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Niche pre-emption increases with species richness in experimental plant communities — Source link

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Abstract

In plant communities, invasion resistance may increase with diversity because empty niche space decreases simultaneously. However, it is not clear if this only applies to exotic species or also to native species arriving at a site with few other native species during community assembly. We tested the latter by transplanting four native species into experimental grassland communities varying in species richness form 1-16 (?60) species. In addition, we tested the hypothesis that invasion is less successful if the invading species belongs to a functional group that is already present in the community. The test invaders included a grass species (Festuca pratensis, FP), a short (Plantago lanceolata, PL) and a tall herb species (Knautia arvensis, KA), and a legume species (Trifolium pratense, TP). The same four functional groups also occurred alone or in all possible combinations in the different experimental communities. The overall performance of the transplants was negatively related to the logarithm of the species richness of host communities. Plant biomass declined by 58%, 90%, 84% and 62% in FP, PL, KA and TP, respectively, from monocultures to 16-species mixtures, indicating lower invasiveness of the two herbs than of the grass and the legume. Resident grasses showed a strong negative effect on the performance of all test invaders, whereas resident small and tall herbs had neutral, and resident legumes had positive effects. The case of the legumes indicates that contributions to invasion resistance need not parallel invasiveness. Communities containing resident species of only one functional group were most inhibitive to transplants of the same functional group. These results indicate that invasion resistance of experimental plant communities is related to the degree of niche overlap between resident species and invaders. This niche overlap can be high due to generally low amounts of empty niche space in species-rich resident communities or due to the occurrence of the same functional group as the one of the invader in the resident community. Stronger within- than between-functional-group invasion resistance may be the key mechanism underlying diversity effects on invasion resistance in grassland and other ecosystems at large.

Niche pre-emption increases with species richness in experimental plant communities

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Running headline:

Niche pre-emption and invasion resistance

Abstract

1. In plant communities, invasion resistance may increase with diversity because empty niche space decreases simultaneously. However, it is not clear if this only applies to exotic species or also to native species arriving at a site with few other native species during community assembly. We tested the latter by transplanting four native species into experimental grassland communities varying in species richness form 1–16 (–60) species. In addition, we tested the hypothesis that invasion is less successful if the invading species belongs to a functional group that is already present in the community.

2. The test invaders included a grass species (*Festuca pratensis,* FP), a short (*Plantago lanceolata*, PL) and a tall herb species (*Knautia arvensis,* KA), and a legume species (*Trifolium pratense*, TP). The same four functional groups also occurred alone or in all possible combinations in the different experimental communities.

3. The overall performance of the transplants was negatively related to the logarithm of the species richness of host communities. Plant biomass declined by 58%, 90%, 84% and 62% in FP, PL, KA and TP, respectively, from monocultures to 16-species mixtures, indicating lower invasiveness of the two herbs than of the grass and the legume.

4. Resident grasses showed a strong negative effect on the performance of all test invaders, whereas resident small and tall herbs had neutral, and resident legumes had positive effects. The case of the legumes indicates that contributions to invasion resistance need not parallel invasiveness. Communities containing resident species of only one functional group were most inhibitive to transplants of the same functional group.

5. These results indicate that invasion resistance of experimental plant communities is related to the degree of niche overlap between resident species and invaders. This niche overlap can be high due to generally low amounts of empty niche space in species-rich resident communities or due to the occurrence of the same functional group as the one of the invader in the resident community.

6. Stronger within- than between-functional-group invasion resistance may be the key mechanism underlying diversity effects on invasion resistance in grassland and other ecosystems at large.

Key words: diversity effects; invasion resistance; invasiveness; niche overlap; phytometers; plant functional groups; The Jena Experiment

Introduction

Understanding the mechanisms behind the relationship between resident species richness and the establishment of non-resident species (i.e. invaders in the broad sense) in natural communities is a major goal in ecology. This relationship has potential applications in conservation, restoration and prediction of community invasion resistance. Elton (1958) and Levine & D'Antonio (1999) provide evidence for a generally negative relationship between diversity and the likelihood that an intruder will be able to establish itself in a community. Such relationships have been found in a large number of experimental studies using temperate plant communities (Tilman, 1997; Knops *et al.*, 1999; Joshi *et al.*, 2000; Naeem *et al.*, 2000; Prieur-Richard *et al.*, 2000; Diemer & Schmid, 2001; Kennedy *et al.*, 2002; Pfisterer *et al.*, 2004). In contrast, observational studies, which necessarily assess invasion by exotic invaders, often report higher numbers of invading species in species-rich than in species-poor plant communities (Stohlgren *et al.*, 1999; Stadler *et al.*, 2000; Pysek *et al.*, 2002; Stohlgren *et al.*, 2002), though Stohlgren *et al.* (1999) found the opposite at one site in their study. The results of observational studies may be attributed to uncontrolled extrinsic factors, whose effect on native and exotic species is the same (Stohlgren *et al.*, 1999; Levine, 2000; Shea & Chesson, 2002). Additionally, observational studies mostly analyse the number of invading species (e.g. Stohlgren *et al.*, 1999; Meiners *et al.*, 2004) whereas many experimental studies also assess the performance of particular invaders (see e.g. Prieur-Richard *et al.*, 2000; Diemer & Schmid, 2001; Hector *et al.*, 2001).

In most cases, species richness is the only component of diversity manipulated in experimental studies (e.g. Prieur-Richard *et al.*, 2000; Troumbis *et al.*, 2002), though some studies have demonstrated the importance of functional diversity in competitive suppression of invaders (Crawley *et al.*, 1999; Hector *et al.*, 2001; Prieur-Richard *et al.*, 2002; Xu *et al.*, 2004; Fargione & Tilman, 2005). Functional groups are sets of species (not necessarily taxonomic) that show close similarities in traits related to ecosystem functioning, e.g. traits related to resource uptake and biomass production. Increasing evidence suggests that the influence of functional diversity in a community might be more important than pure species richness (Diaz & Cabido, 2001; Garnier *et al.*, 2004; Heemsbergen *et al.*, 2004; Petchey *et al.*, 2004).

It is supposed that empty niche space (Hutchinson, 1957) declines with increasing species richness in a community (MacArthur, 1970). As a consequence, species-rich communities can utilize the total resources available in a biotope more completely than do species-poor communities (e.g. Scherer-Lorenzen *et al.*, 2003; Dimitrakopoulos & Schmid, 2004), thereby pre-empting resources for potential invaders (Tilman, 1999; Hector *et al.*, 2001; Fargione *et al.*, 2003). This effect occurs because, generally, an increase in species richness should also increase functional richness, suggesting that the number of functional groups in an experimental community may be a good predictor of these diversity effects. Conversely, the effect should be minimal if species richness is increased without increasing the number of functional groups at the same time. In addition, a community should be more resistant to invaders belonging to functional groups already present among the resident species (e.g. Fargione *et al.*, 2003; Turnbull *et al.*, 2005).

In most cases, invasion studies compare a set of species used as test invaders with a separate set of species used as residents of host communities (Tilman, 1997; Knops *et al.*, 1999; Hector *et al.*, 2001; Prieur-Richard *et al.*, 2002; Fargione *et al.*, 2003; Pfisterer *et al.*, 2004, but see Turnbull et al. 2005). This approach mimics biological invasions into communities by exotic species. For example, the average competitive ability of exotic invaders may change with diversity (e.g. Bossdorf *et al.*, 2004; Colautti *et al.*, 2004; e.g. Vila & Weiner, 2004; Hierro *et al.*, 2005). Here we do not analyze exotic species invasions but rather invasion as a process of community assembly within a pool of native species. In this case, because the host communities and invaders belong to the same species pool, it is possible to distinguish between the *invasiveness* of a particular species or functional group as an invader and its contribution to *invasion resistance* of the host community within the same experiment.

