

 Open access • Journal Article • DOI:10.1007/S00442-010-1735-9

Legume species differ in the responses of their functional traits to plant diversity

— [Source link](#) 

Christiane Roscher, Bernhard Schmid, Nina Buchmann, Alexandra Weigelt ...+2 more authors





Institutions: Max Planck Society, University of Zurich, ETH Zurich, University of Jena ...+1 more institutions

Published on: 01 Feb 2011 - Oecologia (Springer-Verlag)

Topics: Biodiversity, Biomass (ecology), Onobrychis viciifolia and Abundance (ecology)

Related papers:

- [Differential effects of plant diversity on functional trait variation of grass species.](#)
- [The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community](#)
- [Plasticity of functional traits of forb species in response to biodiversity](#)
- [Quantifying the evidence for biodiversity effects on ecosystem functioning and services.](#)
- [Let the concept of trait be functional](#)

Share this paper:    

View more about this paper here: <https://typeset.io/papers/legume-species-differ-in-the-responses-of-their-functional-frzyi7ibpj>



Year: 2011

Legume species differ in the responses of their functional traits to plant diversity

Roscher, C ; Schmid, B ; Buchmann, N ; Weigelt, A ; Schulze, E D

Abstract: Plants can respond to environmental impacts by variation in functional traits, thereby increasing their performance relative to neighbors. We hypothesized that trait adjustment should also occur in response to influences of the biotic environment, in particular different plant diversity of the community. We used 12 legume species as a model and assessed their variation in morphological, physiological, life-history and performance traits in experimental grasslands of different plant species (1, 2, 4, 8, 16 and 60) and functional group (1–4) numbers. Mean trait values and their variation in response to plant diversity varied among legume species and from trait to trait. The tall-growing *Onobrychis viciifolia* showed little trait variation in response to increasing plant diversity, whereas the species with shorter statures responded in apparently adaptive ways. The formation of longer shoots with elongated internodes, increased biomass allocation to supporting tissue at the cost of leaf mass, reduced branching, higher specific leaf areas and lower foliar $\delta^{13}\text{C}$ values indicated increasing efforts for light acquisition in more diverse communities. Although leaf nitrogen concentrations and shoot biomass:nitrogen ratios were not affected by increasing plant diversity, foliar $\delta^{15}\text{N}$ values of most legumes decreased and the application of the ^{15}N natural abundance method suggested that they became more reliant on symbiotic N_2 fixation. Some species formed fewer inflorescences and delayed flowering with increasing community diversity. The observed variation in functional traits generally indicated strategies of legumes to optimize light and nutrient capturing, but they were largely speciesdependent and only partly attributable to increasing canopy height and community biomass with increasing plant diversity. Thus, the analysis of individual plant species and their adjustment to growth conditions in communities of increasing plant diversity is essential to get a deeper insight into the mechanisms behind biodiversity–ecosystem functioning relationships.

DOI: <https://doi.org/10.1007/s00442-010-1735-9>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-42712>

Journal Article

Accepted Version

Originally published at:

Roscher, C; Schmid, B; Buchmann, N; Weigelt, A; Schulze, E D (2011). Legume species differ in the responses of their functional traits to plant diversity. *Oecologia*, 165(2):437-452.

DOI: <https://doi.org/10.1007/s00442-010-1735-9>

1 **Legume species differ in the responses of their functional traits to plant**
2 **diversity**

3

4 Christiane Roscher¹, Bernhard Schmid², Nina Buchmann³, Alexandra Weigelt^{4,5}, Ernst-Detlef
5 Schulze¹

6

7 ¹ Max Planck Institute for Biogeochemistry, POB 100164, D-07701 Jena, Germany

8 ² Institute of Evolutionary Biology and Environmental Studies, University of Zurich,
9 Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

10 ³ Institute of Plant, Animal and Agrosystems Sciences, ETH Zurich, Universitätsstrasse 2,
11 CH-8092 Zurich, Switzerland

12 ⁴ Institute of Ecology, Friedrich Schiller University Jena, Dornburger Strasse 159, D-07743
13 Jena, Germany

14 ⁵ present address: University of Leipzig, Institute of Biology I, Johannisallee 21-23, D-04103
15 Leipzig, Germany

16

17 **Correspondence:** Christiane Roscher, Max Planck Institute for Biogeochemistry, POB
18 100164, D-07701 Jena

19 Phone: ++49 3641 576227; Fax: ++49 3641 577100; Email: croscher@bgc-jena.mpg.de

20

21

22 **MS details:** 292 words in abstract, 8233 words in full text, 4 figures, 3 tables, Supplementary
23 Material

24

25

26 **Abstract**

27 Plants can respond to environmental impacts by variation in functional traits, thereby
28 increasing their performance relative to neighbors. We hypothesized that trait adjustment
29 should also occur in response to influences of the biotic environment, in particular different
30 plant diversity of the community. We used 12 legume species as a model and assessed their
31 variation in morphological, physiological, life-history and performance traits in experimental
32 grasslands of different plant species (1, 2, 4, 8, 16 and 60) and functional group (1 to 4)
33 numbers. Mean trait values and their variation in response to plant diversity varied among
34 legume species and from trait to trait. The tall-growing *Onobrychis viciifolia* showed little
35 trait variation in response to increasing plant diversity, whereas the species with shorter
36 statures responded in apparently adaptive ways. The formation of longer shoots with
37 elongated internodes, increased biomass allocation to supporting tissue at the cost of leaf
38 mass, reduced branching, higher specific leaf areas and lower foliar $\delta^{13}\text{C}$ values indicated
39 increasing efforts for light acquisition in more diverse communities. Although leaf nitrogen
40 concentrations and shoot biomass:nitrogen ratios were not affected by increasing plant
41 diversity, foliar $\delta^{15}\text{N}$ values of most legumes decreased and the application of the ^{15}N natural
42 abundance method suggested that they became more reliant on symbiotic N_2 fixation. Some
43 species formed fewer inflorescences and delayed flowering with increasing community
44 diversity. The observed variation in functional traits generally indicated strategies of legumes
45 to optimize light and nutrient capturing, but they were largely species-dependent and only
46 partly attributable to increasing canopy height and community biomass with increasing plant
47 diversity. Thus, the analysis of individual plant species and their adjustment to growth
48 conditions in communities of increasing plant diversity is essential to get a deeper insight into
49 the mechanisms behind biodiversity–ecosystem functioning relationships.

50

51 **Key words:** biodiversity, functional traits, legumes, species identity, trait variation

52 **Introduction**

53 Growing awareness of widespread reductions in species diversity during the last decades has
54 stimulated intensive research on the consequences of these changes on ecosystem functioning.
55 A number of experimental studies in grassland ecosystems suggest strong and consistent
56 positive effects of biodiversity on several ecosystem processes, e.g. primary productivity or
57 nutrient cycling (see reviews in Hooper et al. 2005, Balvanera et al. 2006). In spite of
58 evidence that complementarity among species contributes to positive biodiversity–ecosystem
59 functioning relationships (Cardinale et al. 2007), the biological mechanisms subsumed under
60 the term “complementarity” are not well understood. Diversity in functional characteristics is
61 generally regarded to increase complementary use of essential resources such as light, water,
62 carbon dioxide, minerals, and space among plant species in a community (Walker et al. 1999,
63 Díaz and Cabido 2001). Resource-use efficiency measured at the community level on average
64 increases with species richness and results in increased community biomass, canopy density
65 and height (Spehn et al. 2000, Lorentzen et al. 2008) and soil nutrient exploitation (Palmberg
66 et al. 2005, Oelmann et al. 2007). However, not all species contribute equally to the overall
67 positive effects of biodiversity on primary productivity, rather some species may overyield
68 whereas others may underyield in plant communities of increasing diversity (e.g. Hector et al.
69 2002, van Ruijven and Berendse 2003, Roscher et al. 2007).

70 Species performance is the net result of a number of morphological, physiological and
71 phenological traits (= functional traits) operating from the cell to whole-plant level (Violle et
72 al. 2007). Environment-induced trait variation (= phenotypic plasticity) is well known as the
73 strategy by which plants maximize their performance under different abiotic and biotic
74 conditions (e.g. Bradshaw 1965, Schlichting 1986, Schmid 1990). Nevertheless, adjustment of
75 a trait is not necessarily adaptive, because it may be due to genetic correlation with other traits
76 or may be a consequence of passive reductions in growth due to resource limitations (van

77 Kleunen and Fischer 2005). According to the “optimal allocation theory” (Bloom et al. 1985,
78 McConnaughay and Coleman 1999), plants tend to adjust their allocation and invest a higher
79 proportion to organs that optimize the acquisition of the most limiting resource. In addition,
80 perennial species often reduce their allocation into reproductive structures in response to
81 resource limitation (Chiariello and Gulmon 1991).

82 So far the relationship between plant community diversity and variation in plant functional
83 traits has attracted little attention in the increasing effort to understand the positive effects of
84 plant species diversity on ecosystem processes (Callaway 2007). In the present study carried
85 out in a large biodiversity experiment located on a nutrient-rich floodplain site (Jena
86 Experiment, Roscher et al. 2004) we focus on legumes, which are often considered as a
87 relatively homogeneous plant functional group in grasslands. They are unique in their ability
88 to fix symbiotically atmospheric nitrogen. Several biodiversity experiments have shown that
89 legumes are keystone species in generating the observed biodiversity effects on ecosystem
90 processes (Hooper et al. 2005). Nevertheless, effects associated with legume presence are
91 highly variable, probably due to the identity of particular legume species and different
92 environmental conditions (Spehn et al. 2002). In temperate grasslands, light and nutrients are
93 among the most limiting factors that affect plant growth. Increasing canopy height and
94 productivity at the community level with increasing species richness alter the amount and
95 quality of available resources for individual species within these communities. Although
96 legumes do not directly depend on the available soil nitrogen, the rates of energy-demanding
97 N₂ fixation may be reduced under high soil nitrogen supply (Marschner 1995). Thus, we
98 recorded data on shoot morphology, biomass allocation to different aboveground plant organs
99 and measured leaf and shoot nitrogen concentrations as traits which were supposed to reflect
100 strategies of light and nitrogen acquisition and retention by individual plants and may indicate
101 changes in the growth environment. We used foliar C isotope ratios ($\delta^{13}\text{C}$) as integrated long-

102 term measure of photosynthetic activity and stomatal conductance, which depend on light
103 availability, air humidity and plant nutritional status (Farquhar et al. 1989). We determined
104 foliar N isotope ratios ($\delta^{15}\text{N}$) and applied the ^{15}N natural abundance method (Amarger et al.
105 1979) to assess plant diversity effects on N_2 fixation in legumes. In addition, we studied
106 legume plant characteristics that may serve as indicators for plant individual performance
107 such as shoot biomass or number of inflorescences. We related these plant characteristics to
108 plant diversity — in terms of species and functional group richness — and community
109 characteristics — in terms of canopy height and community biomass. We tested the following
110 hypotheses: (1) Increasing plant diversity affects variation in trait values associated with
111 strategies in light and nitrogen acquisition and retention. (2) Plant diversity effects are partly
112 but not fully mediated by concomitant increases in community biomass and canopy height.
113 (3) Plant diversity effects on trait variation vary among legume species, suggesting different
114 strategies of species to respond to their biotic environment in ways which may increase
115 complementary resource use.

116

117 **Material and methods**

118

119 *Experimental set-up*

120 The study was carried out as part of the Jena Experiment, a large integrated biodiversity
121 experiment started in 2002 (Roscher et al. 2004). The experimental site lies in the floodplain
122 of the river Saale near to the city of Jena (Thuringia, Germany, 50°55'N, 11°35'E, 130 m
123 a.s.l.) and was used as an agricultural field for 40 years prior to the establishment of the
124 biodiversity experiment. The area around Jena has a mean annual air temperature of 9.3 °C
125 and a mean annual precipitation of 587 mm (Kluge and Müller-Westermeier 2000). The soil
126 of the experimental site is a Eutric Fluvisol developed from up to 2 m thick loamy fluvial

127 sediments. Due to flooding dynamics, soil texture ranges from sandy loam near the river to
128 silty clay with increasing distance from the river.

129 Sixty grassland species typically occurring in Central European semi-natural, species-rich
130 grasslands (*Arrhenatherion* alliance according to the vegetation classification of Ellenberg,
131 1988) were selected as species pool for the experiment. Species were divided into four
132 functional groups following the results of a cluster analysis with a literature-based trait
133 matrix: grasses (16 species), legumes (12 species), small herbs (12 species) and tall herbs (20
134 species). The design of the Jena Experiment ensures that the presence/absence of each
135 functional group (FG) is minimally confounded with species number (SR, see Roscher et al.
136 2004). In total, the main experiment comprises 82 plots of 20×20 m size: 16 monocultures (1
137 FG), 16 two-species mixtures (1 or 2 FG), 16 four-species mixtures (1 to 4 FG), 16 eight-
138 species mixtures (1 to 4 FG), 14 sixteen-species mixtures (1 to 4 FG) and four replicates with
139 a mixture of the complete species pool. The number of replicates with sixteen species was
140 lower because pure legume or small herb mixtures were not possible at this species-richness
141 level. Particular species compositions were compiled by independent random draws with
142 replacement. In addition, all species were established in replicated monocultures of 3.5×3.5
143 m. Sown density aimed to establish 1000 seedlings per m^2 in a substitutive design, in which
144 constant total density was achieved by reducing sowing densities of individual species
145 according to the number of species in the mixture (Jolliffe 2000). Number of sown seeds was
146 adjusted for germination rates from preliminary laboratory tests. Plots were grouped into four
147 blocks parallel to the river, each of them containing the same number of experimental
148 communities per species-richness level. All plots were mown twice a year in early June and
149 September corresponding to the typical management regime for extensive meadows in the
150 region and were not fertilized during the experimental period. Plots were weeded twice per
151 growing season when the vegetation was low and the canopy not completely closed (early

152 April at the beginning of the growing season and early July after mowing). For further details
153 see Roscher et al. (2004).

