation in small-scale richness across communities is described by the size of community species pool (Liira and Zobel 2000a) and the possible effect of shoot plasticity would be shaded in absolute richness measures.

Permanent plot data (intra-community study)

Small-scale species richness data was collected from a mesic calcareous wooded grassland in western Estonia (Laelatu wooded meadow, 58°35′N, 23°34′E), in a

Table 1 Characteristics of the studied 17 herbaceous communities

Site nr.	Community type	Size of community species pool	Average number of species in 500-ramet plots
1 (1)	Mesic calcareous wooded meadow	136	44.5
2 (2)	Hepatica site-type forest	58	19.3
3 (3)	Dry alvar meadow (ungrazed)	75	30.6
4 (4)	Dry alvar meadow (grazed)	74	32.0
5 (6)	Corylus site-type forest	36	15.7
6 (9)	Dry/wet periodically flooded meadow	35	14.0
7 (10)	Dry floodplain meadow	65	28.3
8 (11)	Filipendula site-type forest	52	23.3
9 (12)	Moist calcareous meadow	47	14.7
10 (13)	Occasionally flooded seashore meadow	18	8.3
11 (15)	Vaccinium site-type forest	26	10.0
12 (19)	Flooded riverplain meadow	41	15.3
13 (21)	Dry calcareous wooded meadow	69	32.0
14 (22)	Dry occasionally flooded meadow	44	18.3
15 (23)	Moist calcareous wooded meadow	69	31.0
16 (25)	Moist calcareous wooded meadow	108	35.7
17 (26)	Calamagrostis site-type forest	50	19.3

Community type, size of community species pool and average number of species growing in three replicate 500-ramet plots are shown. Site numbers in parentheses match those in Tables 1 and 2 in Zobel and Liira (1997)

Table 2 The relationships between *mean species shoot plasticity* across locally coexisting species (the average shoot plasticity estimate; S1) and *relative richness per square metre* (species richness per square metre/size of community species pool), *relative richness per 500 ramets* (species richness per 500 adjacent ramets/size of community species pool), variation coefficient of mean canopy height (*CV(canopy height)*) and *Log(ramet density)*, in the 17 herbaceous communities

Dependent variables	Model		Independent variables			
	df	*Adj. R*^{2}	Species mean shoot plasticity		Log(mean ramet biomass)	
			F	*P*	*F*	*P*
Relative richness per sq. m	1	0.33	9.04	**0.009**		
Relative richness per 500 ramets	1	−0.01	0.91	0.355		
CV(canopy height)	1	0.46	14.57	**0.002**		
Log(ramet density)	2	0.52*F* = 9.69 **P = 0.002**	11.32	**0.005**	6.68	**0.022**

When analysing the effect of plasticity on ramet density, *Log(mean ramet biomass)* was included as the additional independent variable. Error degrees of freedom (df) is 15 (14 for *Log(ramet density)*). Significant *P*-values are in boldface

5-year permanent-plot study (see Eek and Zobel 1997, 2001 for details). The meadow has a scattered tree layer with *Quercus robur, Fraxinus excelsior, Corylus avellana, Betula* spp. and *Populus tremula* as the most abundant species. Average coverage of the tree canopy is ca. 20%. 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 rich in species at a small scale—the greatest recorded vascular plant richness figures are 25 in a 0.01-m^2 quadrat and 68 in a 1-m^2 quadrat (Kull and Zobel 1991). The majority of species in the herbaceous layer are forbs (incl. tree seedlings; 71%), 29% are graminoids (mostly grasses and sedges). The average ramet density in the herbaceous layer is ca. 3,700 plant ramets m^{-2} (Zobel and Liira 1997).

Vascular plant species were registered from 24 permanent plots of 40×40 cm, in early July, in five consecutive years (1994–1998). Unfortunately, since the plots are marked for long-term surveillance, and since the measurement of ramet density cannot be performed without severely disturbing the vegetation in the permanent plot, we could not collect ramet density data for this dataset.

