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## **Species richness and identity affect the use of aboveground space in experimental grasslands**

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1 **Species richness and identity affect the use of aboveground space in**  
2 **experimental grasslands**

3

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18

19 **Running title:** Aboveground space use in experimental grasslands

20 **Abstract**

21 Complementary resource use is regarded as a mechanism that contributes to positive  
22 relationships between biodiversity and ecosystem functioning. Here, we used a biodiversity  
23 experiment composed of nine potentially dominant species (grasses: *Alopecurus pratensis*,  
24 *Arrhenatherum elatius*, *Dactylis glomerata*, *Phleum pratense*, *Poa trivialis*, legumes:  
25 *Trifolium pratense*, *T. repens*, non-legume herbs: *Anthriscus sylvestris*, *Geranium pratense*) to  
26 test for differences among monocultures and mixtures and for effects of species richness and  
27 the presence of particular species on the use of aboveground space. The number of rooting  
28 shoots determined in a line transect increased from monocultures to mixtures. Particularly, the  
29 presence of *A. elatius* in mixtures caused a higher shoot density at the community level. The  
30 number of pin contacts per sampling point (cumulative cover) at the community level,  
31 analyzed with the point intercept method, was higher in mixtures than monocultures, and  
32 higher in mixtures with than without *A. elatius*. The effect was attributable to increased  
33 densities across the strata of the vertical stand profile as well as to an increase in community  
34 height. The impact of species richness on the use of aboveground space differed considerably  
35 between individual species. *Arrhenatherum elatius* achieved increased densities across all  
36 strata of the stand profile, while *D. glomerata* reached higher densities with a more  
37 pronounced use of space in the upper strata with increasing species richness of mixtures.  
38 Cumulative cover of *P. pratense* and *A. pratensis* was not affected by species richness, while  
39 the remaining species decreased space use mostly in the upper strata with increasing species  
40 richness or in mixtures with the competitively superior *A. elatius*. Our study shows that  
41 potentially dominant species are limited in their ability for adaptive responses to canopy  
42 shading. Nevertheless, the differential responses to species richness of individual species with  
43 regard to vertical niche occupation resulted in positive diversity effects on aboveground space  
44 use at the community level.

Lorentzen et al.

45

46 **Keywords:** *Arrhenatherum elatius*, biodiversity effects, complementarity, light competition,

47 The Jena Experiment, vertical structure

48 **Introduction**

49 A number of manipulative biodiversity experiments found positive effects of plant species  
50 richness on ecosystem processes such as aboveground productivity (e.g. Hector et al., 1999;  
51 Tilman et al., 2001; Spehn et al., 2005; Roscher et al., 2005; van Ruijven and Berendse, 2005;  
52 Balvanera et al., 2006). The underlying mechanisms of these experimental results have been  
53 discussed controversially (Hooper et al., 2005). The sampling-effect hypothesis describes the  
54 mechanism of increasing probability to include a highly productive species in a randomly  
55 selected species-rich mixture (Aarssen, 1997; Huston, 1997; Tilman, 1997; Cardinale et al.,  
56 2006). The niche-complementarity hypothesis is based on the assumption that differences  
57 among species decrease niche overlap in diverse communities and lead to a more efficient use  
58 of available resources that finally causes the positive relationship between species richness  
59 and productivity (Tilman, 1997; Tilman et al., 1997; Loreau, 1998; Cardinale et al., 2007).

60 All plant species compete for the same major resources of water, carbon dioxide, mineral  
61 nutrients and light. Complementarity in light exploitation has been proposed as one possible  
62 mechanism that contributes to the positive effects of plant species richness on aboveground  
63 biomass production (Naeem et al., 1994; Spehn et al., 2000, 2005). In addition to  
64 morphological and ecophysiological differences among species, individual plasticity may also  
65 increase resource-use efficiency of species and contribute to complementarity. This could, for  
66 example, occur if species with overlapping vertical distributions of leaves in monoculture  
67 would show a segregation of distributions in mixtures allowing the mixture to cover a larger  
68 vertical profile than each monoculture by itself. Adaptative changes in response to light  
69 availability belong to the best-studied examples of phenotypic plasticity (Schmitt and Wulff,  
70 1993; Valladares et al., 2007). Morphological plasticity in response to light competition  
71 includes enhanced internode and petiole extension, reduced leaf development, increased  
72 apical dominance with reduced branching, increasing the probability to overtop neighbours

73 (Smith and Whitelam, 1990; Huber and Wiggerman, 1997; Anten and Hirose, 1999;  
74 Weijsschedé et al., 2006) and, if these responses are not possible, the formation of shade leaves  
75 which can economically use even low levels of light (Corré, 1983; Schmid and Bazzaz, 1994;  
76 Evans and Poorter, 2001; Anten, 2005).

77 So far, aboveground space use of the plant community, and particularly of individual plant  
78 species, as a function of species richness has received little attention in biodiversity  
79 experiments. In the present study, we used the point intercept method (Levy and Madden,  
80 1933) to get detailed information on the spatial arrangement of individual species in a  
81 biodiversity experiment with a pool of nine potentially dominant species. The experiment was  
82 specifically designed to test for the response of individual species to a species richness  
83 gradient (“dominance experiment” of the Jena Experiment; Roscher et al., 2004). The set-up  
84 of this experiment was motivated by the criticism that positive effects of biodiversity found in  
85 previous experiments were caused by a comparison of species mixtures with monocultures of  
86 species that are not able to grow as monospecific plant stands (Huston and McBride, 2002;  
87 Thompson et al., 2005). Species used in this experiment were selected on the criterion that  
88 they are known for their ability to occur in monospecific patches, to become dominant and to  
89 contribute substantially to biomass production in mixtures in semi-natural grassland. The  
90 species differ in growth form and height and become dominant under different management  
91 regimes, but none of them is normally found in the under-storey of mixed plant communities.  
92 Thus, we investigated the following issues: (1) Does species richness increase the use of  
93 aboveground space if the species pool of an experiment is restricted to potentially dominant  
94 species? (2) Is the use of aboveground space modified by variation in canopy height or  
95 density across the canopy profile? (3) How do individual species change the use of  
96 aboveground space in response to species richness? Specifically, we address the question  
97 whether diversity effects continuously increase with species richness or whether these effects

98 are due to differences between monocultures and mixtures or the inclusion of particular  
99 species in mixtures.

100

## 101 **Methods**

102

### 103 *Experimental site*

104 The experimental site is located in the floodplain of the river Saale in Jena (Thuringia,  
105 Germany, 50°55`N, 11°35`E, 130 m a.s.l.). Mean annual air temperature is 9.3 °C and  
106 average annual precipitations are 587 mm (Kluge and Müller-Westermeier, 2000). The Jena  
107 Experiment (Roscher et al., 2004) was established in spring 2002 on a formerly fertilized field  
108 used for growing cereals and vegetable for at least 40 years up to 2000. The soil is derived  
109 from up to 2-m thick, loamy fluvial sediments and almost free of stones. Due to the fluvial  
110 dynamics of the river, soil textures ranges from sandy loam to silty clay with increasing  
111 distance to the river. Therefore, four experimental blocks were arranged parallel to the river.