154

155 ***Data collection***

156 In this study we analysed all legume species belonging to the experimental species pool
157 (Table 1). Plant modules (individual shoots) served as basic unit for all measurements because
158 the ability of some legume species to grow with above- or belowground runners hampers a
159 distinction of plant genets in dense vegetation. Modules are defined as plant parts that would
160 be able to grow independently if separated from the genet, the plant individual derived from a
161 sexually produced seed (Harper 1977, Schmid 1990). The section of a creeping shoot between
162 two nodes and the leaf formed at the distal node was considered as a module in the case of *T.*
163 *repens*. All data are based on two 10-day harvest periods during early and late summer 2006
164 (June, August) at estimated peak biomass before mowing. Two legumes with an annual
165 overwintering life cycle, *T. campestre* and *T. dubium*, were only investigated during the first
166 harvest period because no adult plants were available in late summer.

167 In each plot where legumes were growing, five modules per species were randomly chosen
168 along transects divided into regular sections (of 50 and 25 cm length in large and small plots,
169 respectively). In the field, module height and canopy height of the immediately surrounding
170 vegetation were determined. Module number per genet was counted for species where genets
171 could be distinguished from each other. The selected modules were cut off near the ground,
172 put in sealed plastic bags and transported in a cool box to the laboratory. The following
173 standard protocol was used for further sample preparation. Stretched module length (=
174 maximum shoot length) and internode length of 3 to 5 internodes in the central part of the
175 main shoot axis were measured. Modules were separated into compartments (supporting
176 parts: stems and secondary axes; leaves; reproductive parts: inflorescences and fruits).

177 Secondary axes, higher-order axes and inflorescences were counted. Phenology was assessed
 178 on a nine-part scale according to different stages of flower and fruit development. Three to ten
 179 (dependent on leaf size and number) fully expanded leaves from the upper module part were
 180 chosen, and leaf area was measured immediately as part of the biomass separation process
 181 (LI-3100 Area Meter, LI-COR, Lincoln, U.S.). Petioles and rachis of compound leaves were
 182 included in leaf area measurements.

183 All plant material was dried (70°C, 48 h) and weighed. Leaf samples as well as the remaining
 184 plant compartments (= bulk samples per species and plot) were ground with a ball mill.
 185 Approximately 20 mg of this material was analysed for carbon and nitrogen concentrations
 186 with an elemental analyzer (Vario EL Element Analyzer, Elementar, Hanau, Germany).
 187 Nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope ratios were measured from leaf material (3 mg and
 188 0.8 mg, respectively) with an isotope-ratio mass spectrometer (Delta C prototype IRMS,
 189 Finnigan MAT); sample ratios of $^{15}\text{N}/^{14}\text{N}$ are given relative to the international standard for
 190 atmospheric N_2 , and sample ratios of $^{13}\text{C}/^{12}\text{C}$ refer to the VPDB standard for C. Values are
 191 expressed in per-mil relative to the standards. To assess N_2 fixation of legumes with the ^{15}N
 192 natural abundance method (Amarger et al. 1979), *Lolium perenne* L. (sown as additional
 193 species into a small area of all large experimental plots; Roscher et al. 2008) and *Taraxacum*
 194 *officinale* Wiggers (included in the experimental species pool and occurring as a weed in near
 195 all plots where the species was not sown; Roscher et al. 2009) were used as non- N_2 -fixing
 196 reference species. Leaf material of these species collected during both harvest campaigns in
 197 all large plots, where these species were available, was analysed for $\delta^{15}\text{N}$. The ^{15}N
 198 abundances in legumes and reference species were used to calculate the proportion of legume
 199 N derived from the atmosphere (pNdfa) as

$$200 \quad \text{pNdfa} = (\delta^{15}\text{N}_{\text{ref}} - \delta^{15}\text{N}_{\text{legume}}) / (\delta^{15}\text{N}_{\text{ref}} - \text{B}) \quad (\text{eq. 1}),$$

201 where $\delta^{15}\text{N}_{\text{ref}}$ and $\delta^{15}\text{N}_{\text{legume}}$ are the ^{15}N abundances in the reference species and the N_2 fixing

202 legume species (Amarger et al. 1979, Högberg 1997). B values describing the $\delta^{15}\text{N}$ of the N_2 -
203 fixing species when grown with N_2 in air as the sole N source were set to the lowest detected
204 $\delta^{15}\text{N}$ for each legume species (Hansen and Vinther 2001, Carlsson et al. 2009). Foliar $\delta^{15}\text{N}$
205 values of the reference species *L. perenne* and *T. officinale* varied depending on spatial
206 location of the experimental plots at the field site (using block identity and geographic
207 coordinates as explanatory terms) and decreased with sown species richness (Appendix Fig.
208 S1 in Supplementary Material). The dependence on plot location may be due to spatial
209 variation in soil $\delta^{15}\text{N}$ at the field site. Declining foliar $\delta^{15}\text{N}$ values with increasing species
210 richness might indicate a shift in the uptake of different N forms, an increasing transfer of N
211 from legumes to co-occurring plants or a larger amount of soil N deposited by legume plants
212 via rhizodeposition or degradation of legume litter (Högberg 1997). Because the mechanisms
213 causing a decrease in $\delta^{15}\text{N}$ values of reference species with increasing species richness or
214 affecting their spatial variation across the field site equally apply to legumes themselves,
215 pNdfa was only calculated if $\delta^{15}\text{N}$ values of reference species growing at the same plot were
216 available. Therefore, small monoculture plots of legumes were excluded from these
217 calculations. Differences in foliar $\delta^{15}\text{N}$ between the reference species were not statistically
218 significant. Thus, pNdfa obtained with either *L. perenne* or *T. officinale* as reference species
219 were used in cases where only one of these species was available and values were averaged in
220 plots where both species could be sampled.

221 Community biomass was recorded in each plot in 20×50 cm rectangles shortly before
222 mowing. Two randomly allocated samples were taken in small plots, and four samples were
223 harvested in large plots. Plant material was cut 3 cm above ground, dried (70°C , 48 h) and
224 weighed.

225

226 ***Data analyses***

227 All trait values were averaged per species and plot for each harvest campaign. Derived
228 variables for further analyses are summarized in Table 2. Measurements of *T. fragiferum* were
229 excluded from all analyses because this species was extinct in a large number of plots (Table
230 1). Data were analysed with mixed-effects models using the *nlme* package of the statistical
231 software R2.6.2 (R Development Core Team, <http://www.R-project.org>). Although the Jena
232 Experiment has a factorial design based on gradients of species and plant functional group
233 richness, the random species allocation to each mixture led to unbalanced occurrences of
234 individual species in the experimental plots that violate the assumption of independence of
235 errors. Mixed-effects models account for this non-independence of errors by modelling the
236 covariance structure given by the random effects as grouping variable (Crawley 2002). Block
237 and plot identity were entered as random effects in a nested sequence. Starting from a
238 constant null model we added the fixed effects sequentially. Firstly, we fitted plant diversity
239 as species richness separated into a monoculture vs. mixture contrast (Mo) and a log-linear
240 term (SR), and functional group number (FG). Secondly, legume species identity (ID) was
241 entered. In the following steps we fitted interaction terms between species identity and the
242 experimental factors (ID \times Mo, ID \times SR, ID \times FG), season (June, August) and interaction
243 terms between season and the previously mentioned terms. We applied the maximum
244 likelihood method and used likelihood ratio (L) tests to assess the statistical significance of
245 model improvement. In alternative models we changed the fitting order of the experimental
246 factors SR and FG because of the slight non-orthogonality between them. However, both
247 fitting sequences yielded very similar results. Furthermore, we tested whether plant functional
248 group composition (presence and absence of grasses, small herbs and tall herbs) explained
249 additional variation in trait values. Because we only rarely observed effects of these
250 explanatory terms, we do not present the corresponding results. To test whether effects of
251 species and functional group number on the values of legume traits operated in an indirect

252 way via increasing the canopy height or community biomass, we fitted these plant community
253 characteristics as covariates before the experimental treatments in a further set of models. R^2
254 statistics for the mixed models were calculated based on likelihood-ratio test statistics
255 comparing the log-likelihood of the model after fitting the explanatory terms with the log-
256 likelihood of the model excluding these terms (Magee 1990).

257 Finally we explored functional traits (excluding performance indicators such as module
258 biomass and traits characterising reproduction) with standardized principal components
259 analysis (PCA). We used the respective constrained ordination technique, redundancy
260 analysis (RDA), with different combinations of explanatory terms and covariates, i.e. (1)
261 species identity, (2) community diversity (monoculture vs. mixture contrast, log-linear species
262 richness, functional group number), (3) canopy height and community biomass, and (4)
263 season in partial analyses to decompose the variation in functional traits explained by each set
264 of explanatory variables following the procedure described in Borcard et al. (1992). In
265 addition, we tested whether the differential responses of individual species explained a further
266 proportion of variation and fitted interaction terms of species identity with community
267 diversity and season. Block and plot identity were always entered as covariates and restricted
268 Monte Carlo tests (999 permutations) were applied to assess the significance of explanatory
269 terms. Ordination analyses were performed with CANOCO 4.5 (ter Braak and Šmilauer
270 2002).

271

272 **Results**

273 Aboveground plant traits of shoots and leaves and performance traits in terms of biomass and
274 investment into reproduction differed significantly among the investigated legume species. In
275 addition, the different legume species varied in their responses to increasing species and
276 functional group number, i.e. plant diversity (Table 3, Appendix Table S1, S2). Community

277 biomass increased from monocultures to mixtures ($L = 17.47$, $P < 0.001$) and with increasing
278 species richness of mixtures ($L = 4.69$, $P = 0.030$). Community biomass before the first
279 mowing was significantly higher than before the second mowing ($L = 31.08$, $P < 0.001$).
280 Community biomass correlated positively with canopy height (May: $r = 0.712$, $P < 0.001$, $n =$
281 57 ; August: $r = 0.751$, $P < 0.001$, $n = 50$), which also increased from monocultures to
282 mixtures ($L = 27.05$, $P < 0.001$) and with increasing species richness of mixtures ($L = 6.86$, P
283 < 0.001).

284 In the following we (1) highlight the most significant effects of plant diversity on trait values
285 of legumes, (2) assess whether the mechanism by which plant diversity affects trait values is
286 primarily due to a diversity-induced change in canopy height or community biomass, or (3)
287 whether there are additional significant direct effects of plant diversity on species-specific
288 differences among legumes which cannot be explained by (2). We were particularly interested
289 in trait variation potentially reflecting different strategies of light and nitrogen acquisition and
290 retention among species.

291

292 ***Legume positioning within the canopy (relative growth height)***

293 On average, relative growth height of legumes, i.e. module height compared with the
294 surrounding vegetation, was significantly less than 1 in early summer (one-sample t-tests, $P \leq$
295 0.050) except for *O. viciifolia* with a relative growth height not significantly different from 1
296 ($t_{14} = 0.547$, $P = 0.593$). In late summer relative growth height of *O. viciifolia* even exceeded
297 canopy height (of all neighboring species) in mixtures ($t_{14} = 4.302$, $P = 0.001$), while relative
298 growth height of the other legumes was mostly close to 1 ($P > 0.05$). Relative growth height
299 generally decreased from monocultures to mixtures, which was primarily attributable to
300 increasing canopy height and community biomass (Table 3; Fig. 1a, 2a, S2a). However, per-
301 species analyses showed that plant diversity affected relative growth height of all species

302 except *O. viciifolia* not only via increased canopy height and community biomass (Table S2).

303

304 ***Legume performance in terms of biomass and investment into reproduction***

305 On average, module mass of legumes did not change in response to plant diversity because
306 some species had lower module mass in monocultures than in mixtures and increased module
307 mass with increasing species richness of mixtures whereas other species showed the opposite
308 or no relationships (see significant interactions “ID × Mo”, “ID × SR”; Table 3, S2; Fig. 1b,
309 S2b). Canopy height and community biomass affected module mass of legumes
310 independently of plant diversity, which had a significant direct effect even after fitting the
311 covariables. Module numbers per genet, counted for species with clearly distinguishable plant
312 genets only, were lower in mixtures than in monocultures, again irrespective of changes in
313 community characteristics described by the covariables (Table S1), however, this effect was
314 not significant in separate analyses for each individual species (Table S2).

315 Overall, the number of inflorescences per module decreased with increasing species richness,
316 but the response of individual species varied greatly (Table S1, S2). Flower or fruit
317 development was generally more advanced in monocultures than in mixtures of increasing
318 species richness (Table S1). This negative effect of mixture environment on reproductive
319 phenology was mainly due to increasing canopy height and community biomass.

320

321 ***Shoot and leaf morphology***

322 Legumes growing in mixtures generally invested more biomass into supporting tissue (stems,
323 secondary axes) at the cost of leaf mass, resulting in lower leaf:stem ratios in mixtures of
324 increasing species richness (Table 3; Fig. 1c). Only two legume species, *M. lupulina* and *O.*
325 *viciifolia*, did not change the investment into stems and leaves when growing in mixtures or in
326 response to increasing species number in mixtures (Table S2). The number of secondary axes

327 generally did not vary in response to community diversity, but individual species differed in
328 their response to some degree (significant interaction “ID × Mo”; Table S1). Four species
329 produced shoots with fewer secondary axes either in mixtures compared with monocultures or
330 with increasing species number in mixtures (Table S2). Shoot length of all species except for
331 *O. viciifolia* and *V. cracca* increased from monocultures to mixtures or with increasing
332 species number in mixtures (Table 3, S2; Fig. 1d, S2d). The formation of longer shoots was
333 mostly correlated with elongated internodes on the main axes (Table S1, S2). All species
334 except *O. viciifolia* increased the SLA from monocultures to mixtures or with increasing
335 species or functional group numbers in mixtures (Table 3, S2; Fig. 1e, S2e). Plant diversity
336 effects on shoot and leaf morphology were due to increasing canopy height and community
337 biomass, but significant interactions between species identity and plant diversity (“ID × Mo”,
338 “ID × SR”, “ID × FG”, Table 3, Fig. 2c-e) remained even after fitting these covariables. This
339 suggested that variation of morphological traits in response to plant diversity differed among
340 the studied legumes.

341

342 ***Leaf nitrogen and isotopic signatures***

343 The relationship between mass-based leaf nitrogen and species richness largely depended on
344 species identity (Table 3; Fig. 1f, S2f). Leaf nitrogen concentrations were either reduced
345 (three legume species), increased (two legume species) or did not change in response to
346 species or functional group richness (Table S2) and were not influenced by canopy height or
347 community biomass.