Using this approach, we selected four native species representative of four functional groups used in a biodiversity experiment as test invaders or "phytometers". Specifically, we wanted to find out: (a) if increasing species richness or number of functional groups in plant communities suppresses the performance of invaders; (b) whether the presence of a particular functional group in a host community enhances suppression of the test invaders; and (c) whether the test invaders are most suppressed by host communities containing species belonging to the same functional group.

Materials and methods

Our study was part of a large biodiversity experiment, The Jena Experiment in Germany (50°55' N, 11°35' E, 130 m altitude). This experiment was established in May 2002 on a former agricultural field in the flood plain of the Saale river (Roscher *et al.*, 2004). Plant communities were assembled by constrained random selection from a pool of 60 species typical to Central European mesophilic grasslands. The species were categorized into the four functional groups: grasses (16 species), small herbs (12 species), tall herbs (20 species), and legumes (12 species), based on multivariate analyses of their traits (Roscher *et al.*, 2004). Analyzed traits included growth form (6 binary traits), lateral clonal spread, height of vegetative and flowering plant, leaf size, depth and type of root system, life cycle, seasonality of foliage, onset and duration of flowering and nitrogen fixation. Seventy-eight plots, each measuring 20 x 20 m, were sown with 1, 2, 4, 8, or 16 species. A factorial design was formed with all possible species richness x functional group richness mixtures. At each level of species richness, 16 replicate mixtures with different species composition were established, except at the highest level with 14 replicates only. Four additional large plots contained mixtures of all 60 species in the pool. The field was partitioned into four blocks following a gradient in soil characteristics perpendicular to the river (Roscher *et al.*, 2004). The plots were mowed twice a year (June, September), as is typical for this type of grassland ecosystem, and weeded twice a year to maintain the original species composition. Mowing and weeding were done block-wise such that these management effects could be accounted for with the block term in statistical analysis.

Our test invaders were pre-grown phytometer individuals of four species that also occurred in a large number of experimental communities as resident species. Clements and Goldsmith (1924) introduced the term "phytometer" for test plants that were used to measure environmental factors. Each of the four species belonged to a functional group used in the experiment: *Festuca pratensis* Huds. (grass), *Plantago lanceolata* L. (small herb), *Knautia arvensis* L. (tall herb) and *Trifolium pratense* L. (legume). They are all perennial plant species, form clearly defined compact individuals and are relatively easy to transplant.

In mid-March 2003, we germinated the phytometers on moist filter paper in a greenhouse. Individual seedlings were planted in 132-cm^3 cells of potting trays filled with a soil-compost-perlite mixture (3:2:1 in terms of volumes), and were exposed to a 14-h light regime with 22^{o}C day temperature and 15^{o}C night temperatures. In mid-April 2003, most of the plants had 4–7 leaves. We placed them outside the greenhouse for hardening and one week later transplanted them into the experimental communities. Five phytometer individuals of each test species were randomly allocated to positions at 28-cm intervals in a 2 x 2-m subplot within each large plot and the initial size determined by counting their number of leaves and number of ramets (the latter only for *F. pratense* and *T. pratense*). Transplanted phytometers were marked by fixing numbered plastic labels next to the plants to ease identification during data collection.

In mid-August, in addition to counting the number of leaves, we measured the maximum height of the phytometers. For *T. pratense* and *F. pratensis,* we also counted the number of ramets as before. We calculated the relative growth rate of the transplants using the formula

$$RGR = \left(\ln l_{t2} - \ln l_{t1}\right) / d,$$

where l_{t2} is the mean number of leaves in August, l_{t1} is the mean number of leaves in April and d is the length of time interval in days (Harper, 1977). As a measure of plant fitness, in August, we also counted the number of inflorescences of *P. lanceolata* and *T. pratense* transplants. No individuals of *F. pratensis* or *K. arvensis* were flowering at this time. In the last week of August 2003, shortly before mowing, transplants were cut at 3 cm above the ground and dried at 70°C for at least 48 h to determine the average biomass of each transplant species per plot. In early June 2004, we once again measured the height of the transplants, counted the number of inflorescences in *P. lanceolata* and *T. pratense*, which were flowering at this time, and harvested the transplants per species per plot to determine the average aboveground biomass as described above.

Before each harvest, we determined the leaf area index (LAI) of the resident community in an undisturbed area next to the phytometers using an LAI-2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, Nebraska, USA).

Statistical analysis

We used general linear models with sequential sum of squares (Type I) for data analysis using Genstat 6th Edition, Release 6.2. (Payne *et al.*, 2002). Since individual plants were pseudo-replicates within plots, we analysed means of the response variables plant biomass, plant height, number of leaves and relative growth rate. The data were transformed if residuals showed deviation from the normal distribution. According to the experimental design, the analysis of variance (ANOVA) model consisted of the terms block, sown species richness (partitioned into log-linear contrast and deviation from log-linear contrast), functional group richness, species composition, phytometer species and phytometer species x diversity interactions. Separate contrasts for the presence/absence of each functional group and their interactions with species richness were tested in alternative models. Similarly, separate contrasts were made to compare each phytometer species and its interactions with diversity terms against the other three phytometer species. The diversity terms (species richness, functional group richness, presence of particular functional groups) had to be tested at the between-plot level (Error = composition) whereas phytometer terms and their interactions with diversity terms could be tested at the within-plot level (Schmid *et al.*, 2002). We also analysed the data of each phytometer species separately. To determine if the effect of diversity terms was related to a change in the leaf-area index (LAI) of the community we did post-hoc analyses with LAI as a covariate. In addition, LAI was tested as a dependent variable itself, using the between-plot ANOVA as explained above.

To test if the phytometer species were more affected by their own than by other functional groups, we used a reduced data set of communities with only one functional group (n = 34 plots). To do this, the resident x transplant functional group interaction was decomposed into a "home versus away" contrast and remainder (taking all "away" treatment combinations together; see Table 3). To illustrate the home versus away contrast we use an equivalent of the relative-neighbour-effect of (Markham & Chanway, 1996), using the formula $(P_h-P_a) / \max(P_h, P_a)$. Here, P_h is the performance (e.g. biomass) of phytometers in communities with their own functional group (home), P_a the performance in communities with other functional groups (away) and $\max(P_h, P_a)$ is the larger of the two.

Results

Effects of species richness and functional richness

Except for plant height in *P. lanceolata* and *K. arvensis*, the measured morphological variables of phytometers were highly correlated with their aboveground biomass (Table 1), indicating that the latter is a good measure of overall phytometer performance.