112

### 113 *Species pool*

114 Typical Central European semi-natural mesophilic grasslands (Arrhenatherion community;  
115 Ellenberg, 1988) served as target community to create a species pool for the experiment.  
116 These formerly species-rich communities locally lost many species over the past decades due  
117 to intensified fertilization and shortened rotation periods. Nine species known to become  
118 potentially dominant in these grassland communities were selected for the experiment: five  
119 grasses (*Alopecurus pratensis* L., *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl et C. Presl,  
120 *Dactylis glomerata* L., *Phleum pratense* L. and *Poa trivialis* L.), two legumes *Trifolium*  
121 *pratense* L. and *T. repens* L.) and two non-leguminous herbs (*Anthriscus sylvestris* (L.)  
122 Hoffm. and *Geranium pratense* L.). Whereas the grass species *A. elatius*, *D. glomerata* and

123 *P. pratense* are characterized by a caespitose growth habit, *A. pratensis* forms belowground  
124 stolons and *P. trivialis* grows with creeping aboveground shoots (Beddows, 1959;  
125 Pfitzenmeyer, 1962; Mühlberg, 1967). The formation of sterile leafy shoots is a property that  
126 distinguishes *A. elatius* from the other grass species. The legumes also differ considerably in  
127 their growth habits. *Trifolium repens* produces aboveground creeping shoots rooting at older  
128 nodes. Older shoot parts eventually die off leading to fragmentation of ramets, rendering the  
129 identification of individuals difficult (Gluch, 1967). In contrast *T. pratense* and the non-  
130 leguminous herbs *G. pratense* and *A. sylvestris* have clearly defined individuals. Both non-  
131 legume herbs are known to establish slowly from seeds (Roberts, 1979; Nikolaeva et al.,  
132 1985). However, during our study carried out in the second year of the experiment all species  
133 were present in those plots where they were part of the sown mixtures.

134

### 135 ***Experimental design***

136 The experiment consisted of 206 plots of 3.5 × 3.5 m size. Species richness varied from  
137 one in monocultures to two, three, four, six and the complete set of nine species in mixtures.  
138 Each species was present in eight mixtures at each species richness level. Additionally, each  
139 possible two-species combination occurred with equal frequency at each species richness  
140 level above one. Each monoculture and each particular species combination of mixtures  
141 (except for the nine-species mixture) was represented by two replicate plots resulting in the  
142 following design: 2 × 9 monocultures, 2 × 36 two-species mixtures (each possible species  
143 combination), 2 × 24 three-species mixtures (each pairwise species combination occurring in  
144 2 mixtures and 4 plots), 2 × 18 four-species mixtures (each pairwise species combination  
145 occurring in 3 mixtures and 6 plots) and 2 × 12 six-species mixtures (each pairwise species  
146 combination occurring in 5 mixtures and 10 plots). The nine-species mixture had 8 replicates  
147 to ensure that each species was present in eight mixtures at each species richness level (except



148 for the monocultures). Thus, the experimental design combined an equal representation of  
149 individual species across the diversity gradient with increasing mixture similarity. For our  
150 study we chose randomly one replicate of each monoculture and mixture (and four replicates  
151 in case of the nine-species mixture).

152 The experimental communities were sown at an initial density of 1000 viable seeds per m<sup>2</sup>  
153 (adjusted for germination rates from preliminary laboratory tests) with an equal distribution of  
154 seeds among species. The experimental plots were grouped into four blocks and each block  
155 contained 51 plots with all species richness levels represented equally. All plots were mown  
156 twice a year to 5 cm height. The mown plant material was removed. The plots were weeded  
157 regularly to prevent invasion of unwanted species (for details see Roscher et al., 2004).

158

#### 159 *Data collection*

160 **Horizontal structure.** A line transect of 2 cm width and 250 cm length was used to record  
161 density of rooted shoots and their distribution along the plot diagonal in July 2003 when  
162 individuals could be easily recognized due to previous mowing. Shoots of each species  
163 rooting in the transect were counted in 1-cm intervals. The data were analysed for (1) total  
164 and species number of rooting shoots, (2) number of transect sections where no rooting shoots  
165 were found, and (3) degree of shoot aggregation estimated as coefficient of variation of shoot  
166 density per cm.

167 **Vertical structure.** The point intercept method (Levy and Madden, 1933) was applied to  
168 analyse vertical vegetation structure. This method is known to be affected by pin diameter,  
169 pin inclination and spatial orientation of plant parts (Warren Wilson, 1959, 1960, 1963). The  
170 magnitude of divergence differs among plant species. Nevertheless the point intercept method  
171 may provide the most detailed non-destructive information on spatial arrangement of  
172 individual species in dense plant stands. A pin frame, consisting of a row of 20 pins with a pin

173 diameter of 3 mm and a distance of 5 cm between the pins, was inserted vertically through the  
174 vegetation down to the soil surface. All contacts of green plant parts (excluding litter) with the  
175 pins were counted per species using 5-cm intervals along the pins.

176 Data were taken at the time of peak biomass before mowing of the plots at the end of May  
177 and August 2003. Only monocultures, two-species mixtures and the nine-species mixture  
178 were measured in May. In August, all species richness levels, including three-, four- and six-  
179 species combinations, were recorded. The two-species mixture of *A. elatius* and *G. pratense*  
180 could not be analysed in May because strong rain flattened the vegetation. The following  
181 variables were derived from the field data:

182 (1) *Cumulative cover* per species (and plant stand) was defined as sum of pin contacts per  
183 species (or all species) with 20 pins divided by 20, measured at plot level. *Vertical density*  
184 was defined as number of pin contacts of plant parts per 5-cm height layer divided by 20. The  
185 vertical resolution was considered in seven height strata: 0–5 cm, 5–10 cm, 10–20 cm, 20–  
186 30 cm, 30–50 cm, 50–70 cm, >70 cm. The cumulative cover is closely related to the Leaf  
187 Area Index (LAI). The difference is only due to the inclusion of non-leaf plant parts (these are  
188 also included in optical measurements of LAI).

189 (2) *Maximum height* (cm) per species (or plant stand) was defined as the highest observed pin  
190 contact of plant parts of a species.

191 (3) *Mean height* (MH or centre of vertical density) (cm) per species (or plant stand) was used  
192 as an integrated measure of the vertical distribution of plant parts. It was computed following  
193 Gibson et al. (1987) by multiplying vertical density of each 5-cm wide layer ( $d_i$ ) with the  
194 mean height of the layer ( $h_i$ ) and dividing the sum of these products by the sum of vertical  
195 densities:

$$MH = \frac{\sum_{i=1}^k h_i d_i}{\sum_{i=1}^k d_i}$$

197

198 **Data analysis**

199 Data analysis was done with S-Plus<sup>®</sup> 7.0 software (Insightful Corp., 2005). Data were  
 200 analysed at community and species level. For data recorded with the point intercept method  
 201 we used repeated-measures analysis of variance (ANOVA), applying the principles described  
 202 in Schmid et al. (2002). The initial statistical model included species richness decomposed  
 203 into a contrast to separate monocultures from mixtures and a log-linear contrast for species  
 204 richness within mixtures. The presence of individual species was used as predictor variable in  
 205 additional analyses to test for effects of species identity. This was possible because in our  
 206 design, like in another recent experiment using microbes (Bell et al., 2005), the presence of  
 207 each individual species was correlated to exactly the same degree with species richness. We  
 208 found a strong contrast for the presence or absence of *A. elatius* in mixtures. Therefore, we  
 209 included this effect (presence or absence of *A. elatius*) before entering log-linear species  
 210 richness in our final statistical models. Together with season (May or August) and their  
 211 interaction it constituted the treatment model. Composition (= monoculture or mixture  
 212 identity) and composition within season were used as error term (Table S1, see Schmid et al.,  
 213 2002). Blocks were not included in the error model because the random selection of one  
 214 replicate per mixture leads to a confounding of the block term with species richness. The  
 215 dependent variables were cumulative cover, maximum height and mean height (MH). For the  
 216 analysis of vertical density, the layer variable, we used a split-plot repeated-measures  
 217 ANOVA in which the split-plot treatment was height (decomposed into linear contrast and  
 218 deviation). All other terms were the same as in the above analysis (see Appendix, Table S1

219 for detailed information). For the analysis of species data, the dependent variables were first  
220 multiplied with species richness to account for the differences in proportions of sown seeds.  
221 This correction transformed these variables to per-individual-sown measures. If necessary,  
222 data were log-transformed to meet the assumptions of normality and homogeneity of  
223 variances.

