Community selection increases biodiversity effects

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Species extinctions from local communities can negatively affect ecosystem functioning[1]. Statistical and ecological mechanisms underlying these impacts are well studied[2-4] but the role of evolutionary mechanisms has rarely been addressed[5,6]. In particular, it is not known to what extent local populations are co-adapted, not only to their environment but also to each other, because such a co-adaption would suggest that species extinctions can result in a larger than expected decline in ecosystem functioning. We used a long-term field biodiversity experiment with 52 plant species to determine if natural selection at the level of entire communities intensified the effects of biodiversity on ecosystem functioning. We re-assembled communities with 8-year co-selection histories adjacent to communities with identical species composition but no history of co-selection on native soil from the experiment and on novel soil. Over four years, selected plant communities were more productive and expressed stronger biodiversity effects than naïve communities. Novel soil increased productivity initially but not in the longer term. Our findings suggest that plant community selection can lead to increased community-level functioning, regardless of the soil in which they were assembled. As a consequence, it may take many years to reconstruct well-functioning communities if one reassembles them with populations lacking a common selection history.

A large number of experiments have shown positive effects of species richness on ecosystem functioning, in particular plant biomass production[1,3,4,7-10]. These effects have been explained by statistical sampling, increasing the chances of including productive species in diverse communities[2,3], or by ecological complementary of species, which allows plant mixtures to extract resources more efficiently from the environment[2,4]. Furthermore, species-rich communities may host more diverse communities of enemies thereby diluting specialist pathogens commonly found in species-poor communities[11].

Functional complementarity between co-occurring species increases over time[8-10], likely through selection for niche differentiation[6]. However, the possibility that evolutionary processes shape the diversity–productivity relationship has rarely been tested, and only at the level of individual species[6] rather than at the level of entire communities. Community selection may be defined as genetically based changes among species constituting the community, which alter species performances and interactions[12]. Such changes may occur via genetic recombination, mutations[13], or sorting-out from standing genetic variation through differential mortality and growth of individuals[14]. Just as Darwinian natural selection can lead to changes in gene frequencies in populations within species, selection at the level of communities can lead to correlated changes in gene frequencies in multiple species[12] in response to one another or to co-varying environmental conditions. However, empirical evidence for community selection so far has only been found in planktonic and bacterial communities[15,16].

Recent evidence suggests that selection of particular genotypes from the total genetic pool of a species may affect ecosystem functioning in field experiments[6,17-22]. We propose that selection at the level of entire communities is even more likely to affect ecosystem functions, because of non-random niche or trait changes in response to other phenotypes in the community that result in filling niche space more fully or evenly. Hence, we expect that a community of species with a shared selection history will show a stronger biodiversity effect in comparison with communities assembled from species without such a shared community selection history. Our specific expectation applies to plant communities, but their interactions with other (living) components of the ecosystem may also play a role. For example, plant–soil feedback experiments have shown that soil biota change in response to different plant species, which can in turn modify the composition and productivity of plant communities[23,24].

Here we compare the diversity–productivity relationships of plant communities that have been intact communities for eight years in a long-term grassland biodiversity experiment (Jena Experiment[25]), and hence likely have evolved together as a community, with naïve plant communities without such a shared selection history. We used experimental plant communities of 1, 2, 4 or 8 species, and with 12 unique species compositions within each species richness level. To connect above- and belowground interactions we factorially combined two community components under selection, plants and soils. We grew selected and naïve plant communities for four years in native soil with a common selection history with the selected plant communities or in novel soil (sterilized soil or neutral soil) without a common selection history with either selected or naïve plant communities (see Methods and Extended Data Fig. 1). In 2010, seeds for selected communities were produced from plants collected in Jena in an experimental garden in Zurich. Seeds for naïve communities were purchased from the original supplier of seeds for the Jena Experiment. Seedlings for selected and naïve communities were propagated in the glasshouse in Zurich and transplanted into the plots of the Jena Experiment in early spring 2011. Community-level plant productivity was measured each spring from 2012–2015 by collecting species-specific aboveground biomass (see Methods). The shape of the diversity–productivity relationship was quantified as a function of the logarithm of species richness using a second-degree polynomial.