At the first harvest in summer 2003, i.e. 4 months after transplanting, the performance of phytometer individuals was negatively related to the logarithm of sown species richness (reduced number of leaves or number of ramets, reduced biomass and reduced growth rate, Fig. 1a, c, d and Table 2a). The height of the phytometers was, however, not affected and even increased with the logarithm of species richness in one of the phytometer species (*F. pratensis*; $F_{1,70} = 9.30$, $p < 0.01$ in separate analysis), suggesting a typical allometric response to increased competition for light (etiolation); i.e. a faster increase in height, independent of size (Fig. 1b, Table 2a; see also lower correlations of plant height than of other variables with biomass in Table 1). The length of the leaves in *F. pratensis* also increased with increasing species richness ($F_{1,73} = 15.64$, $p < 0.001$). The influence of resident species richness on phytometer performance varied among phytometer species; the herbs (*P. lanceolata* and *K. arvensis*) were more strongly affected than the grass (*F. pratensis*) and the legume (*T. pratense*) (see species richness x phytometer species (PS) interaction in Table 2a). The negative effect of species richness on phytometer aboveground biomass was still significant in spring 2004 ($F_{1,73} = 27.80$, $p < 0.001$, Fig. 2b), but again plant height was not affected by species richness ($F_{1,73} = 1.19$, $p < 0.172$, Fig. 2a).

Functional richness had no effect on the performance of the phytometers after controlling for species richness in both seasons ($p > 0.05$). By contrast, if fitted before species richness, functional richness also had significant negative effects on all phytometer variables except height (aboveground plant biomass: $F_{1,67} = 4.74$, $p = 0.03$; plant height: $F_{1,67} = 1.38$, $p = 0.24$; number of leaves: $F_{1,67} = 7.13$, $p = 0.01$; growth rate: $F_{1,67} = 6.12$, $p = 0.01$; Fig. 1e-h); and in addition the species richness effects remained significant ($p < 0.05$) except for plant height, as before. The pattern was the same in spring 2004 (Fig. 2c and d). This highlights the importance of species richness even if functional richness in statistical terms is "held constant", i.e. the species richness effect remains negative within a particular level of functional richness.

Separate analyses showed that increasing species richness (log-scale) led to a significant reduction in number of inflorescences per plant in *P. lanceolata* ($F_{1,70} = 25.58$, $p < 0.001$) and *T. pratense* ($F_{1,69} = 6.07$, $p = 0.01$), the two phytometer species which flowered before the first harvest in August 2003 (Fig. 3a). The same negative effect of species richness on number of inflorescences per plant was observed in *P. lanceolata* ($F_{1,69} = 18.31$, $p < 0.001$) and *K. arvensis* ($F_{1,68} = 18.88$, $p < 0.001$) in spring 2004 (Fig. 3a). Again, the effect of functional richness on the number of inflorescences was not significant after controlling for species richness, but it was highly significant if fitted first (summer 2003: *P. lanceolata*; $F_{1,70} = 11.15$, $p < 0.001$, *T. pratense*; $F_{1,69} = 6.13$, $p = 0.016$; spring 2004: *P. lanceolata*; $F_{1,69} = 12.04$, $p < 0.001$, *K. arvensis*; $F_{1,68} = 14.71$, $p < 0.001$; Fig. 3b), with the effect of species richness fitted afterwards again remaining significant ($p < 0.01$).

Effects of the presence of particular functional groups

The presence of grasses or legumes in the host communities had significant overall effects on phytometers, but this was not the case for the other two functional groups (Table 2a). Grasses significantly reduced number of modules (number of leaves or number of ramets), aboveground biomass, and growth rate of all the phytometer species (Table 2a) as well as number of inflorescences in *P. lanceolata* in summer 2003 ($F_{1,68}$ =

5.66, $p = 0.02$) and spring 2004 ($F_{1,67} = 7.56$, $p = 0.008$). For example, in summer 2003, the average biomass of an individual phytometer (all species together) was 0.8 g in plots with grasses compared to 1.9 g in plots without grasses (Fig. 4). In spring 2004, the figures were 3.5 g and 10.8 g for plots with and without grasses respectively. The presence of legumes had an overall significantly positive effect on the performance of the phytometer species (Table 2a, Fig. 4 and 5). Separate analysis for each phytometer, however, revealed that the presence of legumes actually reduced aboveground biomass of the legume phytometer, *T. pratense*, at least in the spring 2004 ($F_{1,61} = 8.97$, $p = 0.004$). The negative effect of legume presence on the legume phytometer as opposed to a positive effect on the other phytometers is also evident in the significant contrast interaction legume presence x *T. pratense* (LG x TP in Table 2b) and when inspecting the last rows in figure 4 and figure 5.

There were no significant interactions between species richness and the presence of particular functional groups in the communities on phytometer performance. We mention this explicitly because such interactions might be expected if the sown proportion of a functional group would influence invasion resistance; where present, the proportion of a functional group decreases with increasing species richness.

In both seasons, the leaf area index (LAI) of the resident community increased with the logarithm of species richness (August 2003: $F_{1,68} = 6.42$, $p = 0.014$, May 2004: $F_{1,70} = 6.70$, $p = 0.012$) but was not affected by functional richness. Although there was no effect of the presence of any functional group on LAI in August 2003, in May 2004, LAI was high in mixtures containing legumes ($F_{1,68} = 28.01$, $p < 0.001$) and low in mixtures containing small herbs ($F_{1,68} = 6.52$, $p < 0.013$). This suggests that belowground competition may be responsible for the observed high suppression of phytometers in communities containing grasses. As a covariate, in August 2003, LAI had significant negative effects on number of leaves and growth rate, positive effects on plant height ($P < 0.05$) but neutral effects on biomass of the phytometers. In May 2004 however, LAI had negative effects on aboveground biomass, plant height, and number of ramets of the phytometers ($P < 0.05$). However, where present, the effects of LAI did not explain the significant effects of species richness; that is, species richness effects remained significant after controlling for the effect of LAI.

Effects of the functional group of the phytometer species

As suggested by hypothesis (c) in the Introduction, comparing the suppression of invaders by communities containing different functional groups is not the same as looking at the performance of invaders belonging to different functional groups. In the first case (hypotheses (a) and (b) in the Introduction), the panels in Fig. 4 and Fig. 5 are compared row-wise, in the second case they are compared column-wise. If the two approaches are combined, the performance of particular phytometer species in assemblages containing only species of its functional group can be compared with its performance in assemblages containing only the other functional groups (–1 diagonal in Fig. 4 and Fig. 5). We refer to this as a “home-vs.-away” contrast (see e.g. Joshi *et al.*, 2001; Turnbull *et al.*, 2005), for which hypothesis (c) predicts a particularly strong negative effect.

The effect of different single-functional-group assemblages on number of modules (leaves or ramets), aboveground biomass and growth rate of the phytometers was similar (Table 3). However, the height of the phytometers significantly differed among these assemblages: it increased from grass < small-herb < tall-herb < legume communities, suggesting that competition for light increased in this order. Overall, the two herbaceous phytometer species were least affected by differences between these one functional group assemblages, whereas the grass (*F. pratensis*) and the legume (*T. pratense*) phytometer were more affected by these differences. This is evident in Fig. 5 by comparing differences between open and filled symbols in monocultures. A contrast between monocultures versus multi-species assemblages containing one functional group showed that the number of modules (leaves or ramets), aboveground biomass and growth rate of the phytometers was significantly lower in the latter (Table 3). This reinforces the statistical observation made above, that competitive suppression increases with species richness of a community even if functional richness is held constant, in this case at the lowest level. The home-disadvantage was similar in mono-specific and multi-species single-functional-group assemblages (interaction home x mono not significant in Table 3).