224 In further analyses we calculated the differences of mean height for each species pair. The  
225 calculation was based on monoculture values from different plots and all species pairs in the  
226 two- and nine-species mixtures recorded in May. One-sample t-tests were applied to test each  
227 pair for differences between monocultures and mixtures.

228

## 229 **Results**

230

### 231 *Horizontal structure in relation to diversity*

232 **Effects of diversity at community level.** Averaged across all plots, we counted 37 ( $\pm$  21 s.d.)  
233 shoots per metre of transect length. The number of rooting shoots increased from  
234 monocultures to mixtures ( $F_{1;96} = 7.26$ ,  $P = 0.008$ ). It was significantly higher in mixtures  
235 with *A. elatius* ( $F_{1;96} = 25.89$ ,  $P < 0.001$ ) while a further increase of species richness beyond  
236 two had no effect on the number of rooting shoots (Table 1, Fig. 1). The number of gaps (=   
237 unoccupied transect sections) as well as the degree of shoot aggregation, estimated as  
238 coefficient of variation of shoot density per cm, were significantly lower in mixtures with  
239 *A. elatius* (number of gaps:  $F_{1;96} = 11.51$ ,  $P < 0.001$ ; shoot aggregation:  $F_{1;96} = 5.85$ ,  
240  $P = 0.017$ ), but not affected by species richness.

241 **Effects of diversity on individual species.** The number of rooting shoots of individual  
242 species was not higher in mixtures than in monocultures. The legumes *T. pratense* and  
243 *T. repens* showed a significant decrease of rooting shoots per individual if sown in mixtures

244 with *A. elatius*. Increasing species richness of mixtures had generally a negative effect on the  
245 number of rooting shoots of the herb *A. sylvestris*. *Arrhenatherum elatius* was able to increase  
246 the number of rooting shoots per individual sown significantly with the logarithm of species  
247 richness of mixtures. The number of rooting shoots per individual sown of the remaining  
248 species did not change in response to species richness or the presence of *A. elatius* (Table 1).

249

### 250 *Vertical structure in relation to diversity*

251 **Effects of diversity at community level.** The cumulative cover of the experimental  
252 communities was higher in mixtures than in monocultures. This increase was mainly caused  
253 by the presence of *A. elatius* in mixtures, and we observed no further increase with increasing  
254 species richness of mixtures beyond two species (Table 1, Fig. 2a, b). Cumulative cover was  
255 significantly higher in May before first mowing than in August, but the effects of the diversity  
256 treatments did not depend on season (Table 1).

257 While community maximum height was significantly higher in mixtures than  
258 monocultures, community mean height did not differ significantly between monocultures and  
259 mixtures. Mixtures containing *A. elatius* had significantly higher maximum as well as mean  
260 heights (Table 1, Fig. 2c-f). In addition to the effect of this particular species, an increase of  
261 species richness affected these parameters in a positive way.

262 The analysis of strata-level density showed that the higher number of vertical pin contacts  
263 in mixtures was due to increased densities per 5-cm height layer across the whole vertical  
264 stand profile. Strata-level density was higher in mixtures than in monocultures. Besides  
265 positive effects of *A. elatius*, we found a further increase in strata-level densities with  
266 increasing species richness of mixtures beyond two species (Table 2, Fig. 3). These increases  
267 of strata-level density were most pronounced in the upper height strata (see interactions “Ae ×  
268 Stratum (linear)” and “SR × Stratum (linear)” in Table 2). All community parameters of

269 vertical stand structure were higher in May than in August, but the effects of species richness  
270 or the presence of *A. elatius* in the plant communities did not change with season (Table 1 and  
271 2).

272 **Effects of diversity on individual species.** Changes in spatial arrangement in response to  
273 diversity differed strongly among species. Two species, *A. elatius* and *D. glomerata*, were  
274 able to increase cumulative cover on a per-individual-sown basis across the species-richness  
275 gradient. Cumulative cover of *A. elatius* was higher in mixtures than in monocultures and  
276 increased even further with the logarithm of species richness (Table 1). The increasing  
277 cumulative cover of *A. elatius* was accompanied neither by changes in maximum height nor in  
278 mean height (Table 1). Strata-level analysis confirmed that increased densities of *A. elatius*  
279 were not related to a change in vertical distribution of this species (Table 2, Fig. 4a).

280 The difference between monoculture and mixtures was not significant for the cumulative  
281 cover of *D. glomerata*, but cumulative cover of this species increased with the logarithm of  
282 species richness after removing variance explained by the presence of *A. elatius* in mixtures  
283 (Table 1). The analysis of strata-level density gave evidence that space use of *D. glomerata* in  
284 more diverse communities was particularly increased in the upper strata (see interactions “M  
285 × Stratum (linear)”, “Ae × Stratum (linear)” and “SR × Stratum (linear)” in Table 2, Fig. 4b),  
286 although we did not find a significant increase of mean or maximum height of this species  
287 with increasing species richness of mixtures (Table 1).

288 Cumulative cover of *A. pratensis* and *P. pratense* did not differ significantly between  
289 monocultures and mixtures and was not affected either by the presence of *A. elatius* in  
290 mixtures or an increasing species richness of mixtures beyond two species (Table 1, Fig. 4c,  
291 d). Whereas we found a significant decrease in maximum and mean height of *A. pratensis*  
292 with a log-linear increase in species richness, these parameters did not change in response to  
293 species richness in *P. pratense*. However, the analysis of strata-level density indicated that

294 aboveground space use of *P. pratense* in the upper canopy layers increased more strongly in  
295 mixtures with *A. elatius* and with increasing species richness of the plant communities (see  
296 interactions “Ae × Stratum (linear)” and “SR × Stratum (linear)” in Table 2).

297 Cumulative cover of the remaining species was negatively affected either by growing in  
298 mixtures (*A. sylvestris*, *G. pratense*), the presence of *A. elatius* in the mixtures (*G. pratense*,  
299 *T. pratense*, *T. repens*) or an increasing species richness of mixtures (*P. trivialis*) (Table 1,  
300 Fig. 4e-i). The lower cumulative cover was accompanied by reduced maximum and mean  
301 heights. Maximum and mean heights of *A. sylvestris* and *G. pratense* decreased from  
302 monocultures to mixtures and even further with increasing species richness of mixtures  
303 (except for maximum height of *G. pratense*). Both variables also decreased significantly with  
304 increasing species richness for *P. trivialis*. The legumes *T. pratense* and *T. repens* had lower  
305 maximum (only *T. repens*) and mean heights in mixtures with *A. elatius*, while species  
306 richness had no significant effect on vertical space use of these species. Analysis of strata-  
307 level densities confirmed that species whose vertical density was affected negatively by  
308 community diversity had a more pronounced decrease in space use in the upper layers of the  
309 plant stands when they were growing in mixtures, in mixtures with *A. elatius* or with  
310 increasing species richness of mixtures (Table 2).