Data analysis

Plasticity (Π) of plant morphological trait (T) of the i-th species in response to light availability (L; percent of full daylight) was defined as the absolute value of the slope of the reaction norm between T and L (Scheiner 1993; Gavrilets and Scheiner 1993; Mclellan et al. 1997; Schlichting and Pigliucci 1998; Stratton 1998; Pigliucci and Schmitt 1999). Such a plasticity estimate is comparable across different traits and species, provided that the trait value is log-transformed (Log T) and the allometric effect of biomass (B) is considered and removed (Coleman and McConnaughay 1995; Mclellan et al. 1997; Casper et al. 1998; Garcia-Berthou 2001; Cheplick 2003; Gehring 2003). We used Generalized Linear Model (GLZ) with dependent variable logarithmic trait value (Log T) and two continuous independent components:

1. Environmental factor (L), accounting for the plastic size-independent variation in Log T caused by the environmental gradient (light). Parameter estimate of environmental factor L is absolute value of the slope of the reaction norm (plasticity estimate Π_T).
2. Plant size (in our case above-ground biomass) with necessary modifications: Log B_i, Log(Log B_i), B_i^{-1}, B_i^2, $B_i^{0.5}$, accounting for the size-dependent variation in Log T. We used several modifications of biomass, since allometric relationships between plant size and trait values may be extremely complicated and may differ between traits and species (Jolicoeur 1989; Coleman and McConnaughay 1995; Garcia-Berthou 2001). Therefore we used backward stepwise procedure ($P = 0.05$, max. no of steps = 100) to find statistically significant modifications of B, which were included into the final model. Models were applied separately for each trait and species.

With this model it is possible to estimate plasticity as the slope of the reaction norm (Π_T) for any trait as a parameter estimate of independent environmental factor L. Since the effect of biomass is included in the GLZ, this plasticity estimate will be size-independent and should reflect only the adaptive plasticity of the particular trait (Sultan 1995; also called true plasticity, McConnaughay and Coleman 1999) and not the type of phenotypic response to resource availability which is predictable as a function of plant growth and developmental stage (inevitable plasticity, Sultan 1995 or passive plasticity McConnaughay and Coleman 1999). Thus, though, for example, the number of leaves in a plant is a directly growth-related trait, our plasticity estimate includes only the part of the total response in leaf number to light availability that cannot be explained through the variation of plant size (biomass) in different light climates.

We estimated plasticities for all species for two leaf traits—mean area per leaf (Π_{LA}) and leaf number (Π_{LN}). The preliminary data analysis demonstrated that mean leaf area and leaf number plasticities were highly correlated across species ($R=0.88$, $P<0.001$). Thus, not surprisingly, the attempt to study the two plasticity components separately yielded in two sets of qualitatively very similar results. We therefore decided to calculate total shoot plasticity for each species as $\Pi = (\Pi_{LA}^2 + \Pi_{LN}^2)^{0.5}$ (Euclidian distance, the recommended statistic in the case of closely correlated variables; Sokal and Rolf 1995) and use it as an integral trait in further analyses (S1).

To test whether the estimated shoot plasticity of species is related to other plant characteristics, we studied the relationships between the plasticity estimate and several qualities or traits that we presumed to be important for successful competition in dense herbaceous communities. To compare the plasticity of species with different growth forms, we classified them according to basic shoot characteristics—leaf width and presence/absence of leafy stem (Liira and Zobel 2000b). The synecological requirements of species (for light and nutrients) were described using Ellenberg's indicator values (Ellenberg et al. 1991). We also tested for the possible effect of plant species mean height (in the full light treatment of the garden experiment) on shoot plasticity. We used the General Linear Model (GLM, Type III sum of squares) with three continuous fixed factors *mean height, Ellenberg indicator values for light* and *Ellenberg indicator values for nutrients*, two discrete fixed factors *leaf width* (two levels) and *presence/absence of leafy stem* (two levels), and dependent factor Π (shoot plasticity of a species).

The distribution of species with known plasticity estimate among the studied communities is shown in Electronic Supplementary Materials (S1). We calculated mean species shoot plasticity in a plot as the average shoot plasticity of the species for which we had a shoot plasticity estimate that occurred in the plot in a certain year. In the permanent plot study an average of 11.9 species with a known plasticity estimate grew in a 40×40 cm permanent plot, accounting, on average, for 39% of plot richness and 37% of total coverage. A similar calculation of species mean plasticity was carried out for the 17 studied grassland communities—it was assessed as the average across those species, registered in three replicate 500-ramet plots, for which the shoot plasticity estimate (Π) was known. An average of 10.8 species with a known plasticity estimate (an average of 45% of species growing on plots) was registered in 500-ramet plots per one community, accounting, on average, for 39% of ramets growing in a plot. It is important to note here that the set of species for the experimental estimation of autecological plasticity was selected randomly and thus should be treated as representative sample of the total pool of species in the communities under observation.