348 Foliar $\delta^{15}\text{N}$ values of legumes declined from monocultures to mixtures, with increasing
349 species numbers in mixtures and when mixtures were composed of species belonging to
350 different functional groups (Table 3, Fig. 1g, S2g), but significant interaction terms with
351 species identity indicated differential effects of plant diversity on foliar $\delta^{15}\text{N}$ values of the

352 various legume species (Table S2). Although canopy height and community biomass had
353 significant effects on foliar $\delta^{15}\text{N}$ values (Fig. 2g, Table 3), these variables only partly
354 explained plant diversity effects. On average, foliar $\delta^{15}\text{N}$ values of legumes were significantly
355 lower in early summer than in late summer, but these seasonal differences varied among
356 species (Table S2). In contrast, foliar $\delta^{15}\text{N}$ values of two non- N_2 -fixing reference species did
357 not differ significantly between early and late summer (paired t-tests $p > 0.05$; *L. perenne*
358 $\delta^{15}\text{N} = 1.91 \pm 0.84\text{‰}$ SD, *T. officinale* $\delta^{15}\text{N} = 1.90 \pm 1.09\text{‰}$). Proportions of N derived from
359 N_2 fixation (pNdfa) calculated based on the ^{15}N natural abundance method with *T. officinale*
360 and *L. perenne* as reference species, where these reference species were available, differed
361 significantly among legume species ($L = 44.15$, $P < 0.001$). The proportion of N derived from
362 N_2 fixation increased with increasing species numbers in mixtures ($L = 10.42$, $P = 0.012$, Fig.
363 3), and increasing functional group number ($L = 5.77$, $P = 0.016$); it was higher in early
364 summer than in late summer ($L = 23.27$, $p < 0.001$; June 0.80 ± 0.16 , August 0.70 ± 0.22
365 averaged across species and plots).

366 Foliar $\delta^{13}\text{C}$ values decreased from monocultures to mixtures and species-specific values
367 became lower in mixtures of increasing species or functional group number in most legume
368 species (Table 3; Fig. 1h, S2h) except for the tallest species *M. × varia* and *O. viciifolia*
369 (Table S2). Unexpectedly, averaged across all species, foliar $\delta^{13}\text{C}$ values decreased when
370 foliar N concentrations increased (Pearson correlation coefficient for early summer: $r = -$
371 0.412 , $P < 0.001$, $n = 132$; for late summer: $r = -0.260$, $P = 0.004$, $n = 119$), while significant
372 correlations for individual species were rare. Relative module height as surrogate for legume
373 positioning within the canopy was positively related to foliar $\delta^{13}\text{C}$ values averaged across all
374 species (Pearson correlation coefficient for early summer: $r = 0.540$, $P < 0.001$, $n = 132$; for
375 late summer: $r = 0.527$, $P < 0.001$, $n = 119$) and was often correlated in analyses of individual
376 species as well.

377

378 Nitrogen utilization (module biomass:N ratio)

379 Variation in biomass:N ratios at the whole-shoot level in response to plant diversity varied
380 largely among legume species (Table 3, Fig. 1i, S2i) with significant effects in nine species
381 (Table S2). Increasing canopy height and community biomass led to increased shoot
382 biomass:N ratios independent of variation in plant diversity (Fig. 2i).

383

384 Patterns of seasonal variation

385 Values of all traits except for inflorescence number per module differed between
386 measurement dates (early June vs. August; Table 3, S1; Fig. S3). Relative module height,
387 leaf:stem ratio, mass-based leaf nitrogen, foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ achieved larger values later in
388 the growing season. In contrast, module mass, shoot length, SLA and module biomass:N
389 ratios had larger values before first mowing. Seasonal variations in SLA and foliar $\delta^{13}\text{C}$ were
390 mediated by variation in community characteristics between early and late summer, while
391 canopy height and community biomass only partly explained seasonal variation in other traits.

392

393 Multiple trait analysis

394 The three leading axes of the principal components analysis accounted for 67 % of total
395 variation in legume functional traits (first axis 29 %, second axis 22 %, third axis 16 %). The
396 first axis had high loadings for traits related to plant height, i.e. shoot length, internode length,
397 and module biomass:N ratios. This axis separated *O. viciifolia* from the other legumes. The
398 second axis was characterized by traits related to species positioning in the canopy, i.e. SLA,
399 foliar $\delta^{13}\text{C}$ values, and relative module height, while the third axis accounted for variation in
400 mass-based leaf nitrogen and number of secondary axes per shoot. Redundancy analysis
401 (RDA) showed that functional traits were significantly related to the explanatory variables

402 which were included in a model that accounted for 44.9 % of the total variation. The partition
403 into different sets of explanatory variables indicated a large effect of species identity
404 (explaining 33.8 % of variation) and a small, but significant effect of season (Fig. 4). While
405 plant diversity and community characteristics together explained a significant proportion in
406 trait variation, the decomposition of these terms gave evidence that main effects of plant
407 diversity on legume trait combinations were largely explained by canopy height and
408 community biomass. That is, by increasing canopy height and community biomass, plant
409 diversity affected these traits indirectly. Interactions of species identity with community
410 diversity and season explained an additional proportion of variation (12.3 %) leaving in total
411 42.8 % of unexplained variation. These results underscore the differential responses of
412 legume species to community diversity and across season.

413

414 **Discussion**

415 Variation in functional traits to optimize resource capture, to compete with neighbors and
416 finally to produce seed or vegetative offspring are of major importance for the adjustment of
417 plants to their abiotic and biotic environment (Schlichting 1986, Sultan 1995). It is known
418 from many studies that plant species are plastic for numerous ecologically important traits
419 including morphology, physiology, anatomy, development and reproduction (Bradshaw 1965,
420 Sultan 2000, Valladares et al. 2007). These studies also reported large interspecific
421 differences in trait variation, and correlations between traits may vary in different
422 environments (Schlichting 1989). Therefore the study of a large set of traits is required to
423 assess trait variation in relation to complex environmental changes, such as variation in plant
424 diversity and species composition, which affects the availability of multiple resources at the
425 same time.

426 In our study, we focused on traits measured on aboveground plant organs which are known as

427 indicators for strategies of light and nitrogen capturing, because these resources are among the
428 most limiting factors for plant growth in temperate grassland. The complementarity
429 hypothesis in biodiversity research suggests that positive diversity–productivity relationships
430 are related to a more complete use of available resources due to diversity in plant functional
431 characteristics and niche differentiation among species (Tilman et al. 1997). Competition for
432 light and nutrients increases at higher productivity levels. To assess to which extent
433 significant effects of plant diversity on trait variation of legumes were mechanistically
434 explained by diversity-induced increases of canopy height and community biomass, i.e.
435 generalised light competition, we compared the results of analyses unadjusted for these
436 covariables with results of analyses adjusted for these covariables. When in addition to the
437 indirect effect via the two covariables there was a “residual” direct effect of diversity, other
438 covariables which were not measured and thus could not be included in the analysis must
439 have been mechanistically involved in the effect. These residual direct effects were obviously
440 not related to generalised light competition but mostly represented differential effects of plant
441 diversity on the different legume species and were probably related to increasing
442 complementarity among legumes in resource acquisition and retention.

443

444 *Nitrogen acquisition*

445 Because of their ability to fix N₂ symbiotically, legume species are less reliant on growth-
446 limiting soil nitrogen resources than other grassland species. However, the energy-consuming
447 symbiotic N₂ fixation may be suppressed when alternative N sources decrease the need for
448 symbiotically fixed N (Hartwig 1998, Carlsson and Huss-Danell 2003). Because the presence
449 of non-fixing plants that deplete soil mineral nitrogen, or even directly receive nitrogen fixed
450 by legumes by uptake of root exudates or from mycorrhizal links to legumes (Paynel et al.
451 2001, Govindarajulu et al. 2005), increases from legume monocultures to mixtures and in

452 mixtures with increasing species and functional group numbers, it is likely that legumes
453 become more dependent on their symbiotic N source with increasing plant diversity. The
454 application of the ^{15}N natural abundance method with non- N_2 -fixing reference species (*L.*
455 *perenne*, *T. officinale*) to assess proportions of legume-N derived from N_2 fixation (pNdfa)
456 provided consistent evidence that legume dependence on symbiotic N source increased with
457 increasing plant diversity. This variation was only partly driven by increasing community
458 productivity and indicated that interactions between legumes and non-legumes were
459 modulated through other plant-diversity related mechanisms (Fig. 3). In spite of this overall
460 stimulating effect of plant diversity on N_2 fixation, pNdfa values varied among legume
461 species and were particularly high in the short-lived legumes *T. campestre* and *T. dubium*
462 which probably have a lower ability to compete with established perennial species for soil
463 nitrogen. The higher proportions of N derived from N_2 fixation in early summer — when
464 experimental communities reached peak biomass — than in late summer before the second
465 mowing — which correlated with higher leaf nitrogen concentrations and lower biomass:N
466 ratios at the module level — gave further indication that legumes increased their reliance on
467 N_2 fixation when competition for soil N was large.

468

469 ***Light acquisition***

470 Our comparison of canopy height and plant height of individual legumes suggested that their
471 access to direct insolation decreased with increasing plant community diversity, although we
472 could not characterise the light climate experienced by the investigated plant individuals. All
473 species except for the tallest, *O. viciifolia*, did not reach maximum canopy height in mixtures
474 in early summer, whereas they did so in late summer (Fig. S2a, S3a). Canopy profiles are
475 characterised by an exponential decrease of photosynthetic active radiation (Wacker et al.
476 2009) and changes in spectral light quality with a lower red to far red ratio deeper in the

477 canopy (Jones 1992). The disproportionate share of light obtained by larger plants increases
478 the probability that smaller plants are outcompeted by shading (Weiner 1990). Our
479 measurements at the whole-shoot and leaf level revealed that legume species in mixtures
480 usually possessed typical strategies to tolerate or avoid lower light availability to a certain
481 degree. They formed longer shoots with elongated internodes, reduced branching and invested
482 more biomass into supporting tissue at the cost of leaf mass, all mechanisms known to
483 enhance the chance to overtop neighbors in dense canopies (Smith 1982, Poorter and Nagel
484 2000). In addition, legumes generally increased their specific leaf area with increasing plant
485 diversity, which is again a typical response of shaded plants (Corré 1983, Evans and Poorter
486 2001). Although variation in these traits differed among legume species, all of them except
487 for the tall *O. viciifolia* increased shoot and internode length, had a lower leaf:stem ratio and
488 increased SLA in relation to increasing species and functional group numbers (see Table 3).

489 A large amount of variation in these light acquisition traits probably represented generalized
490 competition for light which was independent of the particular species contributing to it
491 because it could be explained by the covariables canopy height and community biomass.
492 Nevertheless, significant proportions of species-specific responses were attributable to
493 residual direct effects of plant diversity not related to these covariables, suggesting that in
494 addition to a generalized component of light competition there were also more specific
495 components encapsulated in our plant diversity factors species richness and functional group
496 number. Because these effects were different for the different legume species, they were
497 probably related to complementary strategies of light acquisition. However, not all shade-
498 avoidance reactions may reflect adaptive strategies, i.e. they may not always increase light
499 acquisition and thus be mal-adaptive. A typical case occurs when the shade-avoidance
500 reaction does not allow plant individuals to overtop their neighbors or reach canopy height
501 (Weinig 2000). Although all legume species established successfully in all experimental plots

502 in the year of sowing in the Jena Experiment (unpubl. data), 4 years after sowing the smallest
503 legume species with an annual overwintering or biannual life cycle, such as *M. lupulina*, *T.*
504 *campestre* and *T. dubium* as well as the creeping *T. fragiferum*, went extinct in many
505 experimental mixtures of higher species richness (see Table 1). This extinction is probably
506 due to their non-sufficient genetic predisposition for adjustment or due to resource limitation
507 of these species to adapt to canopy shade in multi-species mixtures. Even if smaller species
508 may possess a larger trait variation, it might not be sufficient to increase competitiveness in
509 plant communities of increasing diversity (Thein et al. 2008).

510 Foliar $\delta^{13}\text{C}$ values can give further information about plant positioning in the canopy. A wide
511 range of physiological and biochemical processes affect isotopic composition of bulk
512 samples: i) CO_2 source, ii) ratio of intercellular to ambient CO_2 concentrations (C_i/C_a) during
513 assimilation, iii) metabolism and biosynthesis of carbon compounds, iv) cellular carbon
514 budgets (Farquhar et al. 1989, Dawson et al. 2002). Thus, the carbon isotope composition of
515 plants is jointly affected by the abiotic (e.g. irradiance, soil moisture, temperature, nitrogen
516 nutrition) and biotic (e.g. leaf physiology, canopy height) environment of individual plants. In
517 contrast to an expected positive correlation between $\delta^{13}\text{C}$ values and leaf nitrogen
518 concentrations under a nitrogen limitation of C assimilation (Evans 1989), these variables
519 varied largely independently at the species level in our study. Instead, plant canopy
520 characteristics determined variation in foliar $\delta^{13}\text{C}$ values, although this relationship may have
521 several causes. In contrast to studies of foliar $\delta^{13}\text{C}$ in previous biodiversity experiments
522 (Caldeira et al. 2001, Jumpponen et al. 2005), canopy profiles measured in a 60-species plot
523 in our experiment showed an increase in CO_2 concentrations with increasing canopy depth
524 (unpubl. data). This CO_2 enrichment in lower canopies might be related to a decrease in $\delta^{13}\text{C}$
525 values of source CO_2 because soil respiration produces CO_2 with carbon isotope ratios similar
526 to the substrate (Peterson and Fry 1987) and may affect foliar $\delta^{13}\text{C}$ of species growing in the

527 canopy (Farquhar et al. 1989, da Silveira et al. 1989). However, light availability and air
528 humidity in lower canopy levels may also control C_i/C_a ratios *via* stomata aperture and hence
529 affect $^{13}C/^{12}C$ ratios in leaf material. Foliar $\delta^{13}C$ values correlated with relative growth height
530 of legume modules and were significantly higher in late summer when legumes reached a
531 higher relative height than in early summer (Fig. S3h). In contrast, we found no diversity
532 effects on foliar $\delta^{13}C$ values of the tallest legumes *M. × varia* and *O. viciifolia* indicating that
533 light availability was a major control of carbon isotope discrimination, although we cannot
534 exclude effects of source-air isotopic composition.