311 **Pairwise differences in mean height.** Pairwise comparisons of species mean heights gave  
312 further insight how species combinations affected vertical space use of individual species.  
313 *Arrhenatherum elatius*, the species with the largest mean height in monoculture, achieved in  
314 general relatively larger values in mixtures. In contrast, the difference between mean height of  
315 *A. pratensis*, which nearly had the same mean height as *A. elatius* in monoculture, and other  
316 species decreased in mixtures. The relation even reversed in the comparisons of *A. pratensis*  
317 with *P. pratense* or *D. glomerata* which obtained relatively larger values of mean height in  
318 mixtures. Significant relative changes of mean height were also found for other species pairs

319 (Table 3). The variety of response patterns to interspecific competition demonstrates that  
320 species height in monoculture was a poor predictor for the probability that a species reaches  
321 the upper strata of the vertical profile in mixtures (Fig. 5).

322

## 323 **Discussion**

324 Similar to a number of biodiversity experiments (see Hooper et al., 2005), we have shown  
325 in previous analyses that aboveground biomass production increases with species richness in  
326 our experiment composed of nine potentially dominant grassland species (Roscher et al.,  
327 2005). In the present study we analysed the relationship between biodiversity and  
328 aboveground space use and how individual species change their spatial arrangement to  
329 contribute to the response at the community level. Our analyses gave evidence that the use of  
330 aboveground space measured as community shoot density and as cumulative cover of the  
331 plant stands increased from monocultures to mixtures. The higher cumulative cover was  
332 attributable to both, an increase in vertical densities across the whole stand profile and  
333 increased height of the plant stands. In addition, we could show that the presence of individual  
334 species, in particular *A. elatius*, led to a further increase in cumulative cover, while an  
335 increase of species richness within mixtures did not result in significant changes of  
336 community vertical and horizontal density.

337 Spatial complementarity of plant species in natural grasslands is known from stands where  
338 subordinate species exploit successfully less favourable microhabitats such as under-storey  
339 vegetation (Grime, 1998). Tall-statured species obtain a higher fraction of incident photon  
340 flux density, but short-statured species use their biomass more efficiently to capture photons  
341 (Werger et al., 2002; Anten, 2005). We hypothesized that such mechanisms of  
342 complementary light use should be less important among potentially dominant species that  
343 normally do not grow as under-storey species. Our results confirmed this prediction: among



344 the selected potentially dominant species there was none that could assume the role of a  
345 subordinate in mixture with even more dominant species. Rather, only those of the nine  
346 species that could respond to competition by placing their parts into the upper canopy layers,  
347 and overtop neighbouring species that could not do so, were able to reach a high cumulative  
348 cover in mixtures.

349 In plant monocultures, the relative height of neighbouring individuals can predict the  
350 outcome of competition (Ford and Diggle, 1981), because larger plants receive a  
351 disproportionate share of light and are more likely to outcompete smaller plants (Weiner,  
352 1990). Our results indicate that this mechanism is important in our species pool as well.  
353 However, while canopy height is an important predictor for competitive dominance (Gaudet  
354 and Keddy, 1988; Mitchley, 1988; Mitchley and Willems, 1995), the relative height of species  
355 in mixtures was not predictable from their height growth in monocultures (Table 3, Fig. 5). In  
356 contrast to our results, Vojtech et al. (2007) found that levels of light intercepted in grass  
357 monocultures were a good indicator for competitive outcomes between species pairs, but this  
358 findings may be due to the shorter duration of their experiment (18 weeks).

359 *Arrhenatherum elatius* was able to overtop neighbours in mixtures and its vertical  
360 distribution of aboveground plant parts was characterized by the highest mean values in  
361 monocultures and mixtures (Fig. 5). This species was the only one that increased its  
362 abundance (number of rooting shoots) across the whole species richness gradient formed by  
363 the others, reaching the highest biomass values and overyielding in many mixtures (Roscher  
364 et al., 2007). The superiority of *A. elatius* could be explained by the exceptional growth form  
365 of this grass that forms sterile leafy stalks with elevated meristems (Pfitzenmeyer, 1962).  
366 Many grass species are characterized by a basal position of meristems on sterile shoots which  
367 limits their potential for vertical light foraging by leaves (Grime and Mackey, 2002).

368 A rich literature exists on the effects of light quality and quantity on adaptive changes of  
369 plant growth form. Gradients of light availability (photon flux density) and spectral light  
370 quality are developed within closed canopies (Monsi and Saeki, 1953; Jones, 1992). Changes  
371 in light quality perceived by phytochrome may control the activity of axillary buds, tillering  
372 and the formation of reproductive shoots in grass species (Deregibus et al., 1985; Casal et al.,  
373 1986). Abundance and height growth of the creeping legume *T. repens*, and the non-  
374 leguminous herbs *A. sylvestris* and *G. pratense* with predominantly horizontal leaves were  
375 affected negatively by species richness in our experiment. Plastic responses of individuals of  
376 herbaceous plants established under canopy shade conditions may be less pronounced than in  
377 individuals grown under sunlit conditions (McLaren and Smith, 1978). This effect could also  
378 apply for *A. sylvestris* and *G. pratense*, whose establishment was delayed in the experimental  
379 communities. Individuals often developed only basal rosettes. Radiation filtered by plant  
380 canopies reduces branching frequency and the number of nodes in *T. repens* (Solangaarachchi  
381 and Harper, 1987; Thompson and Harper, 1988; Markovitz and Turkington, 2000) and other  
382 stoloniferous species (Schmid, 1986) and would consequently lead to decreased abundances  
383 of such species. Thus, light quality does not only induce shade-avoidance reactions. It is also  
384 important for density regulation of plant populations and could be a reason why we found no  
385 effect of species richness on the number of rooting shoots within mixtures.

386 Spehn et al. (2000) showed in another biodiversity experiment (Swiss site of BIODEPTH  
387 study) that height growth of individuals of several species increased with increasing species  
388 richness, while Dimitrakopoulos and Schmid (2004) and Mwangi et al. (2007) found little  
389 effects of species richness on height growth. In our study species richness did not affect  
390 maximum or mean height of individual species in a positive way. In contrast, height growth  
391 of five out of nine species was affected negatively either by species richness or the presence  
392 of *A. elatius* in mixtures. This result could be a consequence of species selection. Whereas

393 both potentially dominant and subordinate species occurred in the species pool of previous  
394 experiments, we only used potential dominants that proved to have a low ability for adaptive  
395 morphological changes in response to vegetation shade.