Except for plant height, the home vs. away contrast almost fully explained the resident functional group x phytometer species interactions (Table 3). That is, as predicted, the phytometers had significantly lower performance when transplanted into assemblages consisting of the same rather than a different functional group (the effects of home-functional groups were stronger than of away-functional group, i.e. negative bars in Fig. 6). The significant residual RFG x PS interaction for plant height indicates that the home effect on plant height is not as clear-cut; for example, *F. pratense* phytometers were taller in non-grass single function group assemblage whereas *T. pratense* phytometers were shorter in non-legume single functional group assemblages (Fig. 6). The four-phytometer species responded differently to mono-specific versus multi-species single-functional-group assemblages (Table 3): the biomass of *P. lanceolata* declined from 5.3 g in mono-specific to 0.9 g in multi-species single-functional-group assemblages whereas the other three-phytometer species showed little reduction in aboveground biomass. For two phytometer species that also occurred as monocultures, *P. lanceolata* was greatly suppressed by its own monoculture in both seasons. It attained less than 1.5 g in its own monoculture in both seasons compared to an average of 5.6 g and 14.7 g in other monocultures in summer 2003 and spring 2004 respectively. By contrast, *F. pratense* performed well in its own monocultures especially in 2004 (i.e. 19.6 g in its own and 13.5 g in others).

Discussion

Effects of species richness and functional richness

By introducing young plants of native species as test invaders into host communities we have shown that plant diversity enhances competitive suppression of newly arriving individuals during the invasion process. This supports the proposition that species-rich communities contain less empty niches that can be occupied by extra individuals. The performance of the test invaders in our experiment was linearly related to the logarithm of species richness. This indicates an attenuation of invasion resistance in more diverse host communities, probably due to increased niche overlap among resident species. It is conceivable that stronger invasion resistance could have been observed if we had introduced seeds (see e.g. Symstad, 2000; Dukes, 2001) instead of young plants, but then we would have confounded requirements for empty germination niches with those for growing plants. Our results agree with several previous findings referring to invasions by non-native species (e.g. Levine, 2000; Prieur-Richard *et al.*, 2002). With one of the most balanced designs in terms of species and functional diversity achieved so far in biodiversity experiments (Roscher *et al.*, 2004), our results show that in contrast to previous suggestions (Diaz & Cabido, 2001) species richness was a better predictor of invasion resistance than was functional group richness.

Since functional groups are aggregations of species, three observations (that can apply in natural communities) may explain why the effect of species richness in this study was stronger than that of functional group richness. First, aggregating several species into few functional groups makes species richness have a wider range (1–60 species) than functional richness (1–4 functional groups). Second, differential effects of functional richness on different phytometer species leads to an averaging of the overall effect of functional richness in a balanced design, where each functional group is represented equally among the four phytometer species and among the resident plant communities. A case in point is the positive effect of resident legumes on non-legume test-invaders and the negative effect on the legume test-invader. Third, contrasting effects of different functional groups on resources may weaken the overall effect of functional group richness. For example, while legumes enrich soil with nitrogen, grasses deplete this resource (Tilman *et al.*, 1997; Scherer-Lorenzen *et al.*, 2003). These counteracting effects of functional groups on resource pre-emption weaken the overall effect of functional group richness on suppression of test-invaders, supporting resource pre-emption as one mechanism of invasion resistance in plant communities.

Nonetheless, as in the study by Symstad (2000), using seeds instead of transplants as invaders, functional group richness can enhance invasion resistance, if considered alone. Interestingly, Symstad (2000) could not attribute increased invasion resistance by functionally rich communities to resource pre-emption, which indicates that in her case perhaps specific requirements for germination played an important role. Our study showed that pure grass mixtures can be most resistant to invasion after germination, underlying the importance of traits of specific groups (see next section). It remains debatable, of course, if the *a priori* definitions of functional groups that we adopted in The Jena Experiment are adequate to understand the relationship between functional diversity and invasion resistance. Nevertheless, the fact that species richness log-linearly increased invasion resistance even within plant assemblages consisting of a single functional group further exemplifies the importance of species richness as a driver in this particular case of an ecosystem function.

Effects of the presence of particular functional groups

The negative, positive and neutral effect of legumes, grasses and herbs, respectively, on invasion resistance in our study reflects their known patterns of resource use (Fargione *et al.*, 2003; Fargione & Tilman, 2005) and fits with a general theory of invasibility of Davis *et al.* (2000). In our experiment, better performance of the phytometers in communities with legumes corresponded with findings that they actually benefited from nitrogen fixed by legumes (Temperton *et al.*, submitted). It is well documented that legumes, by adding nitrogen to the soil, can promote invasion in nitrogen-limited environments (Yelenik *et al.*, 2004 and reference therein). By actively fixing atmospheric nitrogen, legumes do not rely on soil-nitrogen pools. Thus, a related effect of legumes is the reduction of competition for soil nitrogen. Some previous studies, however, have reported increased invasion resistance due to presence of legumes (Hector *et al.*, 2001; Fargione *et al.*, 2003). It is notable that positive effects of legumes usually correlate with their effect on belowground resources, mainly soil nitrogen (Maron & Connors, 1996; Prieur-Richard *et al.*, 2002) while their negative effects usually correlate with their effect on aboveground resources (Hector *et al.*, 2001; Fargione *et al.*, 2003). Thus, in general legumes may enhance invasion resistance in fertile soils but promote invasion in poor soils. In addition, legumes may have a stronger potential than grasses and herbs to differentially affect different invaders. Notably, as mentioned above, they can have negative effects on other legumes even when they have positive effects on other species.

Suppression of all phytometers was particularly strong in resident communities containing grasses. Due to their extensive root systems, grasses are efficient in taking up resources from the upper soil layers (Fargione *et al.*, 2003), thereby diminishing resources for potential invaders. Other studies have also reported grasses as a keystone functional group reducing the success of invaders (Crawley *et al.*, 1999; Dukes, 2002; Prieur-Richard *et al.*, 2002). Crawley *et al.* (1999) found that an assembly of 80 herbaceous species was more vulnerable to invasion than were assemblies composed of 1–4 grass species. A weak effect of grasses on LAI did not explain the strong negative effect of their presence on invasion resistance, suggesting that their contribution to invasion resistance is mainly through their effect on belowground resources. From these results we can conclude that with regard to functional diversity, functional group identity may be more important than pure number of functional groups (Schmid *et al.*, 2002). This was also observed in the same experiment by Scherber *et al.* (2006), investigating herbivory on a different phytometer species, *Rumex acetosa*.

Effects of the functional group of the phytometer species and niche pre-emption within functional groups as major mechanism of invasion resistance

With regard to the identity of the invader, experimental communities were particularly resistant to a phytometer species if they contained species belonging to the same functional group. For example, although non-legume herbs had no effect on invasion resistance in general, their presence in the resident communities enhanced suppression of their respective phytometers. Likewise, despite notable facilitation by legumes, communities containing only this functional group strongly inhibited the legume test invader, *T. pratense*. Our results and a previous observation that legume monocultures were most resistant to invasion by legumes (Turnbull *et al.*, 2005) indicate that resident legumes also pre-empt other resources that limit legumes, most likely phosphorus, water and light (Vitousek & Howarth, 1991). This is consistent with high niche overlap along several resource-use axes between resident and invading legumes, and further supports niche pre-emption as a mechanism of invasion resistance. Thus, high niche overlap between newly arriving individuals and resident species can reduce chances of an invasion, rate of colonisation or even success of restoration. This corresponds to findings of Fargione *et al.* (2003) in a seed addition experiment, where they concluded that high invasion resistance was due to similar patterns of resource use between the resident species and the invaders. Xu *et al.* (2004) also found that the presence of a functionally similar herb in a resident community increased resistance to invasion by Alligator weed (*Alternanthera philoxeroides*), which was also attributed to niche overlap.