Preliminary inspection of the data revealed that species composition in permanent plots showed considerable annual change (mean Sørensen similarity in a permanent plot between successive years being 0.59). This shows that species turnover in the plots is quite rapid and the use of Repeated measures GLM using within-subjects design is not supported. Therefore, the overall effect of mean species plasticity on species richness was tested using GLM (Type III sum of squares) with dependent variables: continuous fixed factor *mean species shoot plasticity* and random factor *year* (five levels). The effect of mean species shoot plasticity on local species richness was also tested separately for five consecutive years using multiple linear regression analysis.

Relations between mean species plasticity and community characteristics over 17 grassland sites were studied using GLM (Type III sum of squares) with:

1. Dependent variables *Log(ramet density), relative richness per square metre, relative richness per 500 ramets*, and independent variable *mean species shoot plasticity*. When analysing the effect of plasticity on ramet density, *Log(mean ramet biomass)* was included as the additional independent variable.
2. Dependent variables *relative richness per square metre, relative richness per 500 ramets* and *CV(canopy height)*, and independent variables *Log(ramet density)* and *mean species shoot plasticity*. All statistical analyses were performed using Statistica 6.0 software (StatSoft Inc., Tulsa, USA).

Results

The plasticities of species with different growth forms—grasses, sedges, upright forbs and rosette-forming forbs—were not significantly different. Nor was there any relationship between plasticity to light availability and the Ellenberg indicator values for light or nutrients (Ellenberg et al. 1991). There was also no significant effect of species mean height on shoot plasticity.

Log(ramet density) was positively related to *mean species shoot plasticity* in the 17 herbaceous communities (as well as to *Log(ramet biomass)*; Table 2, Fig. 1a). On the other hand, ramet density was a good predictor of *relative richness per square metre* (Table 3, Fig. 2)—a relatively larger proportion of the community pool was represented in 1 m^2 plots in communities with denser vegetation. Given these two relationships, it was not surprising that the estimate of mean species plasticity was positively related to relative richness per unit area (Table 2, Fig. 1b). Obviously the relationship between mean shoot plasticity and relative richness is mainly due to the fact that assemblages of plastic plants allow for denser canopies—there was no relationship between plasticity and relative richness per 500 adjacent ramets (density-independent estimate of relative richness; Tables 2, 3; Fig. 1c).