396 Recently Yachi and Loreau (2007) presented a model of light competition in multi-species  
397 plant communities. They emphasized the importance of competitive balance among species  
398 for a positive net effect of complementary resource use. In our experiment, the most  
399 competitive species, *A. elatius*, and increasing species richness had negative effects on  
400 inferior species. However, the beneficial effects of competitive release for *A. elatius* itself in  
401 mixtures with interspecific neighbors overcompensated for negative effects of competitive  
402 imbalance on some species, while other species showed little response to species richness. In  
403 conclusion, changes in vertical niche occupation in mixtures are either the result of  
404 competitive release for the superior species or of competitive suppression. These effects lead  
405 to an enhanced and complementary use of available space at the community level although  
406 the potential for alternative strategies of light exploitation appeared to be limited among  
407 potentially dominant species.

408

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417

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590

591 **Appendix**

592 The number of plots entering in different levels of the ANOVA is not equal because all  
593 species-richness levels were studied in August and data in monocultures, two- and nine-  
594 species mixtures only were recorded in May. The main effects (monoculture vs. mixture,  
595 presence of *A. elatius*, species richness as log-linear term) were tested across all species  
596 richness-levels (including monocultures, 2-, 3-, 4-, 6- and 9-species mixtures). This part of the  
597 analysis comprises 103 plots (= 100 different compositions because we analysed 4 identical  
598 replicates of the 9-species mixture) in total. The total number of compositions (= 100) served  
599 as error term. The analysis of seasonal effects is complicated because not all compositions  
600 were measured in May. Thus, 49 plots (= 46 different compositions because we analysed 4  
601 identical replicates of the 9-species mixture) had data for May and August, whereas the  
602 remaining ones only had data for August. As a consequence of this imbalance, the effects of  
603 “season” and their interaction with the diversity treatments appear at different levels of the  
604 ANOVA table. According to Heiberger (1989) we used the lower level of appearance of these  
605 variables to test for significance. Nevertheless, the appearance of these variables affects the  
606 mean squares of the error term at the upper level. We excluded these terms from the upper  
607 level. The variable height “stratum” was fitted as linear term and as deviation from linearity  
608 (factor). It has seven factor levels according to the following height strata: 0–5 cm, 5–10 cm,  
609 10–20 cm, 20–30 cm, 30–50 cm, 50–70 cm, >70 cm. Mean values per height level were used  
610 for the linear term (2.5, 7.5, 15.0, 25.0, 40.0, 60.0, 100.0). The effects were tested across all  
611 species-richness levels (including monocultures, 2-, 3-, 4-, 6- and 9-species mixtures). The  
612 mean squares of the error terms (C1, C2, C3) of the different analysis strata were calculated in  
613 the hierarchical ANOVA with treatment and error model (see e.g. Schmid et al. 2002). The  
614 residuals come from the use of 4 (out of 8) identical replicates of the 9-species mixtures  
615 (during each sampling campaign), while we did not analyse identical replicates of the other  
616 mixtures (= compositions).

Table S1: Skeleton analysis of variance for community and species data analyzed at stand level (center) or at the level of vertical height strata (right); (a) degrees of freedom (d.f.) for analyses of community data, (b) d.f. for analyses of species data. For the analysis on the right d.f.s for terms including height stratum were lower for species which did not occur in all strata.

Source of variation	Stand analysis				Strata level analysis			
	d.f. (a)	d.f. (b)	Mean square	Variance ratio	d.f. (a)	d.f. (b)	Mean square	Variance ratio
Mixture (M)	1	1	MS <sub>M</sub>	MS <sub>M</sub> /MS <sub>C1</sub>	1	1	MS <sub>M</sub>	MS <sub>M</sub> /MS <sub>C1</sub>
Presence of <i>Arrhenatherum elatius</i> (Ae)	1	1	MS <sub>Ae</sub>	MS <sub>Ae</sub> /MS <sub>C1</sub>	1	1	MS <sub>Ae</sub>	MS <sub>Ae</sub> /MS <sub>C1</sub>
Species richness (log-linear) (SR)	1	1	MS <sub>SR</sub>	MS <sub>SR</sub> /MS <sub>C1</sub>	1	1	MS <sub>SR</sub>	MS <sub>SR</sub> /MS <sub>C1</sub>
Composition (C1)	96	30	MS <sub>C1</sub>		96	30	MS <sub>C1</sub>	
Season (S)	1	1	MS <sub>S</sub>	MS <sub>S</sub> /MS <sub>C2</sub>	1	1	MS <sub>S</sub>	MS <sub>S</sub> /MS <sub>C2</sub>
Mixture x Season (M x S)	1	1	MS <sub>MxS</sub>	MS <sub>MxS</sub> /MS <sub>C2</sub>	1	1	MS <sub>MxS</sub>	MS <sub>MxS</sub> /MS <sub>C2</sub>
<i>A. elatius</i> x Season (Ae x S)	1	1	MS <sub>AexS</sub>	MS <sub>AexS</sub> /MS <sub>C2</sub>	1	1	MS <sub>AexS</sub>	MS <sub>AexS</sub> /MS <sub>C2</sub>
Species richness (log-linear) x Season (SR x S)	1	1	MS <sub>SRxS</sub>	MS <sub>SRxS</sub> /MS <sub>C2</sub>	1	1	MS <sub>SRxS</sub>	MS <sub>SRxS</sub> /MS <sub>C2</sub>
Composition (C2) (nested within season)	41	6	MS <sub>C2</sub>		41	6	MS <sub>C2</sub>	
Stratum (H1) as linear contrast					1	1	MS <sub>H1</sub>	MS <sub>H1</sub> /MS <sub>C3</sub>
Stratum (H2) as deviation from linearity					5	≤ 5	MS <sub>H2</sub>	MS <sub>H2</sub> /MS <sub>C3</sub>
Mixture x stratum (linear) (M x H1)					1	1	MS <sub>MxH1</sub>	MS <sub>MxH1</sub> /MS <sub>C3</sub>
Mixture x stratum (deviation from linearity) (M x H2)					5	≤ 5	MS <sub>MxH2</sub>	MS <sub>MxH2</sub> /MS <sub>C3</sub>
<i>A. elatius</i> x stratum (linear) (Ae x H1)					1	1	MS <sub>AexH1</sub>	MS <sub>AexH1</sub> /MS <sub>C3</sub>
<i>A. elatius</i> x stratum (deviation from linearity) (Ae x H2)					5	≤ 5	MS <sub>AexH2</sub>	MS <sub>AexH2</sub> /MS <sub>C3</sub>
Species richness (log-linear) x stratum (linear) (SR x H1)					1	1	MS <sub>SRxH1</sub>	MS <sub>SRxH1</sub> /MS <sub>C3</sub>
Species richness (log-linear) x stratum (deviation from linearity) (SR x H2)					5	≤ 5	MS <sub>SRxH2</sub>	MS <sub>SRxH2</sub> /MS <sub>C3</sub>
Season x stratum (linear) (S x H1)					1	1	MS <sub>SxH1</sub>	MS <sub>SxH1</sub> /MS <sub>C3</sub>
Season x stratum (deviation from linearity) (S x H2)					5	≤ 5	MS <sub>SxH2</sub>	MS <sub>SxH2</sub> /MS <sub>C3</sub>
Composition (C3) (nested within season and stratum)					840	≤ 234	MS <sub>C3</sub>	
Residuals	6	6	MS <sub>R</sub>		42	42	MS <sub>R</sub>	

Table 1: Effects of species richness and season on horizontal density and measures of vertical stand architecture of entire plant communities and of individual species within these mixtures.