535

536 ***Fitness consequences***

537 In our experiment, legumes mostly remained or even increased their performance at the
538 module level assessed as module biomass in communities of increasing diversity. At the same
539 time, plant genets often consisted of fewer modules in more diverse plant communities
540 (except for *O. viciifolia*, *T. pratense*), indicating a decreasing performance at the genet level.
541 Biomass allocation to reproductive compartments usually depends on plant size (Harper
542 1977). Reproductive structures have high resource costs and allocation into reproduction is
543 generally greater under resource excess (Bloom et al. 1985). Therefore the observed reduction
544 of inflorescence numbers in several legumes is not surprising, because it is likely that lower
545 light availability — correlated with a decrease in legume module biomass (Table 3) — also
546 affected the investment of legume species into reproduction.

547

548 ***Conclusions***

549 So far, effects of community diversity on plant functional traits and their variation have
550 received little attention although it is known that variation in physiological, morphological
551 and life-history traits may alter direct and indirect interactions of organisms with their abiotic

552 and biotic environment (Callaway et al. 2003, Miner et al. 2005). Our study provided
553 evidence for highly consistent effects of plant diversity on plant traits. Trait variation in
554 particular of traits reflecting strategies for light acquisition were partly attributable to
555 diversity-related changes in community characteristics in terms of canopy height and biomass
556 production. However, plant diversity beyond these community characteristics was mainly
557 responsible for species-specific trait variation of different legume species.

558 In our study we cannot differentiate whether variation of functional traits in legume species
559 growing in plant communities of different diversity is exclusively due to phenotypic
560 responses or whether different growing conditions led to local genetic differentiation at plot-
561 scale, although each species was established with identical seed populations in all plots
562 (Roscher et al. 2004). In addition, the potential plastic response of a species may be larger
563 than what was observed, which might have been limited by resource availability (van Kleunen
564 and Fischer 2005); and the number of replicates of particular legume species at each species-
565 richness level was often small. Nevertheless, our study shows that the investigated legume
566 species are neither redundant in their functional characteristics nor in the variation of these
567 traits in relation to plant diversity. This is in line with previous studies at larger scales (Díaz et
568 al. 2004). The uniqueness of species behavior shows that *a priori* classifications into
569 functional groups are limited in their usefulness to elucidate biodiversity effects on ecosystem
570 processes (Wright et al. 2005, McGill et al. 2006). Therefore, it is important to also consider
571 potential particularities of individual species and interactions between individual species to
572 better understand processes measured at the community level.

573

574 **Acknowledgements**

575 The Jena Experiment is funded by the German Science Foundation (FOR 456) with additional
576 support from the Max Planck Society and the Friedrich Schiller University Jena. We thank all

577 people helping with the management of the experiment, especially the gardeners and many
578 student helpers. We gratefully acknowledge U. Wehmeier, S. Hengelhaupt, A. Höfer, C.
579 Jeschke, A. Mraja and N. Streit for their help during harvest and sample preparation. I. Hilke
580 and H. Geilmann conducted chemical and stable isotope analyses. We acknowledge J.
581 Schumacher for advice on statistical analyses. Finally, we thank four anonymous referees and
582 P. Reich for their valuable comments which helped to improve the manuscript.

583

584 **References**

- 585 Amarger N, Mariotti A, Mariotti F, Durr JC, Bourguignon C, Lagacherie B (1979) Estimate
586 of symbiotically fixed nitrogen in field grown soybeans using variations in ^{15}N natural
587 abundance. *Plant Soil* 52:269-280
- 588 Balvanera P, Pfisterer AB, Buchmann N, He J-S, Nakashizuka T, Raffaelli D, Schmid B
589 (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and
590 services. *Ecol Lett* 9:1146-1156
- 591 Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological
592 variation. *Ecology* 73:1045-1055
- 593 Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants – an economic
594 analogy. *Annu Rev Ecol Syst* 16:363-392
- 595 Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. *Adv Genet*
596 13:115-155
- 597 Caldeira MC, Ryel RJ, Lawton JH, Pereira JS (2001) Mechanisms of positive biodiversity-
598 production relationships: insights provided by $\delta^{13}\text{C}$ analysis in experimental Mediterranean
599 grassland plots. *Ecol Lett* 4:439-443
- 600 Callaway RM, Pennings SC, Richards CL (2003) Phenotypic plasticity and interactions
601 among plants. *Ecology* 84:1115-1128

- 602 Callaway RM (2007) Positive interactions and interdependence in plant communities.
603 Springer, Dordrecht
- 604 Cardinale BJ, Wright JP, Cadotte MW, Carroll JA, Hector A, Srivastava DS, Loreau M, Weis
605 JJ (2007) Impacts of plant diversity on biomass production increase through time because
606 of species complementarity. *Proc Natl Acad Sci USA* 104:18123-18128
- 607 Carlsson G, Huss-Danell K (2003) Nitrogen fixation in perennial forage legumes in the field.
608 *Plant Soil* 253:353-372
- 609 Carlsson G, Palmborg C, Jumpponen A, Scherer-Lorenzen M, Högberg P, Huss-Danell K
610 (2009) N₂ fixation in three perennial *Trifolium* species in experimental grasslands of varied
611 plant species richness and composition. *Plant Ecol* 205:87-104
- 612 Chiariello NR, Gulmon S (1991) Stress effects on plant reproduction. In: Mooney HA,
613 Winner WE, Pell EJ, Chu E (eds) Response of plants to multiple stresses. Academic Press,
614 San Diego, pp 161-188
- 615 Corré WJ (1983) Growth and morphogenesis of sun and shade plants. I. The influence of light
616 intensity. *Acta Bot Neerl* 32:49-62
- 617 Crawley MJ (2002) Statistical computing. An introduction to data analysis using S-Plus. John
618 Wiley & Sons Ltd., Chichester
- 619 da Silveira L, Sternberg M, Mulkey SS, Wright SJ (1989) Ecological interpretation of leaf
620 carbon isotope ratios: influence of respired carbon dioxide. *Ecology* 70:1317-1324
- 621 Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP (2002) Stable isotopes in plant
622 ecology. *Annu Rev Ecol Syst* 33:507-559
- 623 Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem
624 processes. *Trends Ecol Evol* 16:646-655
- 625 Díaz S, Hodgson JP, Thompson K, Cabido M, Cornelissen C, Jalili A, Montserrat-Martí G,
626 Grime JP, Zarrinkamar F, Asri Y, Band SR, Basconcelo S, Castro-Díez P, Funes G,

- 627 Hamzehee B, Khoshnevi M, Pérez-Harguindeguy N, Pérez-Rontomé MC, Shirvany FA,
628 Vendramini F, Yazdani S, Abbas-Azimi R, Bogaard A, Boustani S, Charles M, Dehghan
629 M, de Torres-Espuny L, Falczuk V, Guerrero-Campo J, Hynd A, Jones G, Kowsary E,
630 Kazemi-Saeed F, Maestro-Martínez M, Romo-Díez A, Shaw S, Siavash B, Villar-Salvador
631 P, Zak MR (2004) The plant traits that drive ecosystems: evidence from three continents. *J*
632 *Veg Sci* 15:295-304
- 633 Ellenberg H (1988) *Vegetation ecology of Central Europe*. Cambridge University Press,
634 Cambridge
- 635 Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C₃ plants. *Oecologia*
636 78:9-19
- 637 Evans JR, Poorter H (2001) Photosynthetic acclimation of plants to growth irradiance: the
638 relative importance of specific leaf area and nitrogen partitioning in maximizing carbon
639 gain. *Plant Cell Environ* 24:755-767
- 640 Farquhar GD, Ehleringer J, Hubick KT (1989) Carbon isotope discrimination and
641 photosynthesis. *Ann Rev Plant Physiol Plant Mol Biol* 40:503-537
- 642 Govindarajulu M, Pfeffer PE, Jin H, Abubaker J, Douds DD, Allen JW, Bücking H, Lammers
643 PJ, Shachar-Hill Y (2005) Nitrogen transfer in the arbuscular mycorrhizal symbiosis.
644 *Nature* 435:819-823
- 645 Hansen JP, Vinther FP (2001) Spatial variability of symbiotic N₂ fixation in grass-white
646 clover pastures estimated by the ¹⁵N isotope dilution method and the natural ¹⁵N abundance
647 method. *Plant Soil* 230:257-266
- 648 Harper JL (1977) *The population biology of plants*. Academic Press, London
- 649 Hartwig UA (1998) The regulation of symbiotic N₂ fixation: a conceptual model of N
650 feedback from the ecosystem to the gene expression level. *Perspect Plant Ecol Evol Syst*
651 1:92-120

- 652 Hector A, Bazeley-White E, Loreau M, Otway S, Schmid B (2002) Overyielding in grassland
653 communities: testing the sampling effect hypothesis with replicated biodiversity
654 experiments. *Ecol Lett* 5:502-511
- 655 Högberg P (1997) ^{15}N natural abundance in soil-plant systems. *New Phytol* 137:179-203
- 656 Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM,
657 Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005)
658 Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol*
659 *Monogr* 75:3-35
- 660 Jolliffe PA (2000) The replacement series. *J Ecol* 88:371-385
- 661 Jones HG (1992) Plants and microclimate. A quantitative approach to environmental plant
662 physiology. Cambridge University Press, Cambridge.
- 663 Jumpponen A, Mulder CPH, Huss-Danell K, Högberg P (2005) Winners and losers in
664 herbaceous plant communities: insights from foliar carbon isotope composition in
665 monocultures and mixtures. *J Ecol* 93:1136-1147
- 666 Kluge G, Müller-Westermeier G (2000) Das Klima ausgewählter Orte der Bundesrepublik
667 Deutschland: Jena. *Ber Deutsch Wetterdienstes* 213:1-290
- 668 Lorentzen S, Roscher C, Schumacher J, Schulze E-D, Schmid B (2008) Species richness and
669 identity affect the use of aboveground space in experimental grasslands. *Perspect Plant*
670 *Ecol Evol Syst* 10:73-87
- 671 Magee L (1990) R^2 measures based on Wald and likelihood joint significance tests. *Am*
672 *Statist* 44:250-253
- 673 Marschner H (1995) Mineral nutrition of higher plants. Academic Press, London
- 674 McConnaughay KDM, Coleman JS (1999) Biomass allocation in plants: ontogeny or
675 optimality? A test along three resource gradients. *Ecology* 80:2581-2593

- 676 McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from
677 functional traits. *Trends Ecol Evol* 21:178-185
- 678 Miner BG, Sultan SE, Morgan SG, Padilla DK, Relyea RA (2005) Ecological consequences
679 of phenotypic plasticity. *Trends Ecol Evol* 20:685-692
- 680 Oelmann Y, Wilcke W, Temperton VM, Buchmann N, Roscher C, Schumacher J, Schulze E-
681 D, Weisser WW (2007) Soil and plant nitrogen pools as related to plant diversity in an
682 experimental grassland. *Soil Sci Soc Am J* 71:720-729
- 683 Palmborg C, Scherer-Lorenzen M, Jumpponen A, Carlsson G, Huss-Danell K, Högberg P
684 (2005) Inorganic soil nitrogen under grassland plant communities of different species
685 composition and diversity. *Oikos* 110:271-281
- 686 Paynel F, Murray PJ, Cliquet JB (2001) Root exudates: a pathway for short-term N transfer
687 from clover and ryegrass. *Plant Soil* 229:235-243
- 688 Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293-
689 320
- 690 Poorter H, Nagel O (2000) The role of biomass allocation in the growth response of plants to
691 different levels of light, CO₂, nutrients and water: a quantitative review. *Aust J Plant*
692 *Physiol* 27:595-607
- 693 Roscher C, Schumacher J, Baade J, Wilcke W, Gleixner G, Weisser WW, Schmid B, Schulze
694 E-D (2004) The role of biodiversity for element cycling and trophic interactions: an
695 experimental approach in a grassland community. *Basic Appl Ecol* 5:107-121
- 696 Roscher C, Schumacher J, Weisser WW, Schmid B, Schulze E-D (2007) Detecting the role of
697 individual species for overyielding in experimental grassland communities composed of
698 potentially dominant species. *Oecologia* 154:535-549
- 699 Roscher C, Schumacher J, Weisser WW, Schulze E-D (2008) Genetic identity affects species
700 performance in grasslands of different plant diversity: an experiment with *Lolium perenne*

- 701 cultivars. *Ann Bot* 102:113-125
- 702 Roscher C, Beßler H, Oelmann Y, Engels C, Wilcke W & Schulze E-D (2009) Resources,
703 recruitment limitation and invader species identity determine pattern of spontaneous
704 invasion in experimental grasslands. *J Ecol* 97:32-47
- 705 Schlichting CD (1986) The evolution of phenotypic plasticity in plants. *Annu Rev Ecol Syst*
706 17:667-693
- 707 Schlichting CD (1989) Phenotypic plasticity in *Phlox*. II. Plasticity of character correlations.
708 *Oecologia* 78:496-501
- 709 Schmid B (1990) Some ecological and evolutionary consequences of modular organization
710 and clonal growth in plants. *Evol Trends Plants* 4:25-34
- 711 Smith H (1982) Light quality, photoperception, and plant strategy. *Ann Rev Plant Physiol*
712 33:481-518
- 713 Spehn EM, Joshi J, Schmid B, Diemer M, Körner C (2000) Above-ground resource use
714 increases with plant species richness in experimental grassland ecosystems. *Funct Ecol*
715 14:326-337
- 716 Spehn EM, Scherer-Lorenzen M, Schmid B, Hector A, Caldeira MC, Dimitrakopoulos PG,
717 Finn JA, Jumpponen A, O'Donovan G, Pereira JS, Schulze E-D, Troumbis AY, Körner C
718 (2002) The role of legumes as a component of biodiversity in a cross-European study of
719 grassland biomass nitrogen. *Oikos* 98:205-218
- 720 Sultan SE (1995) Phenotypic plasticity and plant adaptation. *Acta Bot Neerl* 44:363-383
- 721 Sultan SE (2000) Phenotypic plasticity for plant development, function and life history.
722 *Trends Plant Sc* 5:537-542
- 723 ter Braak CJF, Šmilauer P (2002) CANOCO reference manual and CanoDraw for Windows
724 user's guide: software for canonical community ordination (version 4.5). Ithaca

- 725 Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of
726 functional diversity and composition on ecosystem processes. *Science* 277:1300-1302
- 727 Thein S, Roscher C, Schulze E-D (2008) Effects of trait plasticity on aboveground biomass
728 production depend on species identity in experimental grasslands. *Basic Appl Ecol* 9:475-
729 484
- 730 Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity.
731 *New Phytol* 176:749-763
- 732 van Kleunen M, Fischer M (2005) Constraints on the evolution of adaptive phenotypic
733 plasticity in plants. *New Phytol* 166:49-60
- 734 van Ruijven J, Berendse F (2003) Positive effects of plant species diversity on productivity in
735 the absence of legumes. *Ecol Lett* 6:170-175
- 736 Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the
737 concept of trait be functional! *Oikos* 116:882-892
- 738 Wacker L, Baudois O, Eichenberger-Glinz S, Schmid B (2009) Effects of plant species
739 richness on stand structure and productivity. *J Plant Ecol* 2:95-106
- 740 Walker B, Kinzig A, Langridge J (1999) Plant attribute diversity, resilience, and ecosystem
741 function: the nature and significance of dominant and minor species. *Ecosystems* 2:95-113
- 742 Weiner J (1990) Asymmetric competition in plant populations. *Trends Ecol Evol* 5:360-364
- 743 Weinig C (2000) Plasticity versus canalization: population differences in the timing of shade-
744 avoidance responses. *Evolution* 54:441-451
- 745 Wright IJ, Naeem S, Hector A, Lehman C, Reich PB, Schmid B, Tilman D (2005)
746 Conventional functional classification schemes underestimate the relationships with
747 ecosystem functioning. *Ecol Lett* 9:111-120
- 748

749 Figure captions

750

751 Figure 1: Trait values plotted against sown species number. Trait values per species are
752 averaged across different plots and season (June, August) for each species-richness level.
753 Each regression line represents a legume species. For species symbols and line styles see Fig.
754 3.