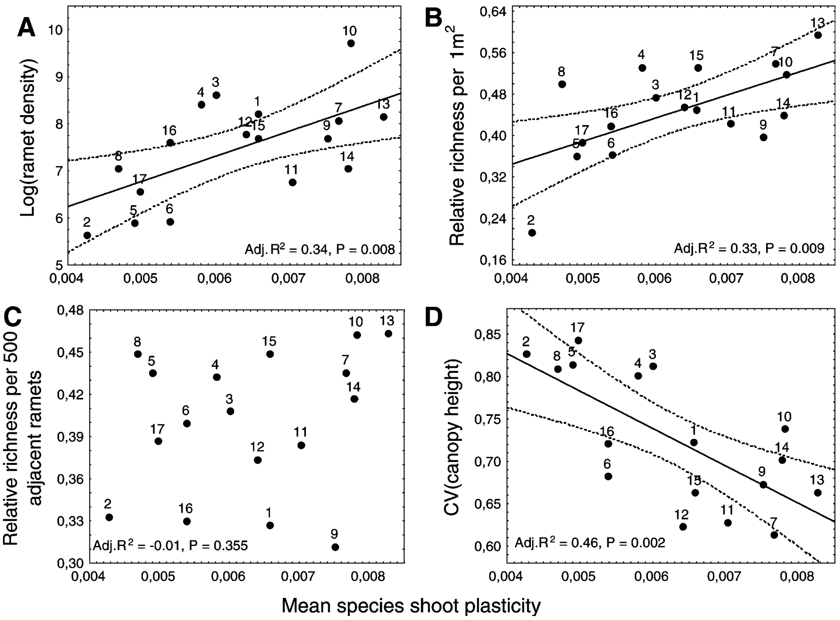

Fig. 1 The effect of *mean species shoot plasticity* on **a** *Log(ramet density)*; **b** *relative richness per* 1 m^2 (species richness per square metre/size of community species pool); **c** *relative richness per 500 ramets* (species richness per 500 adjacent ramets/size of community species pool); **d** variation coefficient of canopy height (*CV(canopy height)*). Communities are numbered as in Table 1. Model determination coefficient (*Adj. R*^{2}) and significance level of independent factor (*P*) are shown

Table 3 Results of GLM analysis for the 17 herbaceous communities, with *Log(ramet density)* and *mean species shoot plasticity* included as independent variables

Dependent variables	Model			Independent variables			
	Adj. R^2	*F*	*P*	Log(ramet density)		Species mean shoot plasticity	
				F	*P*	*F*	*P*
Relative richness per square metre	0.56	10.97	**0.001**	8.43	**0.012**	1.22	0.288
Relative richness per 500 ramets	−0.05	0.60	0.563	0.33	0.577	0.15	0.708
CV(canopy height)	0.51	9.16	**0.003**	2.40	0.144	16.77	**0.001**

Relative richness per square metre, *relative richness per 500 adjacent ramet* and on canopy height variability (*CV(canopy height)*) are considered as dependent variables. In all models model degree of freedom (df) is 1 and error df is 13. Significant *P* values are in boldface

Mean shoot plasticity was related to the spatial distribution of plant biomass in the 17 herbaceous communities. In communities with relatively high shoot plasticity, the variability of herbaceous canopy height (*CV(canopy height)*) was significantly lower (Table 2, Fig. 1d). Further analyses revealed that this relationship was not mediated by ramet density—in a model with *Log(ramet density)* and *mean species shoot plasticity* included as independent variables, only the latter was significantly related to spatial variability of canopy height (Table 3).

Species richness in permanent plots in the Laelatu meadow was positively related to mean shoot plasticity of species growing in this plot (Table 4, Fig. 3). The number of locally co-existing species was higher in microsites with a high concentration of plastic species. This relationship was statistically significant in all 5 years (Fig. 3), although species composition in plots showed considerable annual change (mean Sørensen similarity in a permanent plot between successive years being 0.59). Mean species shoot plasticity described about 50% of local species richness annually (*Adj. R*^{2} ranging from 0.35 to 0.60 in different years; Fig. 3). The effect of interaction term *mean species shoot plasticity* × *year* was not significant, indicating that the slopes of the regression lines in Fig. 3 were not significantly different from each other.

Discussion

Our results strongly imply that shoot plasticity should be considered as a trait that can alter the density of co-existing plant ramets in a herbaceous community (Fig. 1a) and, since the number of species per unit area is a density-dependent variable (Fig. 2), also species diversity in a sample quadrat with fixed area (Fig. 1b, 3). In the inter-community-data, this is reflected in a positive regression of relative richness per unit area on mean species plasticity (relative richness should be used here because most of the variation in absolute quadrat richness is explained by the size of the community species pool; Liira and Zobel 2000a). In the within-community data (permanent plots) the relationship emerges in five

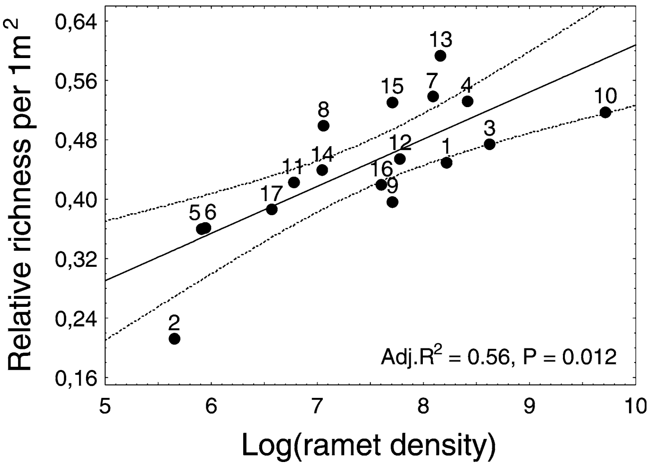

Fig. 2 The effect of *Log(ramet density)* on *relative richness per* 1 m^2(species richness per square metre/size of community species pool). Communities are numbered as in Table 1. Model determination coefficient (*Adj.* R^2) and significance level of independent factor (*P*) are shown