Overall, for each doubling of species richness, community aboveground biomass increased by 100 $g \cdot m^{-2} \cdot y^{-1}$. However, between monocultures and 2- to 4-species mixtures this increase in productivity was steeper for selected plant communities than for naïve plant communities (Fig. 1; $F_{1, 132.3} = 7.219$, $P = 0.008$ for the interaction between community selection treatment and the quadratic term of species richness; Extended Data Table 1). Selected plant communities were also more productive on average than naïve communities ($F_{1,132.4} = 22.12$, $P < 0.001$). Furthermore, productivity increased with time in selected

98 communities but decreased in naïve ones ($F_{1,135.1} = 5.461$, $P = 0.021$). This was related to
99 increased performance of 2- and 4-species mixtures over time in selected communities and
100 the deterioration of monocultures in naïve communities (Fig. 1 and Extended Data Fig. 2).
101 We plotted the diversity–productivity relationships of the first four years (2003–2006, i.e.
102 before selection) of the Jena Experiment (Extended Data Fig. 3), which clearly resembled
103 such relationships in naïve communities but not in selected communities from 2012–2015
104 (Fig. 1).

105 Community productivity initially increased in novel soil and at high diversity (Fig. 2),
106 reflected in an overall main effect of soil treatment ($F_{1,89.6} = 23.91$, $P < 0.001$), a significant
107 soil treatment by year interaction ($F_{1,90.8} = 8.591$, $P = 0.004$) and a significant three-way
108 interaction of the latter with species richness ($F_{1,90.5} = 8.287$, $P = 0.005$). In part this might
109 have been caused by a nutrient flush from gamma-sterilization of the soil[26], which affected all
110 novel but only half of the native soil treatments (see Methods). However, the use of native vs.
111 novel soils did not alter the differences in biodiversity effects between selected and naïve
112 plant communities ($F_{1,131.2} = 0.001$, $P = 0.973$ and $F_{1,132.0} = 0.566$, $P = 0.453$ for the three-way
113 interactions of soil treatment with community selection treatment and log-linear and
114 quadratic species richness terms, respectively).

115 Our results show that eight years of selection in plant communities in a biodiversity
116 experiment can increase the slope of diversity–productivity relationships, suggesting
117 community selection may at least in part explain why biodiversity effects commonly increase
118 over time in such experiments[8-10]. Our community selection treatment increased the
119 biodiversity effect on community productivity especially from monocultures to 2- and 4-
120 species mixtures. In a previous study, we showed that eight years of selection led to increased
121 biodiversity effects in 2-species mixtures compared with monocultures due to character
122 displacement between individual species outside their community context[6]. It is conceivable

123 that such processes become less effective or take more time to evolve when communities of
124 more than 2–4 species are considered. In addition, selection for increased growth in mixture
125 may be compromised by reduced pathogen defence[27]. This may explain why 8-species
126 mixtures were initially much more productive in novel than in native soil (Fig. 2 and
127 Extended Data Fig. 2). Within-species variance in specific leaf area (SLA) decreased in
128 selected and increased in naïve communities with increasing species richness (Extended Data
129 Fig. 4, $F_{1,69.2} = 4.87$, $P = 0.031$). The narrowing of within-species variance with increasing
130 diversity in selected communities may thus underlie character displacement between species.
131 In contrast, species in monocultures may have been selected for niche expansion resulting in
132 increased within-species variance. Species in naïve communities had not yet responded to
133 different diversity treatments with a similar adjustment in within-species variance in the four
134 years of this study; their higher variance at high diversity may stem from a more
135 heterogeneous biotic environment.

136 The focus of our study was community selection; however, our results are consistent
137 with the few studies concerning species selection in biodiversity experiments[6,21,22]. Our
138 community selection treatments led to an increased species-level productivity for most of our
139 species (Fig. 3). Eight years of selection increased biodiversity effects in selected
140 communities, naïve communities however did not catch up in the four years of growth of our
141 study, giving us some insights into the duration of the selection process: even if community
142 selection may occur mainly through sorting out from initial standing variation within plant
143 species, it may not occur immediately during seedling establishment and growth. The
144 inability of naïve communities to adapt could most clearly be seen in the deterioration of
145 monocultures, potentially due to pathogen accumulation[11], both in native and with some
146 delay in novel soil (Extended Data Fig. 2).