Finally, it should be mentioned that alternative hypotheses may also be consistent with the result of stronger within- than between-functional-group invasion resistance (Fukami *et al.*, 2005; Britton-Simmons, 2006). Namely, the presence of a species in a community might build up pathogens, parasites, or herbivores that have negative impacts on invaders from the same functional group (Wardle *et al.*, 2004; Bartelt-Ryser *et al.*, 2005). It is conceivable that such effects are particularly important during the early phases of the life cycle of invaders, e.g. during germination. However, in this study we could not test this because we introduced our test invaders as young plants rather than seeds into the communities.

This study confirms that, first, communities that are more diverse confer high resistance to invasion independent of invasiveness of the introduced species. Secondly, presence of grasses enhances invasion resistance while legumes may promote invasion due to their influence on nitrogen dynamics. Thirdly, communities are more resistant to invaders belonging to functional groups already present among the resident species. Although these results pertain to grassland ecosystems which are regularly "disturbed" by mowing, similar mechanisms may play a role in other terrestrial and in aquatic ecosystems where species richness has been shown to increase invasion resistance (see review of Balvanera *et al.*, in press). However, to our knowledge this has not been investigated in such a systematic way as we did here in grassland systems.

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Table 1 Partial correlation of phytometer vegetative and reproductive traits measured in summer 2003 with aboveground biomass harvested at the same time. Significance levels are, * P<0.05; ** P<0.01; ** P<0.001

Plant Trait	*F. pratense* (N=71)	*P. lanceolata* (N=78)	*K. arvensis* (N=76)	*T. pratense* (N=68)
Number of leaves	0.919***	0.887***	0.855***	0.776***
Number of ramets	0.904***	-	-	0.866***
Height	0.467***	0.128^{ns}	0.228*	0.415***
Number of flowers	-	0.974***	-	0.938***
Relative growth rate	0.804***	0.610**	0.720***	0.680***

Table 2a Summary of analyses of variance of the performance of the four phytometer species in summer 2003. Residual d.f. are [a]=225 and total [b]=308 for number of leaves and plant height and [a]=240 and total [b]=327 for growth rate. Diversity is represented by a log-linear contrast (SR) and the deviation from this contrast. The phytometer species (PS) at the same time represents the functional group of the phytometer. Due to hierarchical design of the experiment, the terms above composition are tested at plot-level error term, i.e. composition. The terms presence of functional groups and their interaction with SR were added alternatively because they are intrinsically related, same communities contained presence/absence of different groups. PS and SR x PS was tested against within-plot error (residual). Significance levels are * P < 0.05; ** P < 0.01; *** P < 0.001.

		BIOMASS		LEAVES		HEIGHT		GROWTH RATE	
Source	d.f.	MS	F	MS	F	MS	F	MS	F
Block	3	6.23	2.63	1.06	1.23	0.79	1.61	<0.01	1.53
Species richness (SR)	1	22.22	**9.39** **	14.84	**17.23** ***	1.17	2.36	<0.01	**13.59** ***
Deviation	3	5.17	2.18	1.26	1.46	0.26	0.53	<0.01	0.71
Composition	70	2.37	**3.28** ***	0.86	**4.28** ***	0.49	**4.30 *** **	<0.01	**3.07 *** **
Grasses (GR)	1	19.52	**9.25** **	3.20	**3.89** *	4.93	**11.66 ****	<0.01	**4.41 ***
SR x GR	1	2.72	1.29	1.10	1.33	0.93	2.19	<0.01	2.98
Composition	68	2.11	**2.89** ***	0.82	**4.21** ***	0.42	**3.82 *** **	<0.01	**3.11 *** **
Short-herbs (SH)	1	3.33	1.41	0.15	0.17	1.06	2.19	<0.01	0.46
SR x SH	1	1.60	0.68	0.00	<0.01	0.77	1.59	<0.01	0.99
Composition	68	2.37	**3.39** ***	0.88	**4.36** ***	0.48	**4.13 *** **	<0.01	**3.07 *** **
Tall-herbs (TH)	1	4.22	1.78	1.27	1.46	0.70	1.41	<0.01	0.04
SR x TH	1	0.06	0.02	0.08	0.09	0.31	0.62	<0.01	<0.01

Composition	68	2.38	**3.31** ***	0.87	**4.23** ***	0.49	**4.38 *****	<0.01	**3.12 *****
Legumes (LG)	1	13.15	**5.86** *	0.82	0.94	7.18	**17.88 *****	<0.01	<0.01
SR x LG	1	0.03	0.01	0.35	0.41	0.08	0.20	<0.01	0.17
Composition	68	2.24	**3.29** ***	0.87	**4.76** ***	0.40	**3.64 *****	<0.01	**3.31 *****
Phytometer species (PS)	3	10.44	**14.47** **	14.82	**73.58** **	13.31	**115.84 ****	<0.01	**82.60 *****
SR x PS	3	2.07	**2.88** *	0.25	1.26	0.17	1.45	<0.01	**3.08** *
Residual	216[a]	0.72		0.20		0.11		<0.01	
Total	299[b]	1.39		0.56		0.34		<0.01	

Table2b Summary of analyses of variance of contrasts of phytometer species and their interaction with the diversity terms. Residual d.f. are [a]=219 for number of leaves and plant height and [a]=234 for growth rate. Contrasts for each phytometer species were added alternatively into model in table 2a and tested against their respective residuals. Abbreviations not included in table 2a are; FP = *Festuca pratensis*, PL = *Plantago lanceolata*, KA = *Knautia arvensis*, TP = *Trifolium pratense*, for the phytometer species.

		BIOMASS		LEAVES		HEIGHT		GROWTH RATE	
Source of variation	d.f.	MS	F	MS	F	MS	F	MS	F
FP	1	<0.01	<0.01	33.52	**171.4** **	25.57	**231.06 ****	<0.01	**36.33 *****
SR x FP	1	3.55	**4.86** *	0.42	2.14	0.50	**4.49 ***	<0.01	2.26
GR x FP	1	0.19	0.26	1.46	**7.48** **	0.01	0.08	<0.01	**18.02** ***
GR x PS	2	0.23	0.32	0.52	2.68	0.34	**3.04 ***	<0.01	**3.89 ***
SR x GR x FP	1	0.38	0.52	0.00	0.02	0.15	1.31	<0.01	2.26
SR x GR x PS	2	0.64	0.88	0.00	0.00	0.40	**3.57 ***	<0.01	0.13
Residual	210[b]	0.73		0.20		0.11		<0.01	0.61
PL	1	1.49	2.13	12.46	**61.43** **	2.15	**18.44 ****	<0.01	**50.16 *****
SR x PL	1	3.68	**5.27** *	0.53	2.60	0.04	0.34	<0.01	0.77
SH x PL	1	1.67	2.39	0.29	1.43	0.05	0.46	<0.01	0.15
SH x PS	2	2.06	2.96	0.06	0.28	0.10	0.84	<0.01	0.66
SR x SH x PL	1	2.01	2.87	0.00	0.01	0.00	0.01	<0.01	0.86
SR x SH x PS	2	0.66	0.94	0.24	1.20	0.03	0.28	<0.01	0.93
Residual	210[b]	0.70		0.20		0.12			
KA	1	14.31	**19.96** **	12.03	**58.72** **	23.91	**212.05 ****	<0.01	**107.17 *****
SR x KA	1	0.56	0.78	0.02	0.11	0.08	0.71	<0.01	3.49
TH x KA	1	0.00	0.00	0.01	0.04	0.18	1.56	<0.01	0.17
TH x PS	2	1.69	2.35	0.15	0.74	0.10	0.89	<0.01	0.75
SR x TH x KA	1	0.02	0.02	0.01	0.03	0.37	3.31	<0.01	0.56