Table 4 Results of GLM for permanent plot data (Laelatu wooded meadow)

	df	Effect	*Adj.* R^2	*F*	*P*
Model	9		0.46	12.43	**< 0.001**
Intercept	1	Fixed		2.40	0.125
Year	4	Random		0.93	0.450
Mean species shoot plasticity	1	Fixed		92.19	**< 0.001**
Mean species shoot plasticity × year	4	Random		1.24	0.298
Error	110				

The effect of *mean species shoot plasticity* (average shoot plasticity estimate across species occurring in a certain plot in a certain year; S1) and *year* of observation (random factor) on species richness in the 40×40 cm permanent plots is presented. Significant *P*-values are in boldface

consecutive years in a positive regression between quadrat richness and mean plasticity across species (absolute richness can be used here because the size of the community species pool is constant). If plants with high shoot morphological plasticity are growing together, reciprocal shading causes mutual adjustments in the number and shape of above-ground organs. Fewer number of plant modules per ramet and elongation of plastic ramets in dense stands reduces the light preemption. As a result, suppression and exclusion of lower ramets decreases (Wilson et al. 2000; Stoll et al. 2002). In other words, higher overall plasticity reduces the intensity of competition for light—competition asymmetry decreases and self-thinning in the canopy is retarded. Consequently, ramet density is significantly higher in those communities where species with high shoot plasticity prevail (Table 2, Fig. 1a), and relatively more species from the community species pool are capable of co-existing in a fixed area (Figs. 1b, 3).

Earlier, relationships between plasticity to light availability and competition asymmetry have been found in experiments with artificially "blinded" plants (Ballaré et al. 1994; Ballaré and Scopel 1997; Schmitt et al. 1999; Stoll et al. 2002). Competition between nonplastic plants has resulted in a considerable variability of plant height, indicating competition asymmetry, while competition between plastic individuals has been more symmetrical. Ramets with high plasticity to light have been demonstrated to be more tolerant of competition and therefore have a much higher probability of being able to adapt and survive in shaded microsites than nonplastic inferior ramets (Ballaré and Scopel 1997; Schmitt et al. 1999; Stoll et al. 2002, reviewed by Callaway et al. 2003). In field conditions, the degree of spatial aggregation of above-ground plant biomass in a grassland has also been shown to increase in the case of light deficit, caused by nutrient addition, indicating that intensified competition for light is reflected in an increased varia-

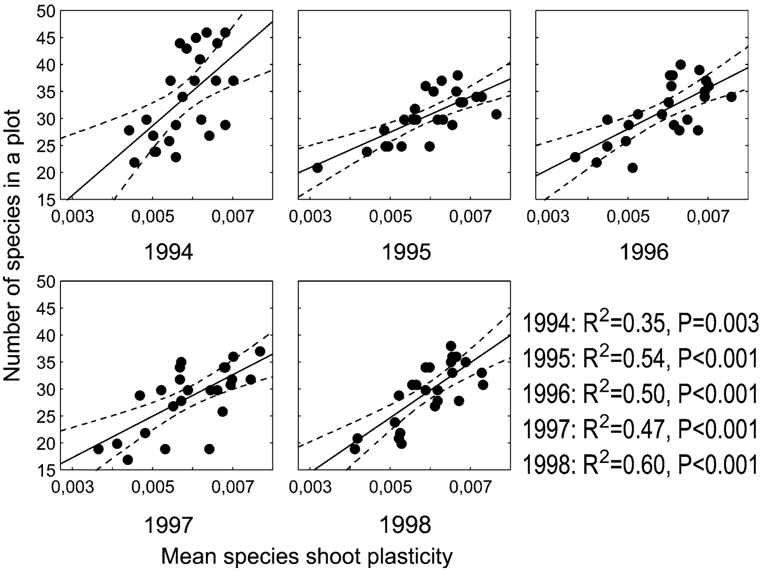

Fig. 3 The effect of *mean species shoot plasticity* on the number of species recorded in 40×40 cm permanent plots in Laelatu wooded meadow, in five consecutive years. Model determination coefficient (*Adj.* R^2) and significance level (*P*; calculated separately for all years) are shown

tion in canopy thickness and height (Eek and Zobel 1997). Our results from the 17 herbaceous communities demonstrate that mean plasticity of co-existing species alters the outcome of above-ground competition—if plants with high shoot plasticity happen to grow together, canopy height variability (and thus ramet height variability) will be significantly lower (Table 3, Fig. 1d).