The generally lower productivity in native soil, and with time in novel soil, may have occurred through nutrient depletion or stronger plant-pathogenic effects compared with plant-mutualistic soil organisms[28]. Previous studies in the context of biodiversity–ecosystem functioning research reported negative plant–soil feedbacks on home soils[24,29], possibly through the accumulation of specialized pathogenic microbes[11]. The relatively rapid approach of the slope and shape of the diversity–productivity relationship in novel soil to the relationship in native soil (Fig. 2) may have been due to the large population sizes and short generation times of most soil organisms, allowing for fast re-assembly and evolution of soil communities[19].

Changes have been observed in the performance of individual species selected in different species diversity and tested under experimental abiotic or biotic conditions in previous studies[6,21,22]. In our study we demonstrated for the first time that changes in the performance of entire plant communities through time may depend on a shared community selection history of the assembled species. An ecosystem with individuals adapted to optimise the use of the local resources by reducing interspecific competition, will be a well-functioning and sustainable system as a whole[30]. Our new findings suggest that it is not sufficient to preserve species outside a community context for the conservation of biodiversity and its beneficial effects on ecosystem functioning and services. To protect species interactions and ecosystem functioning more efficiently, novel strategies should consider the conservation of entire communities or at least subsets of these.

Online content Methods, along with additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author contributions B.S., D.B.F. and G.B.D.D. conceived the project; D.Z-D. and V.Y. set up the experiment; S.J.V.M., T.H., D. Z-D. and V.Y. carried out the experiment; B.S., C.W., S.J.V.M. and T.H. analysed the data; D.B.F. analysed the TRFLP data; B.S., S.J.V.M., T.H. and C.W. wrote the first draft of the manuscript. All authors contributed to the final manuscript.

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263 METHODS

264 **Study site.** The present study was conducted at the Jena Experiment field site (Jena,
265 Thuringia, Germany, 51˚N, 11˚E, 135m a.s.l.) from 2011 to 2015. The Jena Experiment is a
266 long-term biodiversity field experiment located in the floodplain of the river Saale where 60
267 Central European grassland species have been grown in a number of species combinations
268 since 2002[25].

269 **Plant community selection.** The 48 experimental plant communities of this study included
270 twelve monocultures, twelve 2-species mixtures, twelve 4-species mixtures and twelve 8-
271 species mixtures. We used two community selection treatments; plants with eight years of
272 shared community selection in the Jena Experiment (selected communities) and plants
273 without a common selection history in the Jena Experiment (naïve communities). The plant
274 seeds without a common selection history were obtained from the same commercial seed
275 supplier (Rieger Hofmann GmbH, in Blaufelden-Raboldshausen, Germany) as the seeds used
276 for the establishment of the original experimental plant communities. This supplier collected
277 plants of the different species at field sites in Germany and propagated them for at least 5
278 years in monoculture, reseeding them every year. Seeds of selected communities were
279 produced in an experimental garden in Zurich, Switzerland, from cuttings that had been made
280 in the Jena experiment and were then planted in Zurich in the original species combination in
281 plots fenced with plastic netting to reduce pollination between communities. To obtain
282 sufficient numbers of seeds from selected communities a small number was additionally
283 collected directly in the plots of the Jena Experiment. All these seeds were thus offspring of
284 plant populations that had been sown in 2002 and grown until 2010 in plots of the Jena
285 Experiment.

286 The seeds of selected and naïve communities were germinated on potting soil (BF4,
287 De Baat; Holland) in mid-January 2011 in a glasshouse in Zurich. In March 2011, the
288 seedlings were transported back to the Jena Experiment field site within 2 x 2 m subplots of
289 the original plots (Extended Data Fig. 1). There were four 1 x 1 m quadrats with different soil
290 types in each subplot (see next section). Each quadrat was split into two 1 x 0.5 m halves. We
291 transplanted seedlings of selected communities into one half and seedlings of naïve
292 communities into the other half of each quadrat at a density of 210 plants per m^2 with a 6-cm
293 distance between individuals in a hexagonal pattern (Extended Data Fig. 1). Species were
294 planted in equal proportions, but if a species was no longer present in an original plot of the
295 Jena Experiment it was excluded from both selected and naïve communities. Five plant
296 species were excluded in total. The seedlings received water every second day for 6 weeks
297 after transplanting to ensure the plants established.