755

756 Figure 2: Trait values plotted against canopy height including values measured in June
757 (before first mowing) and August (before second mowing). Each regression line represents a
758 legume species. For line styles see Fig. 3.

759

760 Figure 3: Proportion of N derived from N₂ fixation (pNdfa) based on the ¹⁵N natural
761 abundance method plotted against sown species number. Values per species are averaged
762 across different plots and season (June, August) for each species-richness level. Each
763 regression line represents a legume species.

764

765 Figure 4: Summary of Redundancy Analysis (RDA) using different sets of explanatory
766 variables in partial analyses to decompose their effects on legume trait variation. For each set
767 of explanatory variables being species identity, season and plant community (separated into
768 diversity and canopy height and community biomass, respectively) the proportion of
769 explained trait variation, F ratio statistics and P values obtained by Monte Carlo tests (999
770 permutations) are shown. Shared variation indicates the proportion of explained variability
771 that cannot be attributed uniquely to a certain set of predictor variables. An additional
772 proportion of variation may be explained by differential responses of individual species
773 (interactions of species identity with community diversity and season).

Figure 1

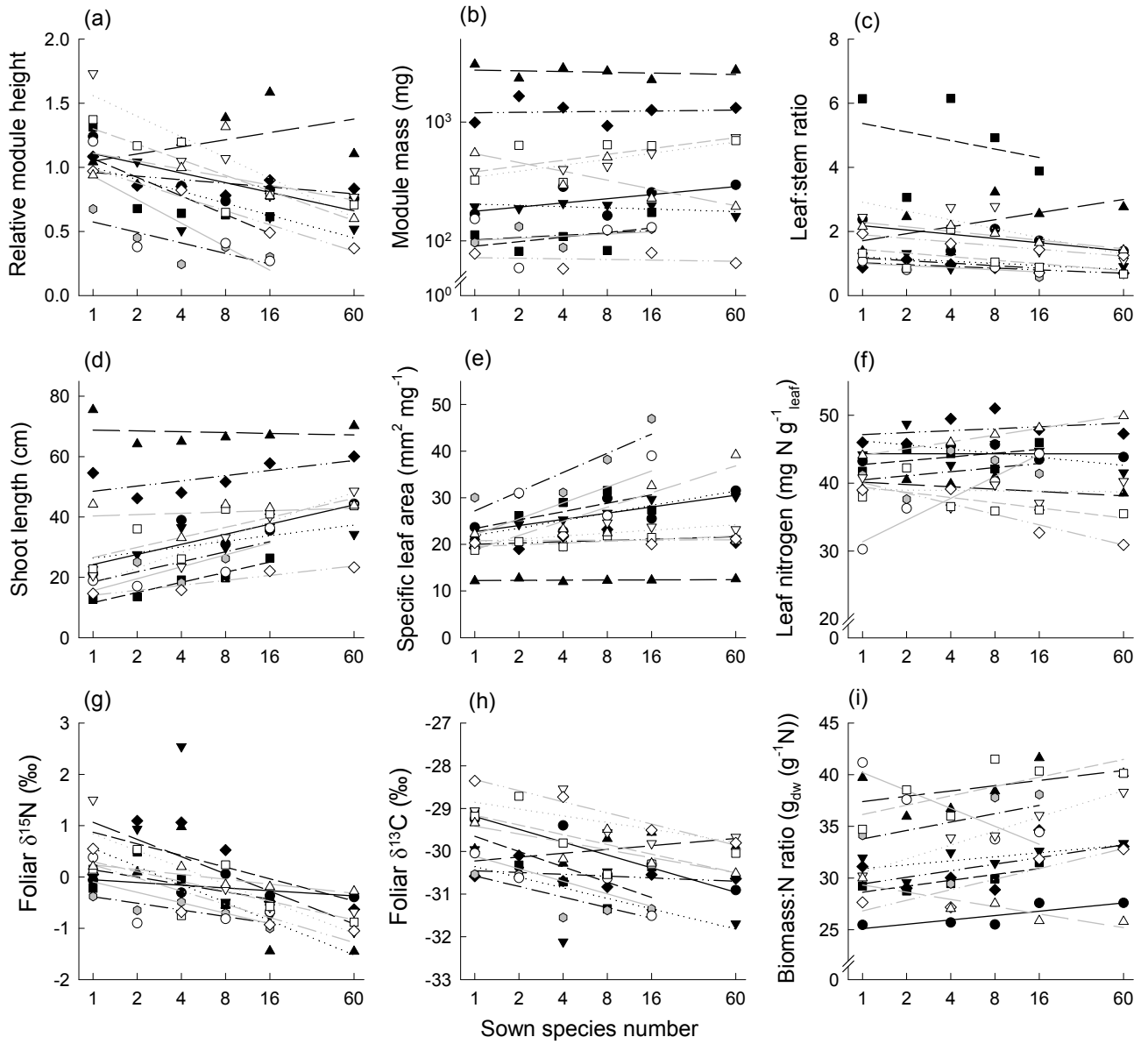


Figure 2

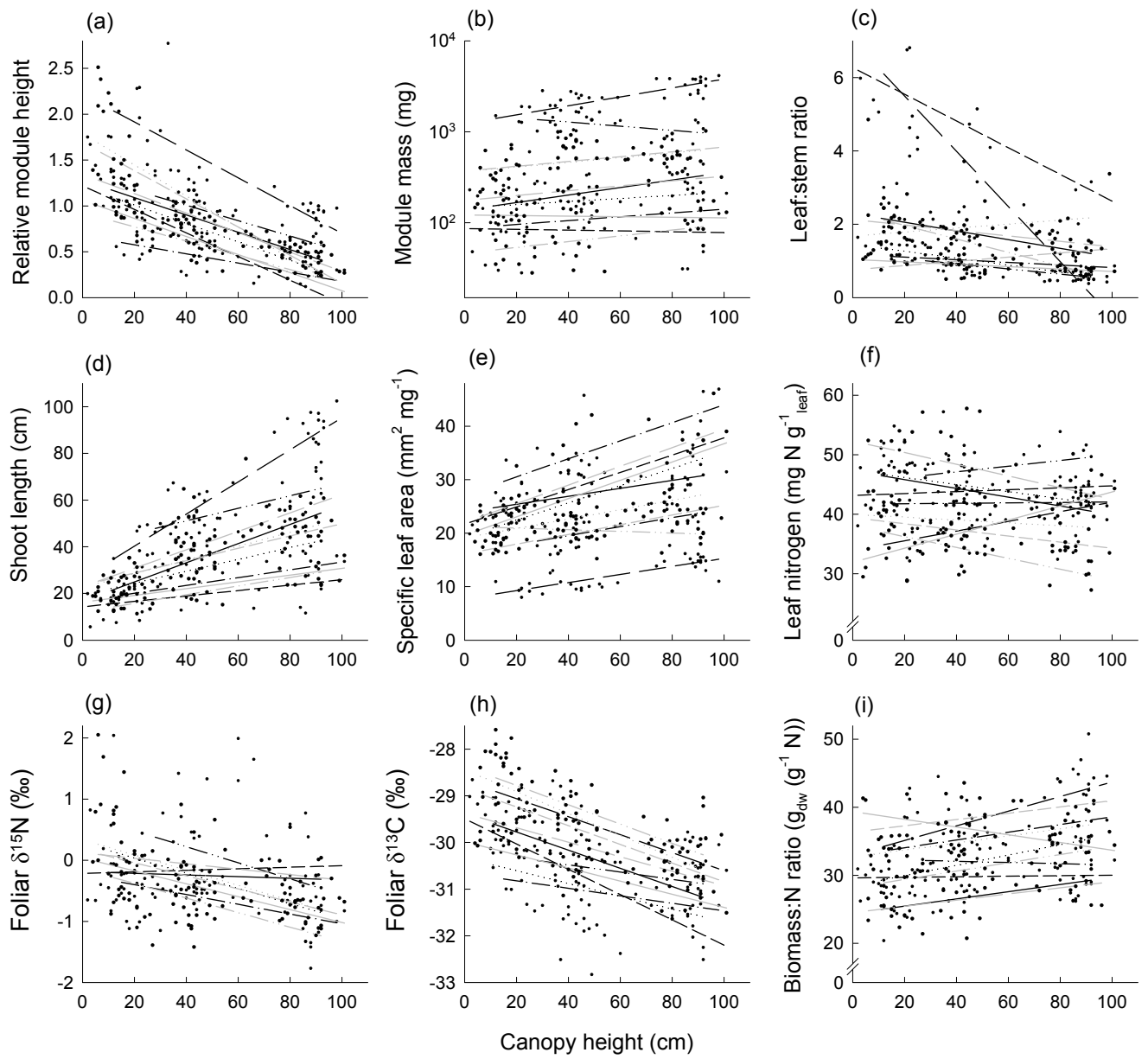


Figure 3

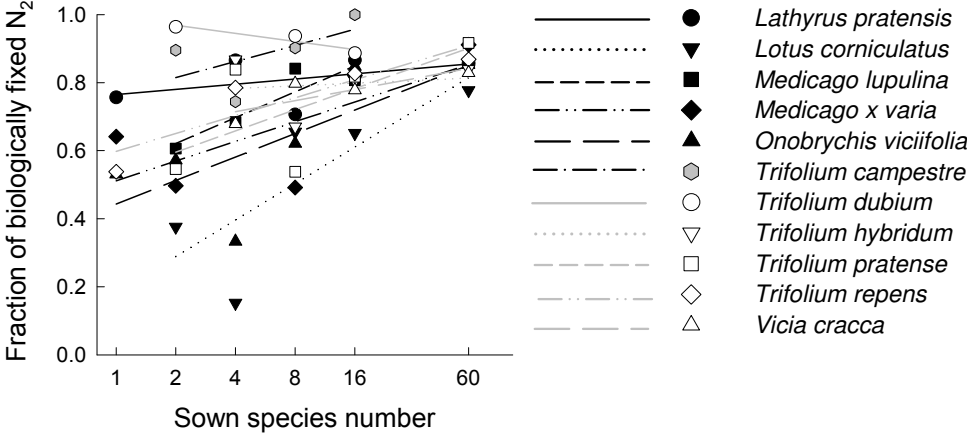


Figure 4

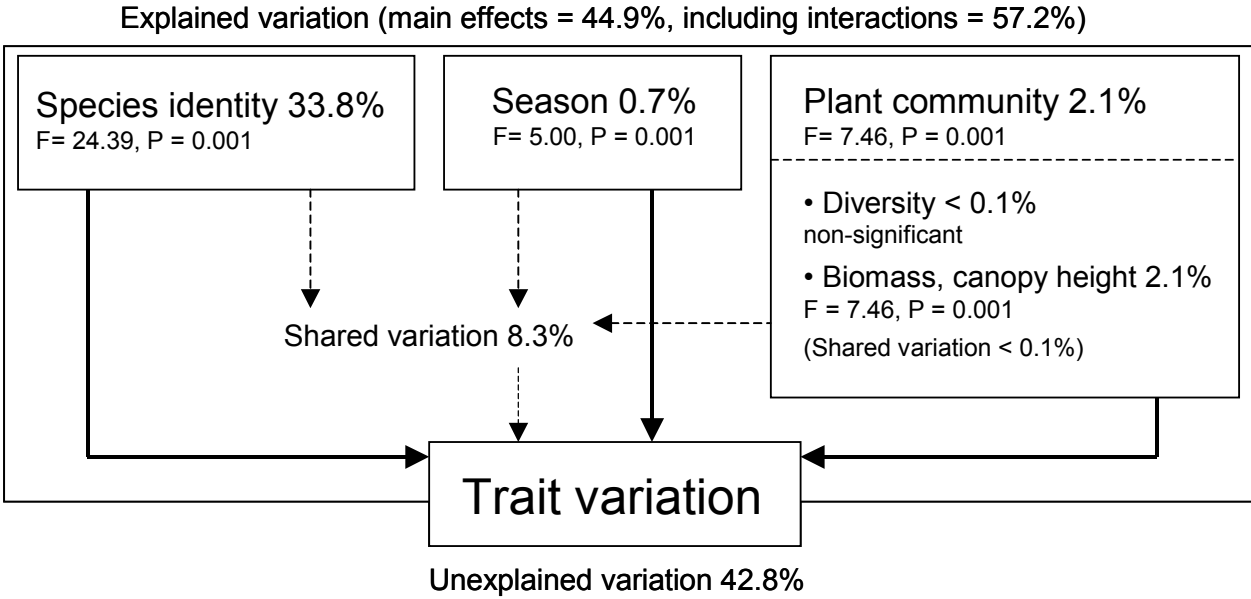


Table 1: Number of plots in which the investigated legumes occurred in the experiment. The number of plots in which the original seed mixtures contained the respective legume species is given in parentheses. Abbreviations for life cycle are: a = annual, ao = annual overwintering, p = perennial