SR x TH x PS	2	0.87	1.22	0.07	0.33	0.21	1.84	<0.01	0.45
Residual	210[b]	0.72		0.20		0.11			
TP		25.83	**37.88** **	1.38	**7.56** **	1.56	**14.17 ** **	<0.01	**144.96 *** **
SR x TP	1	0.56	0.82	0.05	0.28	0.05	0.49	<0.01	**6.25** *
LG x TP	1	8.17	**11.97** **	2.56	**14.02** **	0.44	**3.97 ***	<0.01	**7.61 ****
LG x PS	2	0.76	1.11	0.82	**4.50** *	0.06	0.51	<0.01	2.35
SR x LG x TP	1	0.55	0.81	0.16	0.89	0.54	**4.89 ***	<0.01	0.77
SR x LG x PS	2	1.16	1.71	0.45	2.45	0.31	2.78	<0.01	2.53
Residual	210[a]	0.68		0.18		0.11		<0.01	

Table 3 Summary of analyses of variance of summer 2003 data for home-vs.-away effect on the four phytometer species using plots with resident communities consisting of species from only one functional group. Significance levels are * P < 0.05; ** P < 0.01; *** P < 0.001.

		Biomass		Leaves		Height	
Source	d.f.	MS	F	MS	F	MS	F
Block	3	11.63	**4.09***	2.33	2.08	553.61	8.43
Resident Functional Group (RFG)	3	3.11	1.09	0.26	0.23	962.34	**14.66*****
Monoculture vs. Mixture (Mono)	1	22.02	**7.75***	9.16	**8.19****	49.64	0.76
RFG x Mono	3	0.53	0.19	0.06	0.06	6.44	0.10
Composition	23	2.84	**4.19*****	1.12	**5.61*****	65.66	**1.68***
Phytometer species (PS)	3	3.36	**4.95****	5.99	**30.08*****	1818.79	**46.65*****
Home vs. Away (RFG x PS main diag.)	1	4.25	**6.26***	1.59	**7.98****	169.93	**4.36***
RFG x PS (residual interact.)	8	0.84	1.24	0.22	1.13	191.49	**4.91*****
Phytometer species x Mono	3	2.47	**3.64***	0.28	1.40	42.37	1.09
Home vs. Away x Mono	1	0.19	0.28	0.38	1.89	8.51	0.22
Residual	79	0.68		0.20		38.99	
Total	128	1.68		0.63		128.91	

Figure legends and Figures

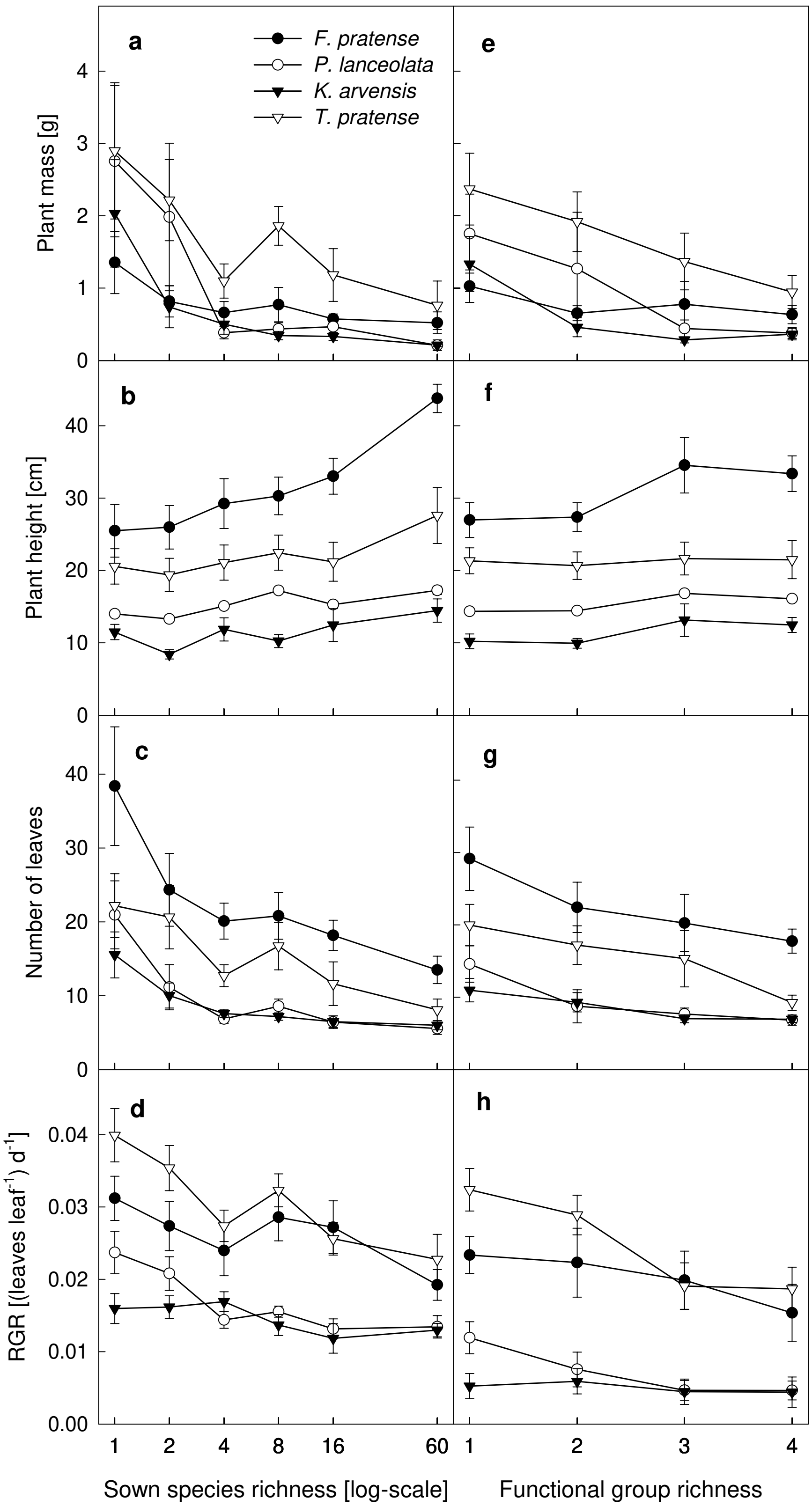

Fig. 1. Effect of plant species richness (a–d) and functional group richness (e–h) on performance of four transplanted phytometer species in the first season (summer 2003). Points and vertical bars represent means ± 1 standard error. All panels use the legend in panel (a).