Listed are F ratios and the levels of significance, where \*:  $P \leq 0.05$ , \*\*:  $P < 0.01$ , and \*\*\*:  $P < 0.001$ . Arrows indicate significant increase (↑) or decrease (↓) of the measures in mixtures compared with monocultures (M), in mixtures with compared with mixtures without *A. elatius* (Ae) or with a logarithmic increase in species richness (SR). M after season means significantly higher values of the measure in May than in August.

	Community	<i>A. pratensis</i>	<i>A. sylvestris</i>	<i>A. elatius</i>	<i>D. glomerata</i>	<i>G. pratense</i>	<i>P. pratense</i>	<i>P. trivialis</i>	<i>T. pratense</i>	<i>T. repens</i>
<i>Horizontal density (line transect data)</i>										
Mixture (M)	7.26** ↑	<0.01	2.32	0.13	3.15	1.11	0.05	0.10	0.14	0.89
Presence <i>A. elatius</i> (Ae)	25.86*** ↑	2.33	0.59		0.20	0.31	0.80	0.11	9.07** ↓	12.92*** ↓
Species richness (SR)	0.01	0.07	5.37* ↓	9.25** ↑	3.46	0.29	0.11	2.43	2.45	0.71
<i>Cumulative cover (point intercept data)</i>										
Mixture (M)	15.92*** ↑	0.03	18.35*** ↓	11.92** ↑	2.00	9.75** ↓	0.44	<0.01	0.18	1.99
Presence <i>A. elatius</i> (Ae)	37.77*** ↑	0.01	0.81		1.02	4.79* ↓	2.61	1.45	6.89* ↓	25.49*** ↓
Species richness (SR)	1.73	2.29	3.28	15.18*** ↑	13.32*** ↑	2.86	2.54	4.32** ↓	0.02	2.38
Season	67.94*** M	9.95* M	0.16	16.39*** M	0.55	0.22	217.53*** M	162.44*** M	9.95* M	11.77* M
M x Season	2.29	0.66	<0.01	1.82	0.20	<0.01	14.14**	0.04	0.17	0.14
Ae x Season	0.09	0.01	0.11		2.65	1.27	72.17***	12.12*	0.14	1.32
SR x Season	0.05	2.90	<0.01	10.22*	15.95**		16.59**	4.42	0.02	0.06
<i>Maximum height</i>										
Mixture (M)	6.84**↑	2.24	6.95* ↓	0.57	1.35	5.44* ↓	0.54	1.27	1.79	2.10
Presence <i>A. elatius</i> (Ae)	84.00***↑	0.21	0.74		0.05	1.63	1.80	0.05	2.80	26.32*** ↓
Species richness (SR)	7.65**↑	16.05*** ↓	7.33* ↓	2.09	1.62	3.92	0.80	5.68* ↓	0.57	2.48
Season	80.69***M	106.70***M	0.21	73.11*** M	1175.35*** M	0.38	205.92*** M	78.59*** M	2.08	30.81*** M
M x Season	0.06	1.23	0.02	2.13	12.22*	0.06	1.84	0.28	0.29	0.07
Ae x Season	1.62	3.79	0.02		<0.01	0.71	2.77	5.42	10.54*	4.80
SR x Season	0.06	0.13	0.15	0.04	2.95		3.17	1.84	2.49	0.22
<i>Mean height</i>										
Mixture (M)	2.17	1.69	5.82* ↓	<0.01	1.23	4.87* ↓	0.24	0.89	0.31	1.22

Presence <i>A. elatius</i> (Ae)	62.12***↑	0.19	0.88		0.13	2.18	0.55	<0.01	6.18* ↓	13.79*** ↓
Species richness (SR)	11.50***↑	9.98** ↓	6.55* ↓	0.14	1.42	5.40* ↓	0.80	4.28* ↓	2.30	1.18
Season	92.55***M	228.74***M	0.34	151.26*** M	729.50***M	0.54	372.06*** M	59.01*** M	17.69** M	14.73** M
M x Season	0.19	2.01	0.04		0.16	0.04	0.07	0.42	11.43*	0.44
Ae x Season	0.33	3.87	0.04	0.23	7.80*	0.12	3.46	5.24	12.70*	4.00
SR x Season	<0.01	0.32	0.23	1.01	0.19		0.47	0.93	4.44	0.03

Table 2: Effects of species richness, season and height stratum on vertical density of the community and of individual species. Listed are F ratios and the levels of significance, where \*:  $P \leq 0.05$ , \*\*:  $P < 0.01$ , and \*\*\*:  $P < 0.001$ . Arrows indicate significant increase (↑) or decrease (↓) of the measures in mixtures compared with monocultures (M), in mixtures with compared with mixtures without *A. elatius* (Ae) or with a logarithmic increase in species richness (SR). M after season means significantly higher values of the measure in May than in August.

	Community	<i>A. pratensis</i>	<i>A. sylvestris</i>	<i>A. elatius</i>	<i>D. glomerata</i>	<i>G. pratense</i>	<i>P. pratense</i>	<i>P. trivialis</i>	<i>T. pratense</i>	<i>T. repens</i>
<i>Strata-level interval density</i>										
Mixture (M)	13.21** ↑	0.22	16.95*** ↓	6.52* ↑	0.07	17.09*** ↓	<0.01	0.27	0.64	3.38
<i>A. elatius</i> (Ae)	79.89*** ↑	1.04	0.85		1.88	5.64* ↓	3.77	0.98	8.25** ↓	30.85*** ↓
Species richness (SR)	6.21* ↑	8.53** ↓	4.68* ↓	3.91	1.88	3.58	0.27	2.32	0.63	4.25* ↓
Season (S)	142.48*** M	51.03***	0.07	35.17*** M	48.18*** M	<0.01	228.85*** M	264.46*** M	15.95** M	26.15** M
M x Season	3.99	0.41	<0.01	1.40	0.06	0.01	6.43*	0.17	0.70	0.10
Ae x Season	0.08	1.90	0.12		4.27	0.70	8.17*	17.13**	0.44	2.63
SR x Season	0.01	2.20	0.04	17.47**	6.02*		15.02**	1.33	0.01	0.31
Stratum (linear) (H1)	1420.28***	322.88***	11.47***	192.44***	870.86***	12.85***	300.83***	179.64***	196.56***	271.73***
Stratum (deviation from linearity) (H2)	40.58***	30.28***	0.35	56.32***	56.76***	6.96***	12.30***	17.64***	15.22***	4.28**
M x Stratum (linear) (H1)	3.77	3.09	21.61*** ↓	1.02	7.82** ↑	3.72	0.57	0.37	0.14	4.31* ↓
M x Stratum (deviation from linearity) (H2)	0.97	0.06	3.49	0.29	0.66	0.37	0.18	0.19	0.20	0.28
Ae x Stratum (linear) (H1)	46.57*** ↑	1.19	0.71		6.01* ↑	3.50	20.32*** ↑	0.66	8.19** ↓	68.51*** ↓
Ae x Stratum (deviation from linearity) (H2)	33.01***	2.38*	0.41		2.29*	0.38	3.04*	0.40	0.73	1.30
SR x Stratum (linear) (H1)	28.76*** ↑	0.02	4.73* ↓	2.13	21.81*** ↑	1.33	5.57* ↑	16.25*** ↓	0.07	5.56* ↓
SR x Stratum (deviation from linearity) (H2)	6.30***	1.00	0.21	0.97	3.60**	1.06	1.85	0.90	1.50	0.15
S x Stratum (linear) (H1)	151.78***	78.74***	0.24	300.86***	277.89***	0.47	63.24***	50.33***	0.04	1.28
S x Stratum (deviation from linearity) (H2)	18.44***	13.61***	0.90	9.35***	37.18***	0.35	53.85***	8.43***	0.68	5.92***

Table 3: Differences of mean height (MH) for each species pair. Values are based on data recorded in monocultures, two- and nine-species mixtures in May 2003. Differences between species monocultures were used to compare average height differences between species in mixture. Negative values indicate that species in the respective column achieved a lower mean height in comparison to the species in the respective row. Asterisks indicate significant differences between monocultures and mixtures (\*:  $P \leq 0.05$ , \*\*:  $P < 0.01$ ; t-tests). Arrows show significant increase ( $\uparrow$ ) or decrease ( $\downarrow$ ) of the measures in mixtures compared to monocultures.