Species	Life cycle	Species richness					
		1	2	4	8	16	60
<i>Lathyrus pratensis</i> L.	p	2 (2)	0 (0)	1 (1)	2 (2)	4 (4)	3 (3)
<i>Lotus corniculatus</i> L.	p	2 (2)	1 (1)	1 (1)	4 (4)	4 (4)	3 (3)
<i>Medicago lupulina</i> L.	ao, p	2 (2)	2 (2)	3 (3)	3 (4)	2 (2)	0 (3)
<i>Medicago x varia</i> Martyn	p	2 (2)	1 (1)	2 (2)	1 (1)	3 (3)	3 (3)
<i>Onobrychis viciifolia</i> Scop.	p	2 (2)	1 (1)	2 (2)	4 (4)	5 (5)	3 (3)
<i>Trifolium campestre</i> Schreb.	a, ao	2 (2)	1 (1)	1 (1)	2 (4)	1 (5)	0 (3)
<i>Trifolium dubium</i> Sibth.	a, ao	2 (2)	1 (1)	0 (0)	2 (3)	1 (3)	0 (3)
<i>Trifolium fragiferum</i> L.	p	1 (2)	0 (0)	1 (1)	1 (4)	0 (3)	0 (3)
<i>Trifolium hybridum</i> L.	p	2 (2)	0 (0)	1 (1)	4 (4)	5 (5)	3 (3)
<i>Trifolium pratense</i> L.	p	2 (2)	1 (1)	1 (1)	1 (1)	2 (2)	3 (3)
<i>Trifolium repens</i> L.	p	2 (2)	0 (0)	1 (1)	0 (0)	6 (6)	3 (3)
<i>Vicia cracca</i> L.	p	2 (2)	0 (0)	2 (2)	1 (1)	6 (6)	3 (3)

Table 2: Overview of traits investigated on aboveground plant organs in this study

Variable	Unit	Description
Relative module height	cm cm ⁻¹	Module height divided by canopy height of the surrounding vegetation
Module biomass	mg	Aboveground dry mass per module
Leaf : stem ratio	mg _{leaf} mg ⁻¹ _{stem}	Leaf dry mass per dry mass of supporting tissue
Shoot length	cm	Stretched module length
Specific leaf area (SLA)	mm ² _{leaf} mg ⁻¹ _{leaf}	Leaf area per leaf dry mass
Leaf nitrogen	mg N g ⁻¹ _{leaf}	Foliar nitrogen concentration (Nitrogen mass per leaf dry mass)
Biomass:N ratio	g _{dw} (g N) ⁻¹	Module biomass per unit nitrogen
Foliar δ ¹⁵ N	‰	¹⁵ N isotopic signature of leaves
Foliar δ ¹³ C	‰	¹³ C isotopic signature of leaves
Module number		Number of modules per plant individual
No. secondary axes		Number of secondary and higher order lateral axes per module
Internode length	cm	Length of the longest internode per module
No. inflorescences		Number of inflorescences per module
Phenology		Phenology of flower and fruit development (ordinal scale)

Table 3: Summary of mixed-effects model analyses of functional traits combining all legume species

Model	Relative height		Module mass		Leaf:stem ratio		Shoot length		Specific leaf area	
	A	B	A	B	A	B	A	B	A	B
	R ²	p	R ²	p	R ²	p	R ²	p	R ²	p
R ² statistics	0.70	0.89	0.87	0.89	0.52	0.56	0.88	0.91	0.84	0.89
	L ratio	p	L ratio	p	L ratio	p	L ratio	p	L ratio	p
Canopy	--	141.62 ***↓	--	36.78 ***↑	--	16.61 ***↓	--	133.03 ***↑	--	53.04 ***↑
Biomass	--	5.52 *↓	--	4.63 *↑	--	1.68	--	16.85 ***↑	--	0.84
Mo	15.29 ***↓	0.26	0.60	0.08	0.34	1.53	10.21 ***↑	0.60	4.23 *↑	0.19
SR	2.25	1.01	1.07	0.27	5.13 **↓	1.66	11.10 ***↑	4.40 *↑	0.41	0.09
FG	0.24	0.82	0.85	0.76	1.11	0.84	1.76	1.81	<0.01	<0.01
ID	104.89 ***	156.21 ***	345.03 ***	325.99 ***	64.09 ***	65.78 ***	237.31 ***	234.52 ***	230.27 ***	266.33 ***
ID x Canopy	--	40.23 ***	--	16.04 .	--	23.92 **	--	15.43	--	42.36 ***
ID x Biomass	--	8.38	--	15.97	--	12.53	--	8.24	--	31.49 ***
ID x Mo	34.91 ***	17.11 .	33.01 ***	26.68 **	4.30	1.74	61.24 ***	27.45 **	29.22 **	5.87
ID x SR	5.00	11.44	26.00 **	34.90 ***	3.08	5.83	36.37 ***	45.36 ***	40.69 ***	41.39 ***
ID x FG	11.12	26.88 **	12.79	17.67 .	8.38	10.00	11.19	21.08 *	15.67	27.62 **
Season	64.54 ***A	2.93 .	43.74 ***M	34.00 ***M	17.42 ***A	11.01 ***A	116.15 ***M	26.96 ***M	43.09 ***M	0.02
Season x Canopy	--	65.36 ***	--	5.21 *	--	0.61	--	19.65 ***	--	2.00
Season x Biomass	--	0.12	--	0.40	--	1.31	--	0.34	--	0.62
Season x Mo	2.36	0.02	0.01	4.12 *	0.11	1.05	0.70	6.08 *	3.16 .	0.25
Season x SR	1.95	4.37 *	0.31	0.32	0.84	0.06	0.06	1.17	0.96	2.04
Season x FG	26.25 ***	0.76	3.30 .	3.68 .	0.04	0.03	3.02 .	1.53	1.36	0.43
Season x ID	36.91 ***	65.49 ***	43.28 ***	34.38 ***	81.73 ***	52.95 ***	51.23 ***	58.74 ***	91.24 ***	82.37 ***

Model	Mass-based leaf N		Foliar δ ¹⁵ N		Foliar δ ¹³ C		Biomass:N ratio	
	A	B	A	B	A	B	A	B
	R ²	p	R ²	p	R ²	p	R ²	p
R ² statistics	0.73	0.76	0.61	0.66	0.65	0.75	0.80	0.82
	L ratio	p	L ratio	p	L ratio	p	L ratio	p
Canopy	--	4.61	--	19.00 ***↓	--	83.70 ***↓	--	45.51 ***↑
Biomass	--	0.05	--	5.76 *↓	--	0.07	--	5.01 *↑
Mo	0.66	2.51	10.88 **↓	6.22 *↓	14.60 ***↓	3.17 ↓	0.69	1.12
SR	2.87 ↓	1.52	14.44 ***↓	11.04 ***↓	0.20	0.90	2.26	0.32

FG	0.11	0.10	9.23 **↓	10.13 **↓	0.04	0.20	0.01	0.08
ID	171.11 ***	168.60 ***	71.13 ***	67.94 ***	103.89 ***	117.73 **	231.14 ***	214.81 ***
ID x Canopy	--	46.06 ***	--	9.53	--	14.05	--	26.95 **
ID x Biomass	--	12.53	--	5.61	--	12.32	--	10.52
ID x Mo	25.90 **	14.71	22.91 *	27.14 **	24.79 **	19.57 *	35.19 ***	24.66 **
ID x SR	22.96 *	26.77 **	19.31 *	23.29 **	7.95	11.78	17.24	26.02 **
ID x FG	18.03	24.78 **	17.04	19.30 *	28.31 **	37.09 ***	19.43 *	26.01 **
Season	16.51 ***A	12.82 ***A	26.45 ***A	20.64 ***A	43.27 ***A	1.90	41.32 ***M	14.52 ***M
Season x Canopy	--	4.23 *	--	2.10	--	17.76 ***	--	1.24
Season x Biomass	--	0.12	--	1.55	--	3.40 .	--	0.47
Season x Mo	0.07	0.58	4.69 *	0.89	0.66	0.05	<0.01	0.07
Season x SR	0.13	0.11	7.68 **	12.03 ***	0.82	0.02	0.49	0.04
Season x FG	0.10	1.17	1.95	0.09	4.07 *	0.35	1.32	0.44
Season x ID	72.25 ***	40.50 ***	34.44 ***	31.95 ***	33.78 ***	28.86 **	56.19 ***	30.24 ***

Models were fitted by stepwise inclusion of variables. Listed are the results of likelihood ratio tests that were applied to assess model improvement (= L ratio), the statistical significance of the explanatory terms, where . $P \leq 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. R^2 statistics is based on likelihood ratio test statistics in comparison to the intercept-only model. The first columns for each trait show models (= model A) where only the experimental factors were fitted. They are followed by columns with models (= model B) where canopy height and community biomass were fitted before the experimental factors. Arrows indicate a significant increase (↑) or decrease (↓) of trait values with increasing community diversity, biomass or canopy height. J (= June) or A (= August) indicate a significant increase or decrease of trait values from the first to the second sampling period, respectively. Abbreviations: ID = species identity, Canopy = canopy height, Biomass = community biomass, Mo = monoculture vs. mixture contrast, SR = species number (log-scale), FG = functional group number, Season = time of sampling (early summer = June, late summer = August).

Supplementary online materialRoscher C, Schmid B, Buchmann N, Weigelt A, Schulze E-D. **Legume species differ in the responses of their functional traits to plant diversity**

Table S1: Summary of mixed-effects model analyses of functional traits combining all legume species

Model	Module number		No. inflorescences				Phenology				No. secondary axes				Internode length			
	A		B		A		B		A		B		A		B			
	L ratio	P	L ratio	P	L ratio	P	L ratio	P	L ratio	P	L ratio	P	L ratio	P	L ratio	P		
R ² statistics	0.59	0.66	0.82	0.87	0.84	0.87	0.78	0.84	0.91	0.94								
Canopy	--	1.72	--	2.04	--	27.14 ***↓	--	51.25 ***↓	--	117.65 ***↑								
Biomass	--	4.33 *	--	2.61	--	10.34 **↓	--	9.16 **↓	--	29.29 ***↑								
Mo	3.90 *↓	6.28 *↓	2.24	0.92	3.06 ↓	0.66	0.37	2.20	6.11 *↑	1.94								
SR	0.53	1.05	5.51 *↓	5.04 *↓	3.50 ↓	0.44	<0.01	1.39	6.44 *↑	0.68								
FG	0.06	<0.01	0.08	<0.01	0.02	0.01	0.99	1.54	0.42	0.09								
ID	79.46 ***	72.50 ***	184.85 ***	190.03 ***	180.68 ***	177.89 ***	185.36 ***	186.34 ***	240.35 ***	215.43 ***								
ID x Canopy	--	7.11	--	68.29 ***	--	15.39 .	--	16.28 .	--	105.36 ***								
ID x Biomass	--	1.70	--	19.99 *	--	11.04	--	10.14	--	12.42								
ID x Mo	10.69	12.05 .	28.18 ***	40.34 ***	16.69	37.67 ***	13.09	24.27 **	40.92 ***	17.80 *								
ID x SR	5.72	7.75	8.76	21.39 *	12.47	29.48 ***	17.44 *	15.99 .	19.85 *	17.37 *								
ID x FG	11.54	19.74 **	8.51	22.80 **	10.09	15.59 .	9.49	14.98 .	11.01	10.65								
Season	16.90 ***M	23.74 ***M	3.51 .	0.01	63.89 ***A	50.67 ***A	63.05 ***A	4.43 *A	85.74 ***M	36.42 ***M								
Season x Canopy	--	6.35 *	--	5.00 *	--	4.88 *	--	14.56 ***	--	0.59								
Season x Biomass	--	0.46	--	0.11	--	0.50	--	0.11	--	6.01 *								
Season x Mo	0.04	2.59	3.23 .	<0.01	1.93	0.18	2.08	7.15 **	6.03 *	4.53 *								
Season x SR	<0.01	1.29	0.38	<0.01	0.20	0.49	5.95 *	0.28	0.07	0.18								
Season x FG	2.57	0.12	2.21	0.18	1.22	1.61	2.27	1.10	0.36	0.67								
Season x ID	27.71 ***	21.05 **	150.21 ***	82.73 ***	126.32 ***	82.05 ***	49.97 ***	53.91 ***	140.91 ***	55.33 ***								

Models were fitted by stepwise inclusion of variables. Listed are the results of likelihood ratio tests that were applied to assess model improvement (= L ratio) and the statistical significance of the explanatory terms, where . $P \leq 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. R² statistics is based on likelihood ratio test statistics in comparison to the intercept-only model. The first columns for each trait shows models (= model A) where only the experimental factors were fitted. They are followed by columns with models (= model B) where canopy height and community biomass were fitted before the experimental factors. Arrows indicate a significant increase (↑) or decrease (↓) of trait values with increasing community

diversity, biomass or canopy height. J (= June) or A (= August) indicate a significant increase or decrease of trait values from the first to the second sampling period, respectively. For abbreviations see Table 3.