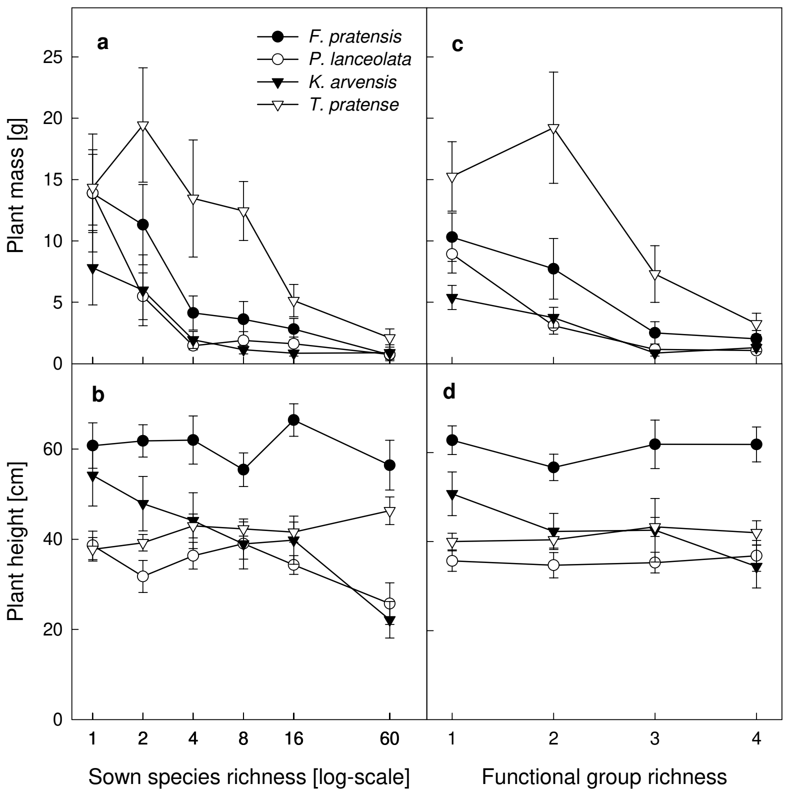

Fig. 2. Effect of plant species richness (a–b) and functional group richness (c–d) on performance of four transplanted phytometer species in the second season (spring 2004). Points and vertical bars represent means ± 1 standard error. All panels use the legend in panel (a).

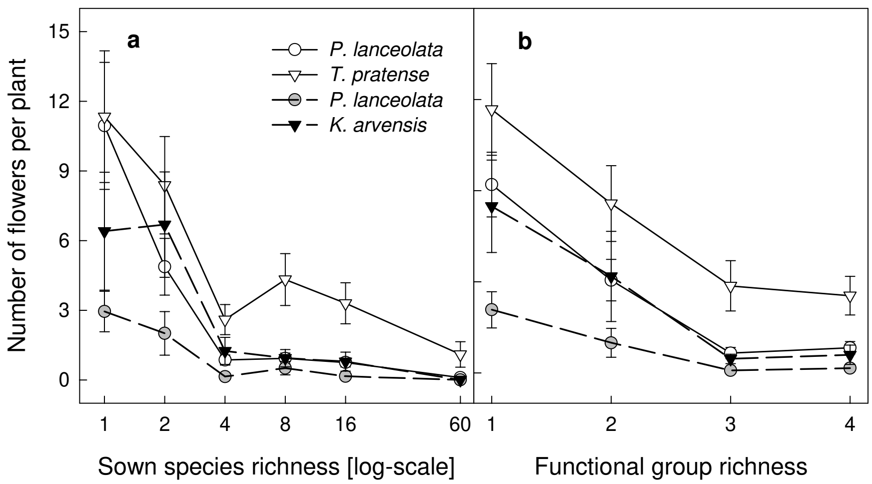

Fig. 3. Effect of plant species richness (a) and functional groups richness (b) on number of inflorescences of four transplanted phytometer species in summer 2003 (solid lines) and spring 2004 (broken lines). Points and vertical bars represent means ± 1 standard error.

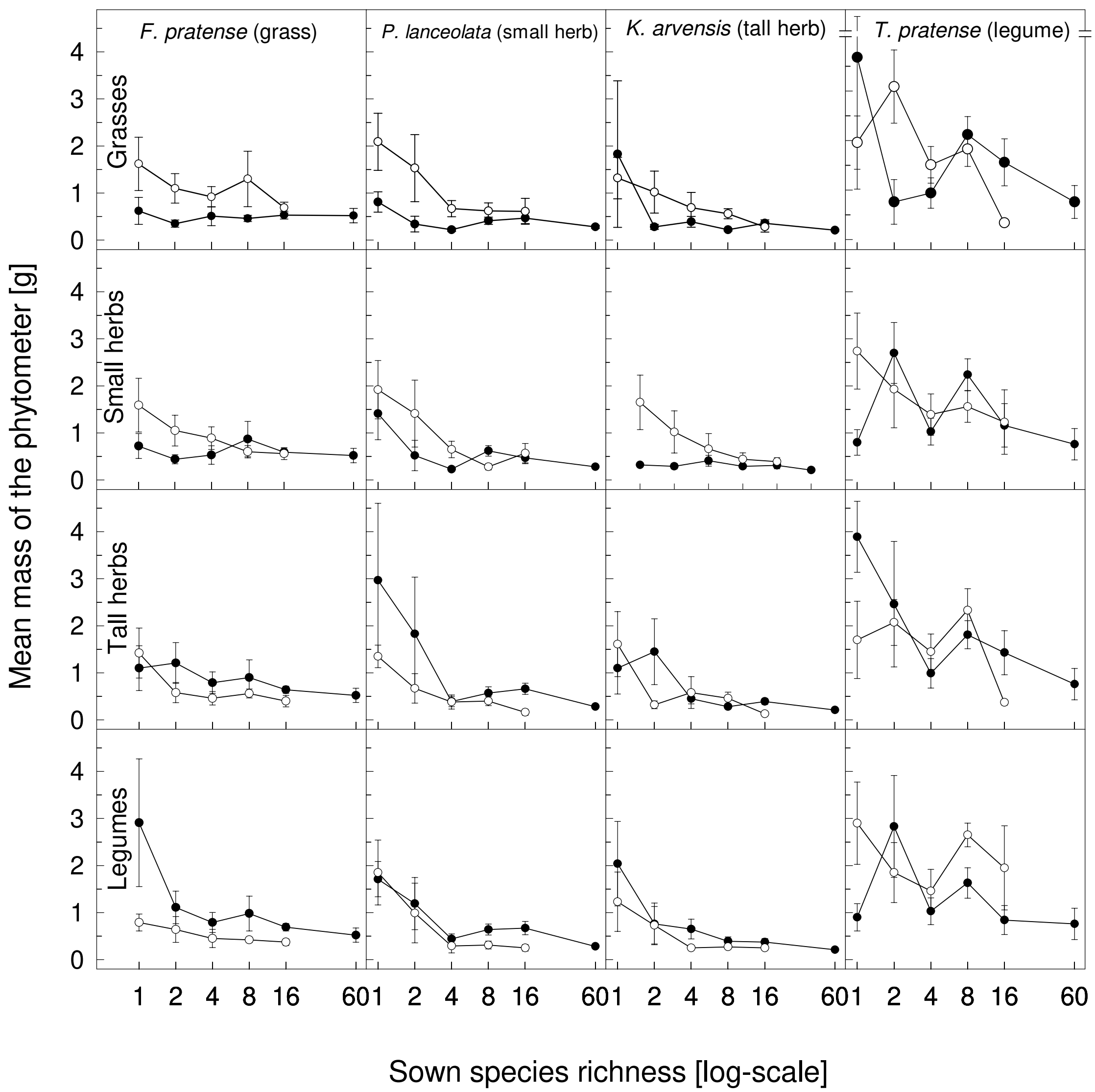

Fig. 4. Effect of plant species richness and presence/absence of different functional groups on biomass of four transplanted phytometer species in the first season (summer 2003). Columns represent phytometers species *F. pratensis*, *P. lanceolata*, *K. arvensis* and *T. pratense* from left to right and rows represent presence/absence of grasses, small-herbs, tall-herbs and legumes from top to bottom. Closed and open symbols indicate, respectively, presence and absence of the corresponding functional groups in the resident

communities. For example, the second panel in the first row shows the response of *P. lanceolata* to species richness in the plots containing grasses (closed symbols) and in plots without grasses (open symbols). Points and vertical bars represent means ± 1 standard error.