	<i>A. elatius</i>	<i>A. pratensis</i>	<i>D. glomerata</i>	<i>P. pratense</i>	<i>G. pratense</i>	<i>P. trivialis</i>	<i>T. pratense</i>	<i>T. repens</i>
<i>Alopecurus pratensis</i>								
Monoculture	0.57							
Mixture	31.72* $\uparrow$							
<i>Dactylis glomerata</i>								
Monoculture	4.65	4.08						
Mixture	21.65* $\uparrow$	-9.15						
<i>Phleum pratense</i>								
Monoculture	8.40	7.83	3.75					
Mixture	21.18* $\uparrow$	-10.23* $\downarrow$	-0.16					
<i>Geranium pratense</i>								
Monoculture	19.09	18.52	14.44	10.69				
Mixture	54.74* $\uparrow$	18.07	31.15** $\uparrow$	28.48** $\uparrow$				
<i>Poa trivialis</i>								
Monoculture	25.65	15.08	21.01	17.25	6.57			
Mixture	34.14	6.21	14.73	14.47	-12.46			
<i>Trifolium pratense</i>								
Monoculture	27.55	26.98	22.90	19.15	8.46	1.89		
Mixture	43.69	11.97* $\downarrow$	22.07	21.07	-10.64** $\uparrow$	8.25		
<i>Trifolium repens</i>								
Monoculture	30.97	30.39	26.32	22.57	11.88	5.31	3.42	
Mixture	52.39* $\uparrow$	19.03	29.64	29.35	1.38* $\downarrow$	16.22	10.83	
<i>Anthriscus sylvestris</i>								
Monoculture	35.22	34.65	30.57	26.82	16.13	9.56	7.67	4.25
Mixture	56.41* $\uparrow$	27.00	35.58	35.79** $\uparrow$	5.41** $\downarrow$	21.24* $\uparrow$	12.72	4.11



Figure captions

Figure 1: Number of rooting shoots as function of species richness (log-scale). Plots with *A. elatius* are shown with filled circles; plots without *A. elatius* are shown with open circles. The lines connect arithmetic means calculated for each species-richness level (solid line = plots with *A. elatius*, broken line = plots without *A. elatius*).

Figure 2: Cumulative cover (a, b), maximum height of pin contacts (c, d), and mean height of pin contacts (e, f) recorded in May (left panel) and August 2003 (right panel) as a function of species richness (log-scale). Plots with *A. elatius* are shown with filled circles; plots without *A. elatius* are shown with open circles. The lines are arithmetic means for all assemblages per diversity level (solid line = plots with *A. elatius*, broken line = plots without *A. elatius*).

Figure 3: Vertical density (number of pin contacts per 5-cm height layer per pin) for the three species-richness levels measured both in May (a) and August 2003 (b): monocultures = dotted lines, two-species-mixtures = broken lines, nine-species-mixtures = solid lines. Horizontal lines show average mean height.

Figure 4: Vertical density (number of pin contacts per 5-cm height layer per pin, corrected for reduced species proportions in mixtures by multiplication with species richness) for individual species in May: monocultures = dotted lines, two-species mixtures = broken lines, nine-species mixtures = solid lines. Horizontal lines show average mean height.

Figure 5: Species mean height in mixtures plotted against species mean height in monoculture for data recorded in May in monocultures, two- and nine-species mixtures. Points above the

Lorentzen et al.

broken line indicate cases where individual species obtained larger mean heights in mixtures than in monoculture.

Abbreviations of species names: ae = *Arrhenatherum elatius*, ap = *Alopecurus pratensis*, as = *Anthriscus sylvestris*, dg = *Dactylis glomerata*, gp = *Geranium pratense*, pp = *Phleum pratense*, pt = *Poa trivialis*, tp = *Trifolium pratense*, tr = *Trifolium repens*.