It has been found that species richness is relatively higher in stands with higher between-species morphological variability (Cody 1991) and in stands with higher within-species genetic variability (Booth and Grime 2003). Since phenotypic plasticity also increases phenotypic variability of ramets, it may be assumed that the effect is similar. Unfortunately, in the mentioned studies (Cody 1991; Booth and Grime 2003) species richness was measured only per unit area and not per number of ramets, making it impossible to guess whether the positive relationship between phenotypic variability and species richness was only due to higher ramet density or whether the relationship would hold also for a fixed number of ramets. Our experience from the 17 herbaceous stands shows that the relative proportion of species from the community pool, represented among 500 adjacent ramets, is independent of the mean plasticity of species in sample quadrats (Fig. 1c). Thus, we have evidence about an increase of richness due to increased density, but no evidence about enhanced richness per fixed density. Surely, only further experiments using artificial stands with variable density and phenotypic variability (manipulated through varying within-genotypic variability as well as varying plasticity of species) could clarify this problem with certainty.

As it was impossible to obtain ramet density data from the Laelatu grassland permanent plots, we can only speculate about the true mechanisms behind the highly significant and consistent relationship between species mean plasticity estimate and seasonal richness (Fig. 3). However, experience from the across-communities study would indicate that it is highly probable that mean plasticity and number of species are closely related because of a higher ramet density in plots with a higher concentration of plastic species (higher plasticity → higher ramet density → more species per fixed area). We can also claim that the mechanism behind plasticity and community structure is remarkably stable in time—the regression between diversity and species mean plasticity showed no annual change (Table 4).

We cannot say with certainty whether high shoot plasticity, which apparently favours the coexistence of ramets, has evolved because, among other reasons, it also slows down mutual competitive exclusion of species in dense stands, or whether it is simply a co-product of light acclimation (Dononhue et al. 2001; Alpert and Simmis 2002; Schlichting and Smith 2002). Natural selection should favour superior competitors that pre-empt resources and become dominant over other plants (Falster and Westoby 2003). In plants, with only a few critically important resources to compete for, adaptations that are directed towards escaping intense competitive pressure and making competition more symmetric are probably quite common (Schmitt et al. 1999; Agrawal 2001). Evidently, there are two ways of escaping intense competitive pressure. The first one is by becoming a superior competitor who pre-empts resources and easily suppresses other plants (Falster and Westoby 2003). In this case, further investment into high shoot plasticity is not necessary. For example, *Filipendula ulmaria*, a clearly dominant species in fertile moist grasslands (where it can form high and almost monospecific stands), was the species with the lowest shoot plasticity estimate in our garden experiment ($\Pi = 0.10 \times 10^{-11}$; S1). The other way of escaping competitive pressure seems to be characteristic to those species which are usually growing in dense multi-species communities with small above-ground productivity (or in those regularly mown or grazed) and little chance for massive suppression of competitors by faster-growing species. These species exhibit high shoot plasticity to light availability (e.g. *Dactylis glomerata, Festuca rubra, Plantago lanceolata*; S1). In conditions where it is not likely to outcompete neighbours consistently, reduced competition between ramets via increased shoot plasticity may significantly increase fitness. This is especially true for clonally reproducing plants (reviewed by Schwinning and Weiner 1998), which also prevailed in the communities analysed in this study.

The use of observational data from natural communities does not allow one to detect with certainty the mechanisms behind the formation of higher ramet density and increased species number per fixed area in stands inhabited by plastic species. For this, further experiments with artificial communities are needed. However, we may conclude that experimentally estimated shoot plasticity has a certain value for predicting the outcome of interactions in complicated multi-species systems. Knowledge about the autecology of species has enabled the taking of a closer look at the possible community processes behind the observed diversity pattern, both small- and large-scale.

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