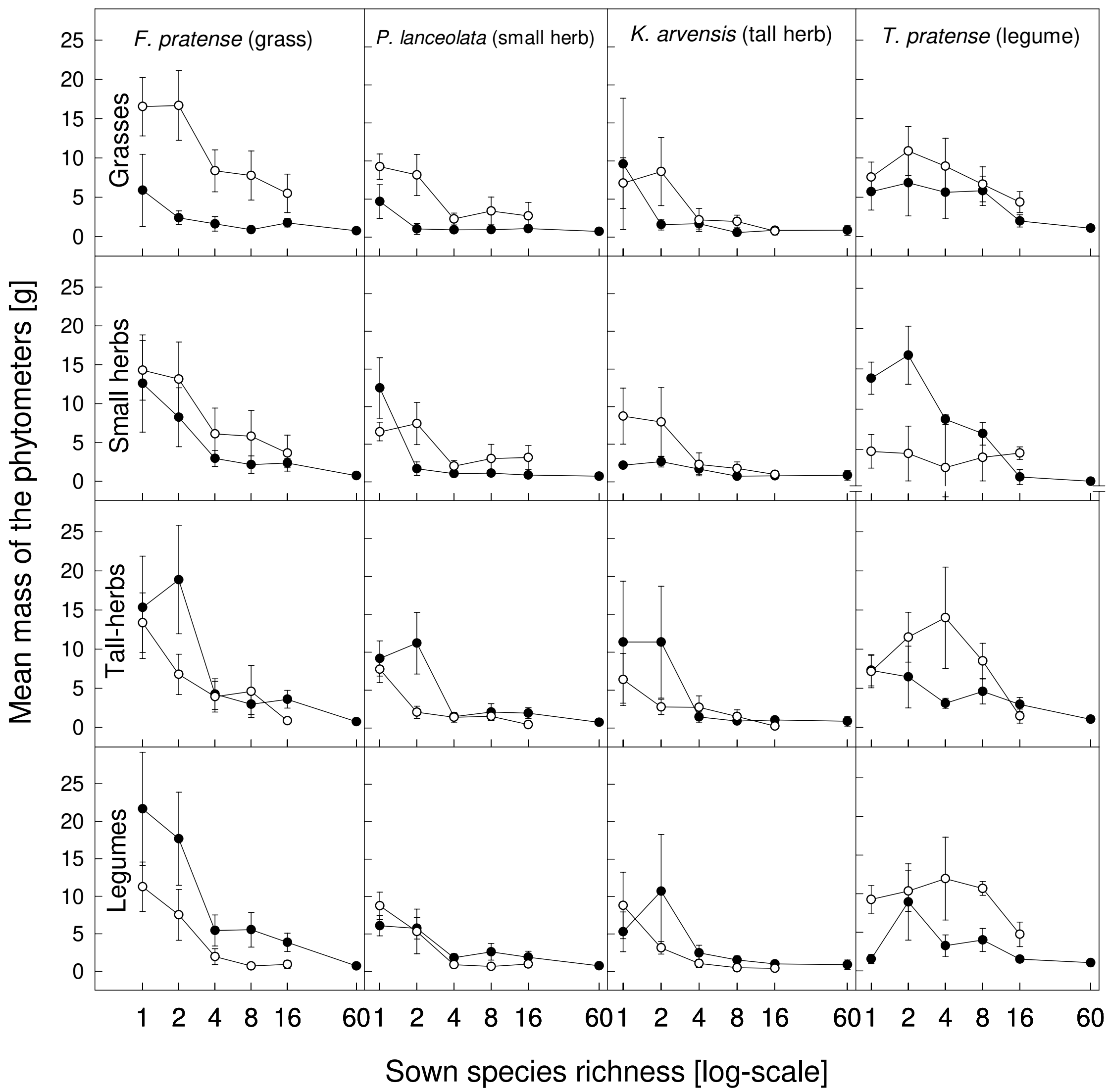

Fig. 5. Effects of plant species richness and presence/absence of different functional groups on biomass of four transplanted phytometer species in the second season (spring 2004). Columns represent phytometers species *F. pratensis*, *P. lanceolata*, *K. arvensis* and *T. pratense* from left to right and rows represent presence/absence of grasses, small herbs, tall herbs and legumes from top to bottom. Closed and open symbols indicate,

respectively, presence and absence of functional groups in the resident communities. Points and vertical bars represent means ± 1 standard error.

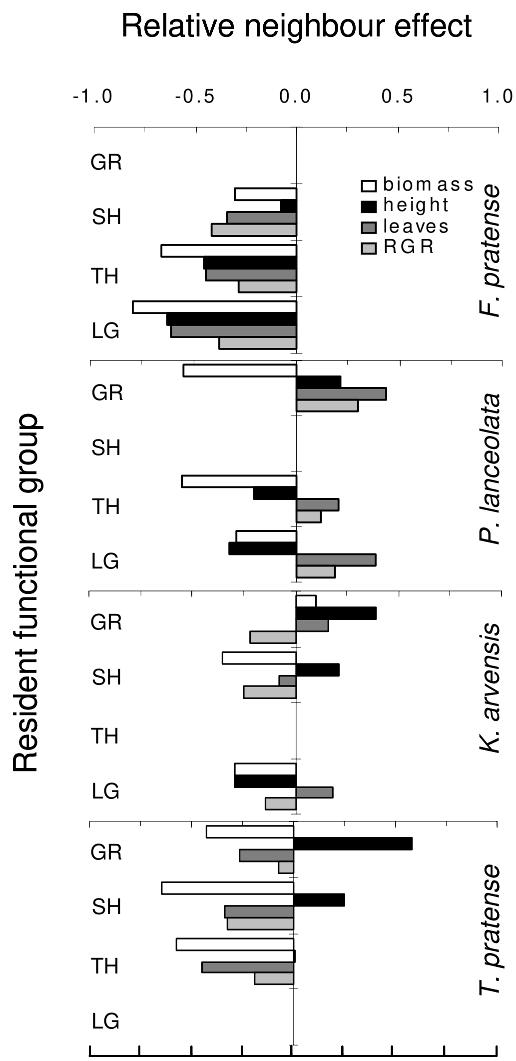

Fig. 6. Performance of phytometers transplanted into single-functional-group assemblages of grasses (GR), small herbs (SH), tall herbs (TH) and legumes (LG) relative to performance in mono-functional group assemblages of their own functional group. Negative values indicate negative "home" effects, i.e. that resident species belonging to a functional group different from that of the phytometer were less inhibitive, while positive values indicate positive home effects.