Figure 1

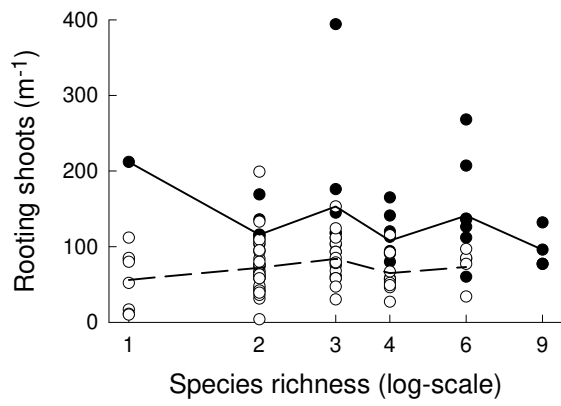


Figure 2

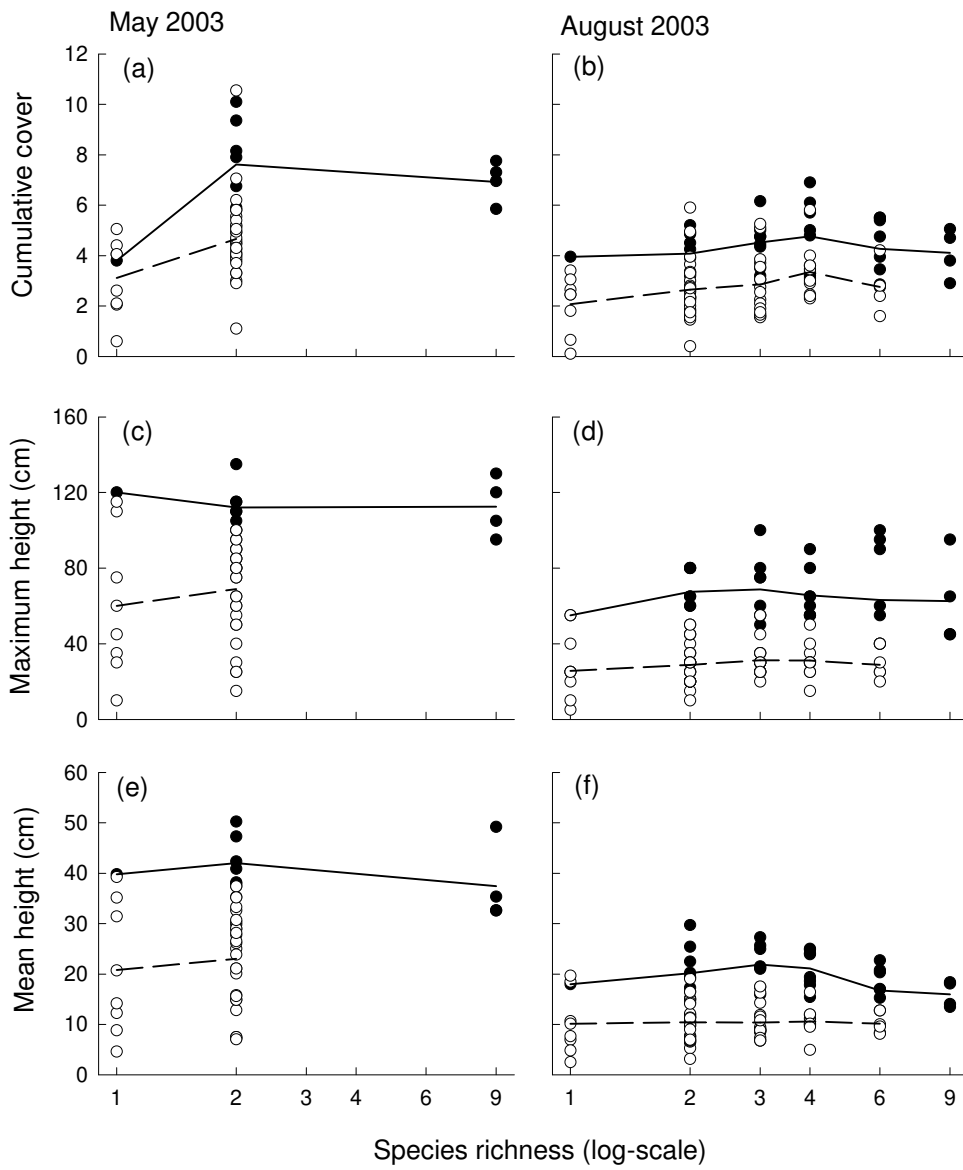


Figure 3

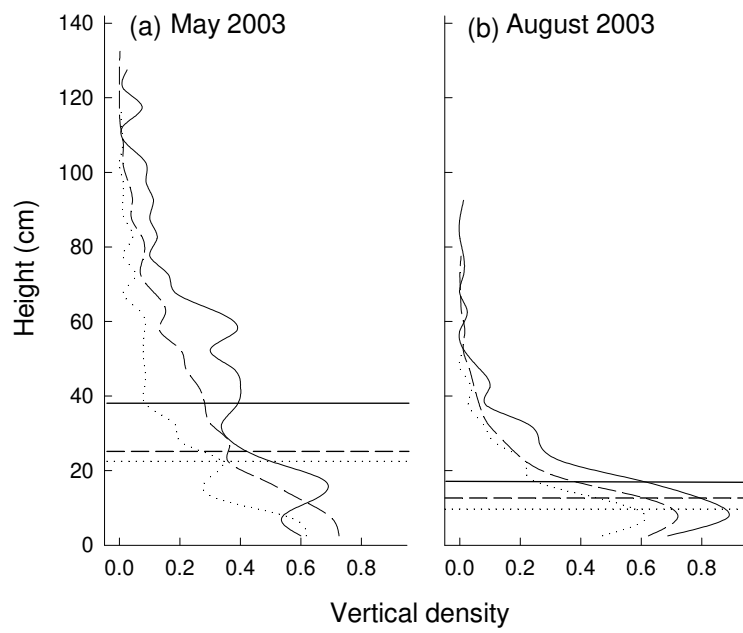


Figure 4

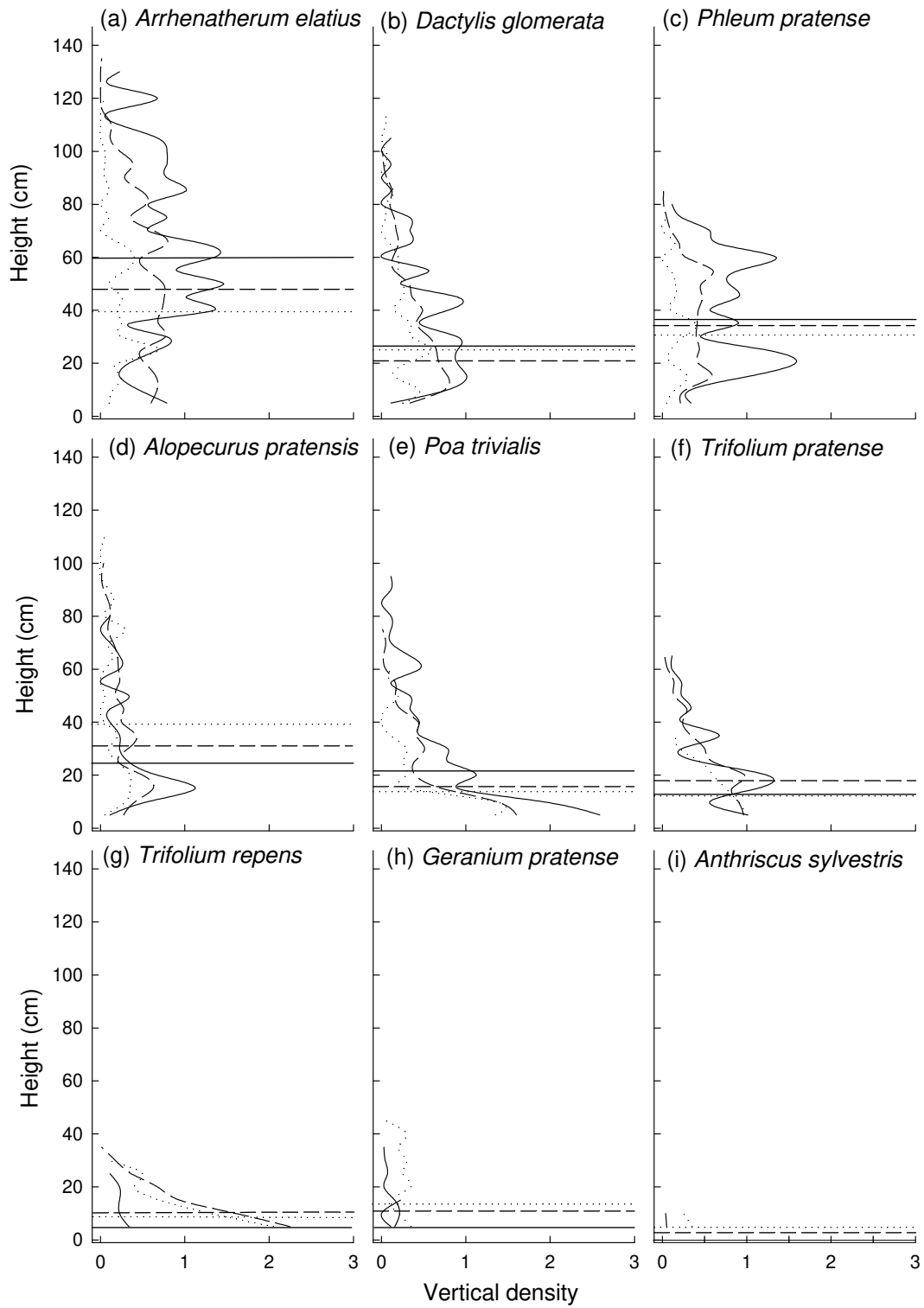


Figure 5