298 **Soil treatment**. Within each 2 x 2 m subplot of the 48 plots of the Jena Experiment used for
299 the present study, the original plant cover was removed in September 2010 (and used for the
300 plant propagation in the experimental garden in Zurich, see above), and the soil was
301 excavated to a depth of 0.35 m and sieved. To minimize exchange of soil components
302 between quadrats within subplots and with the surrounding soil, two 5-cm layers of sand
303 were added to the bottom of the plots and separated with a 0.5 mm mesh net. The borders of
304 the quadrats and the subplots were separated by plastic frames (Extended Data Fig. 1). Using
305 the excavated original soil from each of the plots, four soil treatments were prepared. First,
306 half of the soil (approximately 600 kg per plot) was gamma-sterilized to remove the original
307 soil community. Half of the gamma-sterilized soil was then inoculated with 4 % (by weight)
308 of live sugar-beet soil and 4 % of sterilized original soil of the corresponding plot ("novel
309 soil" obtained by inoculation). Live sugar-beet soil was added to create a natural, but neutral
310 soil community and was previously collected in an agricultural sugar-beet field not associated

311 with the Jena Experiment, but with comparable soil properties. The other half of the gamma-
312 sterilized soil was inoculated with 4 % (by weight) of live sugar-beet soil and 4 % of live
313 original soil of the corresponding plot ("native soil" obtained by inoculation). The other half
314 of the soil was unsterilized and used for the other two soil treatments. Half of this soil was
315 filled back into one quadrat of the corresponding plot ("native soil"). The other half of the
316 unsterilized soil was mixed among all 48 plots and filled into the remaining quadrats. This
317 fourth soil treatment was abandoned after two years because the plant community was
318 excavated for another experiment. Therefore, this treatment is not included in the present
319 study.

320 Before the soils were added into the quadrats in December 2010, they were rested in
321 the field in closed bags to allow for the soil chemistry to equalize and to encourage soil biota
322 of the inocula to colonize the sterilized soil before planting. After the soil was added, all
323 quadrats were covered with a net and a water permeable black sheet to avoid spilling between
324 quadrats until the seedlings were transplanted in March 2011.

325 **Maintenance and data collection.** We maintained the test communities by weeding three
326 times a year and by cutting the plants to 3 cm above ground twice a year at typical grassland
327 harvest times (late May and August) in central Europe. To measure above ground biomass,
328 we harvested plant material 3 cm above ground from a 50 x 20 cm area in the center of each
329 half-quadrat, sorted it into species, dried it at 70°C and weighed the dry biomass.

330 **T-RFLP assay.** Terminal restricted fragment length polymorphism (T-RFLP) targeting the
331 16S RNA was used to characterize the composition of the soil bacterial communities[31]. In
332 April 2011, four soil samples per quadrat were extracted and pooled to assess the
333 establishment of soil microbial communities and to test whether soil treatments were distinct.
334 In 2012, a further set of soil samples was taken and analysed to confirm the establishment of
335 different soil biotic treatments. T-RFLP soil analyses revealed that bacterial communities of

336 the soil treatments remained distinct: each soil treatment had a characteristic bacterial
337 composition both one and two years after planting, with some overlap (Extended Data Fig. 5,
338 Extended Data Table 2).

339 **Statistical analysis.** For the present study, we analysed the data from four spring harvests
340 (2012, 2013, 2014 and 2015), which correspond to peak aboveground plant biomass values.
341 We analysed plant biomass (g/m^2) as a function of the design variables using mixed models
342 and summarized results in analyses of variance (ANOVA) tables (Extended Data Table 1).
343 Significance tests were based on approximate F-tests using appropriate error terms and
344 denominator degrees of freedom.

345 The fixed terms in the model were log-transformed species richness of the original
346 plots of the Jena Experiment (linear and quadratic), year of harvest (linear contrast and factor:
347 lH and fH, respectively), soil treatment (native vs. novel soil: SH), plant community selection
348 treatment (selected vs. naïve communities: PH) and interactions of these. The random terms
349 were plot, quadrat, half-quadrat and their interactions with time. Statistical analyses were
350 conducted using the software product R, version 3.2.3[32]. Mixed models using residual
351 maximum likelihood (REML) were fitted using the package ASReml for R[33].