Table S2: Summary of mixed-effects model analyses of functional traits per legume species

	Relative module height		Module mass		Module number		No. inflorescences		Phenology		Leaf:stem ratio		No. secondary axes		Shoot length		Internode length		Specific leaf area		Mass-based leaf N		Foliar $\delta^{15}\text{N}$		Foliar $\delta^{13}\text{C}$		Biomass:N ratio	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
<i>Lathyrus pratensis</i>																												
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.44	0.84	0.75	0.78	NA	NA	0.59	0.70	0.55	0.57	0.60	0.87	0.51	0.67	0.80	0.86	0.81	0.86	0.45	0.73	0.53	0.62	0.56	0.82	0.56	0.74	0.54	0.80
Canopy	--	↓***	--	↑**	--	--	--	↓*	--	ns	--	↓***	--	ns	--	↑***	--	↑***	--	ns	--	ns	--	ns	--	↓**	--	↑**
Biomass	--	ns	--	ns	--	--	--	ns	--	ns	--	ns	--	↓*	--	ns	--	↑.	--	↑.	--	ns	--	ns	--	ns	--	↑*
Mo	↓*	ns	↑.	ns	--	--	↑*	ns	ns	ns	↓**	ns	ns	↓.	↑**	ns	↑**	ns	ns	ns	ns	↓*	ns	ns	↓*	↓*	ns	ns
SR	ns	.	↑.	ns	--	--	ns	ns	↓.	↓.	↓.	ns	ns	↓.	↑*	ns	↑.	ns	↑*	ns	ns	ns	ns	ns	↓*	↓.	ns	ns
FG	ns	ns	↑**	↑**	--	--	ns	ns	↓*	↓*	ns	ns	↓.	ns	ns	.	ns	ns	ns	↑.	ns	ns	↓**	↓**	↓*	↓*	ns	ns
Season	ns	*	**	*	--	--	***	**	ns	ns	ns	ns	*	ns	**	ns	***	*	ns	***	***	***	.	***	ns	ns	**	ns
Season x Canopy	--	*	--	ns	--	--	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	.	--	ns	--	*	--	*
Season x Biomass	--	ns	--	ns	--	--	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	*	--	ns	--	ns	--	.	--	**
Season x Mo	.	ns	.	*	--	--	*	***	ns	.	**	**	ns	ns	**	**	***	***	.	ns	ns	ns	ns	**	ns	ns	ns	.
Season x SR	ns	ns	ns	ns	--	--	ns	ns	.	ns	ns	***	ns	**	ns	.	ns	*	ns	ns	ns	ns	ns	*	ns	ns	ns	ns
Season x FG	ns	ns	*	*	--	--	ns	ns	*	.	ns	ns	.	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
<i>Lotus corniculatus</i>																												
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.77	0.94	0.46	0.54	0.53	0.68	0.30	0.34	0.38	0.39	0.63	0.77	0.58	0.69	0.68	0.79	0.82	0.88	0.62	0.71	0.65	0.73	0.66	0.72	0.47	0.72	0.72	0.87
Canopy	--	↓***	--	ns	--	ns	--	ns	--	ns	--	↓***	--	↓***	--	↑***	--	↑***	--	↑***	--	↓.	--	↓*	--	ns	--	↑**
Biomass	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	↓*	--	ns	--	↑*	--	ns	--	ns	--	↓.	--	ns	--	ns
Mo	↓**	ns	ns	ns	↓*	↓*	ns	ns	↓*	ns	↓*	ns	ns	↓**	↑**	ns	↑**	↑.	↑*	ns	ns	↓.	ns	ns	↓.	ns	ns	↑**
SR	↓*	ns	ns	↓.	ns	ns	ns	ns	↓*	↓*	ns	ns	ns	ns	ns	ns	↑.	ns	↑*	ns	↓**	↓.	↓**	↓**	ns	ns	↑*	ns
FG	ns	ns	ns	ns	↓.	↓*	ns	ns	ns	ns	ns	ns	ns	ns	↑.	.	ns	ns	ns	ns	ns	ns	↓**	↓*	↓*	↓*	↑*	ns
Season	***	ns	*	.	ns	ns	ns	ns	ns	ns	***	ns	***	ns	***	ns	***	***	***	ns	*	*	*	.	ns	.	***	*
Season x Canopy	--	***	--	ns	--	***	--	ns	--	ns	--	**	--	ns	--	*	--	ns	--	ns	--	**	--	*	--	ns	--	***

Season x Biomass	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	**
Season x Mo	ns	ns	*	*	**	ns	ns	ns	ns	ns	ns	ns	**	ns	ns	ns	**	*	ns	ns	**	ns	ns	ns	.	*	*	*
Season x SR	.	.	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	.	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns
Season x FG	*	ns	*	**	.	ns	ns	ns	ns	ns	ns	ns	ns	.	.	ns	ns	ns	ns	*	**	***	*	ns	ns	***	*	ns

Medicago lupulina

Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
R ² statistics	0.45	0.89	0.52	0.79	0.66	0.82	0.34	0.63	0.65	0.73	0.37	0.67	0.51	0.74	0.69	0.79	0.82	0.87	0.59	0.89	0.19	0.28	0.42	0.57	0.45	0.82	0.43	0.61	
Canopy	--	↓***	--	ns	--	↓.	--	↓*	--	↓**	--	ns	--	↓.	--	↑.	--	↑*	--	↑***	--	ns	--	ns	--	↓***	--	ns	
Biomass	--	ns	--	ns	--	ns	--	↓*	--	↓*	--	ns	--	ns	--	ns	--	ns	--	↑***	--	ns	--	ns	--	ns	--	ns	
Mo	↓*	ns	ns	ns	↓*	↓*	ns	ns	ns	↓**	ns	ns	ns	ns	↑.	ns	↑**	ns	↑*	ns	ns	ns	ns	ns	↓*	↓.	ns	ns	
SR	ns	ns	↑.	↑*	ns	ns	ns	ns	ns	ns	ns	ns	ns	↓.	↑**	↑**	↑***	↑**	ns	ns	ns	ns	↓.	↓.	ns	ns	*↑	*↑	
FG	ns	↓*	ns	ns	ns	ns	ns	↓.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	↓*	↓*	ns	ns	ns	ns	
Season	ns	*	**	***	***	***	ns	ns	***	*	***	***	***	***	***	***	***	***	**	ns	ns	ns	.	*	ns	**	ns	*	
Season x Canopy	--	ns	--	ns	--	*	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	
Season x Biomass	--	**	--	ns	--	ns	--	*	--	.	--	*	--	*	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	
Season x Mo	.	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
Season x SR	ns	*	ns	**	ns	**	ns	ns	ns	ns	ns	*	ns	.	.	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	*
Season x FG	.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	**	ns	ns	ns	.	*	ns	ns	ns	

Medicago x varia

Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.80	0.90	0.34	0.45	0.60	0.67	0.80	0.85	0.78	0.91	0.67	0.82	0.83	0.86	0.59	0.80	0.71	0.83	0.65	0.88	0.25	0.66	0.52	0.58	0.19	0.84	0.31	0.49
Canopy	--	↓***	--	↓*	--	ns	--	ns	--	ns	--	↓***	--	↓.	--	↑***	--	↑***	--	↑**	--	ns	--	ns	--	↓*	--	ns
Biomass	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns
Mo	↓**	ns	ns	↓*	ns	ns	ns	↓*	ns	ns	ns	ns	ns	↓**	↑**	ns	ns	↑***	↑.	ns	ns	ns	ns	ns	ns	ns	ns	ns
SR	ns	↓**	ns	ns	↓**	↓***	ns	↓.	ns	↓.	↓**	*	ns	ns	ns	ns	↑*	ns	ns	↑***	ns	ns	↓***	↓***	ns	ns	↑*	↑*
FG	ns	ns	ns	ns	↓.	ns	↓*	↓***	↓.	↓*	ns	ns	ns	↓**	ns	ns	ns	**	↑**	↑*	ns	ns	ns	ns	ns	ns	ns	ns
Season	***	**	**	.	*	.	***	***	***	***	**	ns	***	***	*	ns	***	ns	***	ns	ns	ns	.	.	ns	ns	ns	ns
Season x Canopy	--	ns	--	ns	--	ns	--	.	--	***	--	**	--	ns	--	*	--	.	--	ns	--	ns	--	ns	--	ns	--	ns
Season x Biomass	--	ns	--	ns	--	ns	--	.	--	ns	--	ns	--	ns	--	ns	--	ns	--	***	--	*	--	ns	--	ns	--	ns
Season x Mo	ns	ns	ns	ns	ns	ns	ns	ns	ns	.	ns	**	ns	ns	.	**	*	ns	ns	ns	ns	**	ns	ns	ns	***	ns	.
Season x SR	*	ns	ns	ns	.	ns	ns	*	ns	ns	ns	ns	ns	*	ns	.	ns	ns	ns	ns	ns	.	ns	ns	ns	***	ns	ns
Season x FG	ns	ns	ns	ns	ns	.	**	ns	.	ns	.	ns	*	.	ns	ns	ns	*	ns	ns	ns	.	ns	ns	ns	ns	ns	ns

Onobrychis viciifolia

Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
R ² statistics	0.52	0.92	0.51	0.62	0.29	0.42	0.72	0.79	0.37	0.46	0.46	0.77	0.49	0.60	0.74	0.84	0.77	0.88	0.66	0.66	0.44	0.52	0.66	0.76	0.62	0.80	0.61	0.62	
Canopy	--	↓***	--	↑***	--	ns	--	↑***	--	↓*	--	↓***	--	↓*	--	↑***	--	↑***	--	↑***	--	↓***	--	ns	--	↓***	--	↑***	
Biomass	--	**	--	ns	--	ns	--	ns	--	↓.	--	ns	--	↓*	--	↑*	--	ns	--	ns	--	ns	--	↓*	--	↓.	--	ns	
Mo	ns	ns	↑.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	↓.	ns	ns	ns	ns	ns	ns	ns	↓.	↓.	ns	ns	ns	ns	
SR	ns	ns	ns	ns	ns	ns	ns	↓.	ns	ns	ns	ns	ns	↓.	ns	ns	ns	↓.	ns	ns	ns	↓.	↓***	↓***	ns	↓**	ns	↓.	
FG	ns	ns	ns	ns	ns	ns	↓*	↓.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	↓.	ns	ns	ns	ns	ns	
Season	***	***	***	ns	ns	.	***	.	***	***	***	ns	***	***	***	**	***	***	***	***	***	ns	*	*	***	ns	***	*	
Season x Canopy	--	*	--	ns	--	.	--	.	--	.	--	**	--	*	--	ns	--	ns	--	ns	--	ns	--	*	--	ns	--	ns	
Season x Biomass	--	ns	--	ns	--	ns	--	*	--	ns	--	***	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	
Season x Mo	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	
Season x SR	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**	**	ns	ns	ns	ns	
Season x FG	***	ns	.	ns	.	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
<i>Trifolium campestre</i>																													
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
R ² statistics	0.65	0.98	0.42	0.98	0.69	0.95	0.40	0.96	0.45	0.87	0.78	0.85	0.94	0.96	0.94	0.98	0.93	0.99	0.88	0.99	0.62	0.86	0.67	0.99	0.39	0.91	0.33	0.81	
Canopy	--	↓**	--	ns	--	↓**	--	ns	--	↓*	--	ns	--	ns	--	↑*	--	↑*	--	ns	--	ns	--	↓***	--	ns	--	ns	
Biomass	--	ns	--	↓.	--	↓.	--	↓*	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	↓.	--	ns	--	↓*	--	ns	
Mo	ns	↓**	ns	↓*	ns	ns	ns	↓*	ns	ns	ns	↓**	ns	↓**	ns	↑**	ns	↑**	ns	↑**	ns	ns	ns	↓**	ns	ns	↑.	↓*	
SR	ns	↓**	ns	ns	↓*	ns	ns	ns	ns	ns	↓*	↓*	↓***	↓**	↑***	↑**	↑***	↑*	↑***	↑*	ns	ns	ns	↓***	↓.	ns	ns	↓.	
FG	↓*	ns	↓.	↓***	ns	↓***	ns	↓***	ns	↓*	↓.	ns	ns	ns	ns	ns	ns	ns	↑***	ns	↑***	ns	↓**	↓*	↓*	ns	↓**	↑.	↓.
<i>Trifolium dubium</i>																													
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
R ² statistics	0.56	1.00	0.88	0.99	0.66	0.98	0.81	0.85	0.58	0.99	0.69	0.99	0.68	0.99	0.94	1.00	0.85	1.00	0.73	0.99	0.71	0.91	0.58	0.99	0.64	1.00	0.61	0.99	
Canopy	--	↓***	--	--	--	--	--	--	--	--	--	↓***	--	--	--	↑***	--	--	--	↑***	--	ns	--	--	--	↓***	--	↑***	
Biomass	--	--	--	↓***	--	↓.	--	↓*	--	↑***	--	--	↓**	--	--	↑***	--	--	--	↑***	--	--	--	↓***	--	--	--	--	
Mo	↓*	ns	ns	ns	↓*	↓**	ns	ns	↑*	ns	↓*	ns	↓*	ns	ns	ns	ns	ns	↑.	ns	↑.	ns	↓*	↓*	↓.	↓.	↑.	ns	
SR	ns	ns	↑**	ns	ns	ns	↓.	ns	ns	ns	ns	ns	ns	ns	↑**	ns	↑*	ns	ns	ns	↑.	ns	ns	↓**	ns	ns	ns	ns	
FG	ns	ns	↑*	ns	ns	ns	↓*	ns	ns	ns	↓.	ns	ns	↓*	↑**	ns	↑*	ns	↑*	ns	ns	ns	ns	↓**	ns	ns	ns	ns	
<i>Trifolium hybridum</i>																													
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
R ² statistics	0.84	0.94	0.51	0.56	0.55	0.78	0.69	0.72	0.86	0.89	0.54	0.64	0.52	0.59	0.79	0.87	0.78	0.81	0.66	0.75	0.19	0.26	0.64	0.66	0.73	0.88	0.64	0.68	
Canopy	--	↓***	--	↑**	--	↓*	--	↓***	--	ns	--	ns	--	↓***	--	↑***	--	↑***	--	↑***	--	ns	--	ns	--	ns	--	↑**	

Biomass	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	↑*	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns
Mo	↓***	ns	ns	ns	↓.	ns	ns	ns	ns	ns	ns	ns	ns	ns	↑***	↑.	↑**	↑.	↑.	ns	ns	ns	↓***	↓***	↓.	ns	↑**	↑*
SR	↓.	ns	↑**	↑**	↓*	↓*	ns	ns	ns	ns	↓*	↓**	↓.	↓**	↑***	↑***	↑**	↑**	ns	ns	ns	ns	ns	ns	ns	ns	↑***	↑**
FG	ns	ns	ns	ns	ns	↓*	ns	ns	↓**	↓**	↓**	↓*	ns	ns	↑.	↑.	↑.	↑.	↑**	↑***	ns	ns	↓.	↓.	↓*	↓*	ns	↑.
Season	***	**	ns	ns	ns	***	***	***	***	***	.	*	***	ns	**	.	**	ns	***	ns	ns	ns	ns	*	***	ns	ns	ns
Season x Canopy	--	***	--	.	--	**	--	ns	--	ns	--	ns	--	ns	*	*	--	**	--	.	--	ns	--	ns	--	***	--	ns
Season x Biomass	--	ns	--	ns	--	ns	--	ns	--	ns	--	.	--	ns	--	.	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns
Season x Mo	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	***	ns	**	ns	ns	ns	ns	ns	*	ns	ns	**	ns	ns
Season x SR	*	ns	ns	ns	**	.	ns	ns	ns	**	*	.	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	.	ns	ns	ns
Season x FG	**	*	ns	ns	ns	ns	ns	ns	*	.	.	.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	.	ns	ns	ns

Trifolium pratense

Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.85	0.97	0.52	0.72	0.38	0.46	0.59	0.70	0.88	0.89	0.61	0.83	0.68	0.76	0.79	0.92	0.79	0.84	0.87	0.99	0.49	0.80	0.84	0.97	0.69	0.74	0.62	0.87
Canopy	--	↓***	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	↑***	--	↑**	--	↑***	--	↓*	--	↓.	--	↓***	--	ns
Biomass	--	ns	--	↓.	--	ns	--	↓.	--	↓*	--	↓*	--	ns	--	↑**	--	↑**	--	ns	--	ns	--	ns	--	↓*	--	ns
Mo	↓**	ns	↑*	↑*	ns	↓*	↑.	↑*	ns	↓*	ns	↓*	ns	↑**	↑**	↑**	↑**	↑*	↑*	ns	ns	ns	ns	ns	↓*	ns	↑**	↑**
SR	↓**	ns	ns	ns	ns	ns	ns	ns	ns	↓.	↓*	↓***	ns	ns	↑*	↑*	↑*	↑.	ns	ns	↓*	↓*	↓**	↓*	↓.	ns	ns	ns
FG	ns	↓*	↓.	↓*	ns	ns	ns	ns	ns	ns	↓*	↓.	ns	ns	↑**	↑**	↑***	↑.	↑*	ns	ns	ns	↓***	↓***	ns	ns	↑*	↑**
Season	**	*	ns	ns	*	.	**	*	***	***	.	ns	*	*	**	*	ns	.	***	*	ns	ns	ns	↓*	***	.	ns	ns
Season x Canopy	--	**	--	ns	--	ns	--	*	--	**	--	ns	--	**	--	ns	--	ns	--	.	--	ns	--	**	--	ns	--	ns
Season x Biomass	--	ns	--	ns	--	ns	--	.	--	ns	--	.	--	ns	--	ns	--	.	--	***	--	.	--	ns	--	ns	--	ns
Season x Mo	ns	ns	ns	ns	ns	ns	ns	ns	**	ns	ns	***	ns	ns	ns	ns	ns	ns	***	ns	ns	.	ns	.	ns	ns	ns	ns
Season x SR	ns	**	ns	ns	ns	ns	ns	ns	.	ns	ns	*	*	ns	ns	ns	ns	ns	ns	ns	ns	**	*	***	ns	ns	ns	***
Season x FG	**	***	ns	ns	ns	ns	ns	ns	ns	ns	.	ns	ns	*	ns	ns	.	ns	ns	ns	*	**	*	*	ns	ns	ns	*

Trifolium repens

Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
R ² statistics	0.72	0.96	0.62	0.99	0.69	0.86	NA	NA	0.34	0.57	0.92	0.95	NA	NA	0.77	0.85	NA	NA	0.54	0.63	0.63	0.71	0.77	0.84	0.57	0.91	0.55	0.62	
Canopy	--	↓***	--	ns	--	ns	--	--	--	ns	--	↓***	--	--	--	↑***	--	--	--	ns	--	↓***	--	↓.	--	↓***	--	↑**	
Biomass	--	ns	--	ns	--	ns	--	--	--	↓*	--	↓*	--	--	--	↑**	--	--	--	ns	--	↓*	--	ns	--	ns	--	↑*	
Mo	↓**	↓**	ns	↓*	↓*	↓.	--	--	ns	ns	↓**	ns	--	--	↑**	ns	--	--	ns	ns	↓**	ns	↓***	↓***	↓*	ns	↑*	ns	
SR	↓**	↓*	ns	↓*	↓*	↓**	--	--	ns	ns	↓.	↓***	--	--	↑*	ns	--	--	ns	ns	↓**	↓.	↓.	ns	ns	ns	↑*	ns	
FG	ns	ns	ns	ns	↓*	↓**	--	--	↓.	ns	ns	↓*	--	--	ns	ns	--	--	↑.	ns	ns	↓.	ns	ns	↓*	↓*	ns	↑*	
Season	**	ns	***	***	--	--	--	--	--	--	***	***	--	--	***	ns	--	--	*	ns	*	ns	ns	ns	ns	ns	**	**	.

Season x Canopy	--	***	--	ns	--	--	--	--	--	--	ns	--	--	--	ns	--	--	--	*	--	ns	--	ns	--	***	--	ns	
Season x Biomass	--	ns	--	ns	--	--	--	--	--	--	ns	--	--	--	ns	--	--	--	ns	--	ns	--	*	--	.	--	ns	
Season x Mo	ns	ns	ns	ns	--	--	--	--	--	*	ns	--	--	ns	ns	--	--	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
Season x SR	ns	*	ns	ns	--	--	--	--	--	ns	ns	--	--	ns	ns	--	--	.	ns	ns	ns	ns	ns	ns	ns	ns	ns	
Season x FG	ns	ns	ns	ns	--	--	--	--	--	**	.	--	--	ns	ns	--	--	*	*	ns	ns	ns	ns	.	**	ns	ns	
<i>Vicia cracca</i>																												
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.59	0.87	0.68	0.77	NA	NA	0.79	0.84	0.69	0.74	0.44	0.80	0.44	0.60	0.72	0.74	0.76	0.79	0.47	0.85	0.69	0.79	0.49	0.65	0.47	0.86	0.70	0.76
Canopy	--	↓***	--	↑.	--	--	--	ns	--	ns	--	↓*	--	↓.	--	↑***	--	↑***	--	↑**	--	ns	--	↓*	--	↓***	--	ns
Biomass	--	ns	--	ns	--	--	--	↓*	--	↓*	--	↓.	--	↓*	--	ns	--	↑*	--	↑*	--	ns	--	↓**	--	ns	--	ns
Mo	ns	ns	↓**	↓**	--	--	↓***	↓***	↓***	↓***	↓.	ns	ns	ns	ns	↑*	ns	ns	↑.	ns	↑*	↑.	↓*	ns	↓*	↓*	↓**	↓**
SR	↓*	ns	ns	↓*	--	--	ns	ns	ns	ns	↓**	↓**	ns	ns	ns	ns	↑*	ns	↑**	↑**	↑.	↑**	↓**	↓*	ns	ns	ns	↓**
FG	↓*	ns	↓.	.	--	--	ns	ns	ns	ns	ns	ns	ns	ns	ns	↑.	ns	ns	ns	ns	↑.	ns	ns	ns	ns	ns	ns	ns
Season	**	*	***	**	--	--	*	**	ns	*	ns	*	**	**	***	*	***	*	ns	***	***	***	ns	ns	ns	***	***	*
Season x Canopy	--	*	--	*	--	--	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns
Season x Biomass	--	ns	--	ns	--	--	--	ns	--	ns	--	**	--	ns	--	ns	--	ns	--	*	--	.	--	ns	--	***	--	ns
Season x Mo	ns	ns	ns	*	--	--	***	**	*	.	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	**	ns	*	ns	.	ns	**
Season x SR	ns	ns	.	ns	--	--	ns	ns	ns	ns	ns	*	.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	*	ns
Season x FG	*	ns	ns	ns	--	--	ns	ns	ns	.	ns	.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	*	ns	ns

Models were fitted by stepwise inclusion of variables. Listed are the results of likelihood ratio tests that were applied to assess model improvement and the statistical significance of the variables, where . $P \leq 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. R² statistics is based on likelihood ratio test statistics in comparison to the intercept-only model. The first column for each trait shows models (= model A) where only the experimental factors were fitted, the second column for each trait shows models (= model B) where canopy height and community biomass were fitted before the experimental factors. Note that the number of replicates was too low to include both covariates in models for *T. dubium*. Here, we separately tested each canopy height and community biomass and selected the model with the larger R². Arrows indicate a significant increase (↑) or decrease (↓) of trait values with increasing community diversity, biomass or canopy height. Dashes indicate absence of measurements or terms not fitted in the respective model. For abbreviations see Table 3.

Figure S1: Foliar $\delta^{15}\text{N}$ values of (a) *Lolium perenne* and (b) *Taraxacum officinale* used as non- N_2 -fixing reference species with the ^{15}N natural abundance method plotted against sown species number. All values are plot means of values measured in samples collected in June (before first mowing) and August (before second mowing) 2006. The lines are arithmetic means for values per species-richness level.

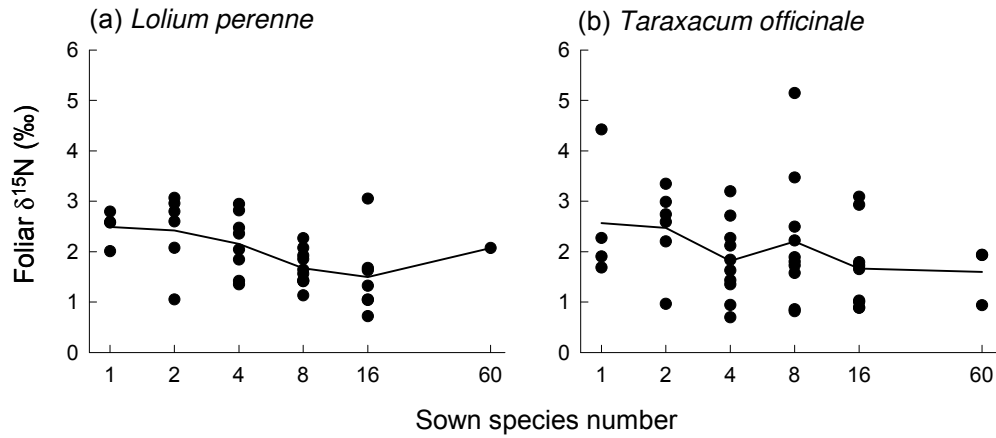


Figure S2: Trait values in mixtures (Mix) plotted against trait values in monocultures (Mono). All values are means of values measured in June (before first mowing) and August (before second mowing). Monoculture values are averaged between two replicated plots per species. Values above the diagonal line indicate cases where trait values in mixtures were larger than in monoculture. For species symbols see Fig. 3.

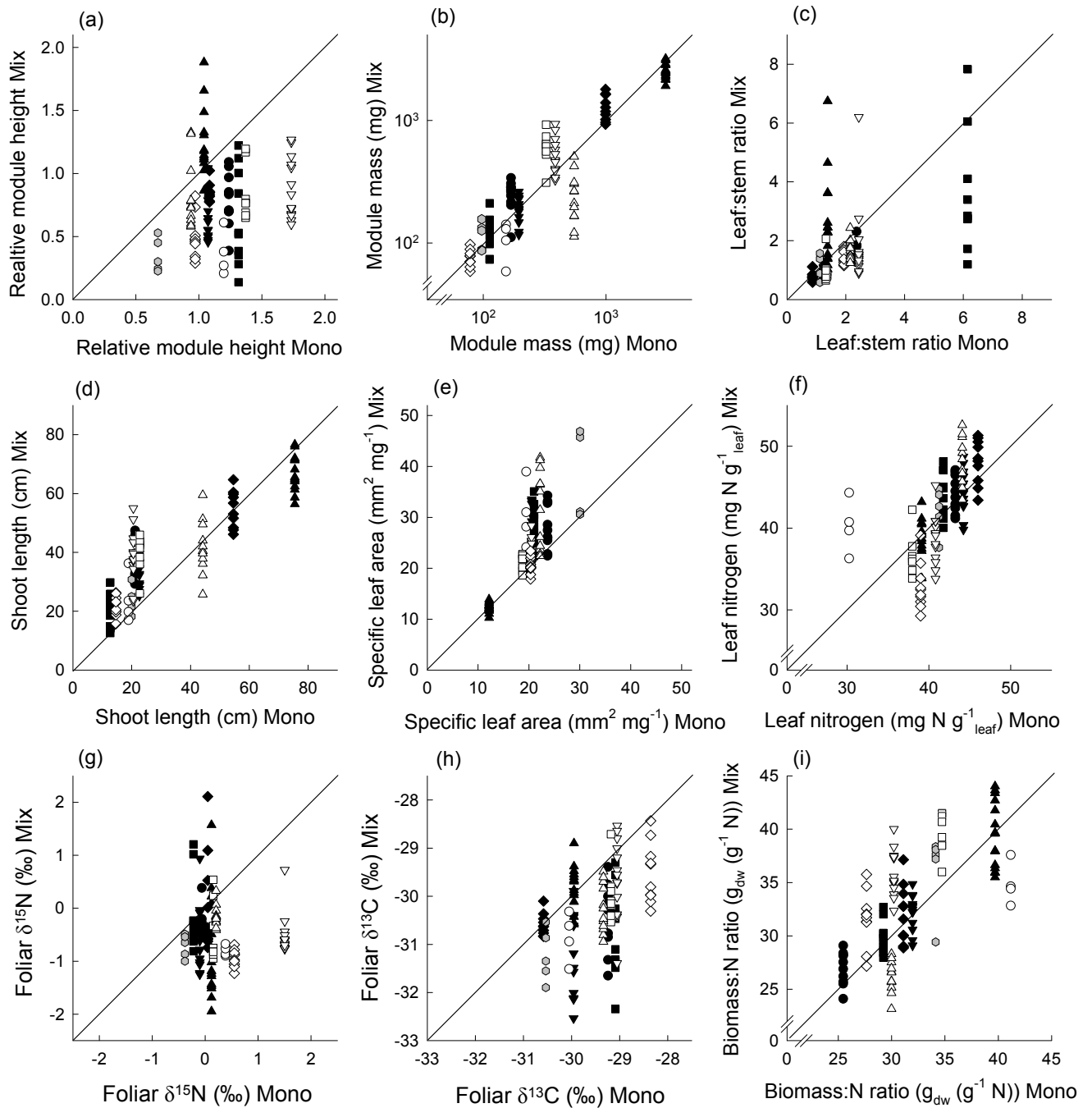


Figure S3: Trait values per species averaged across all plots (mean \pm SE) in late summer (before second mowing: Aug) plotted against trait values in early summer (before first mowing: June). For species symbols see Fig. 3.