352 The calculation of operational taxonomic units (OTUs) from the T-RFLP raw data
353 (restriction enzyme products) was done using the T-RFLP processing software T-REX[34] for
354 each soil treatment and year separately and the soil-specific outputs were then compared with
355 an analysis of similarities (anosim() function of the vegan package[35]). R-values and P-values
356 were extracted and the results were visualized using NMDS ordination[36].

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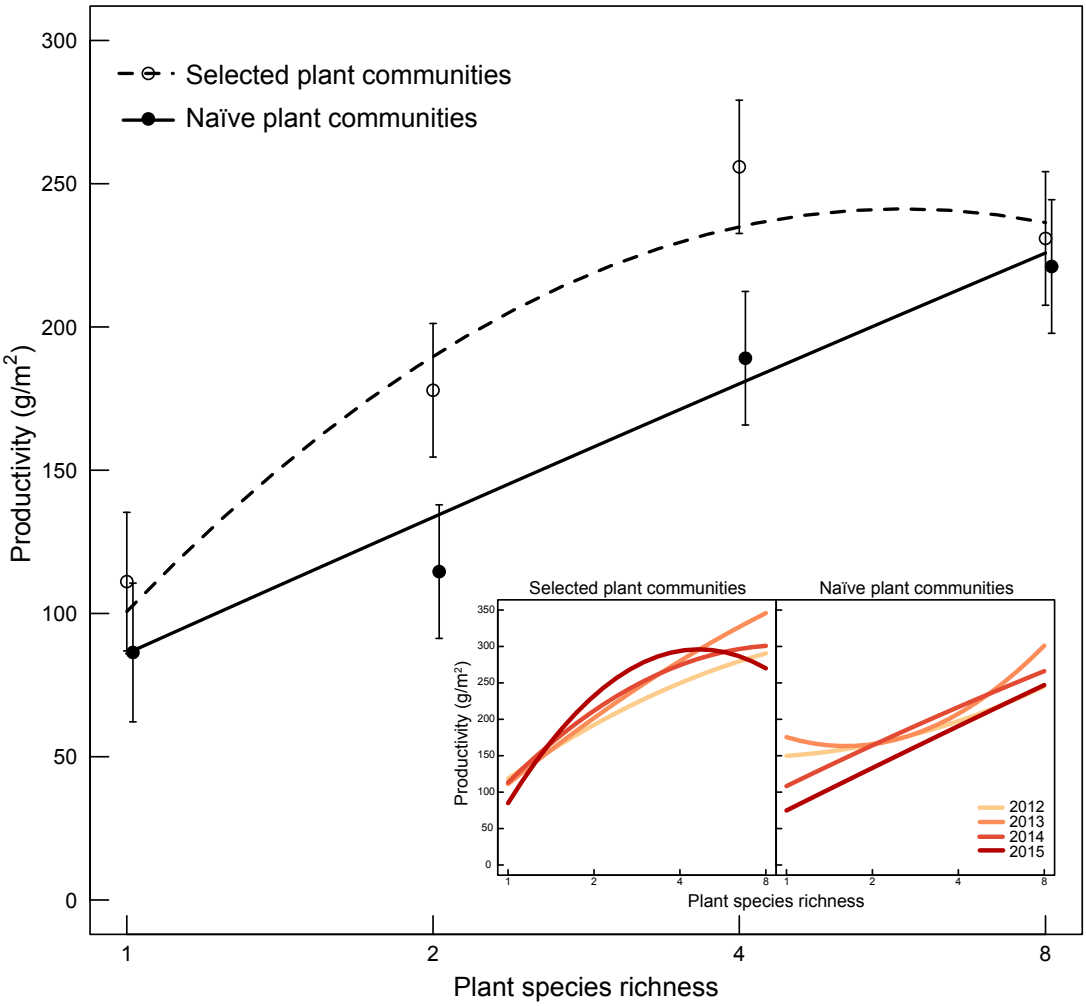

Figure 1 | Selected plant communities show stronger biodiversity effects than naïve plant communities. In selected plant communities, the increase in productivity from monocultures to 2- and 4-species mixtures was stronger than in naïve plant communities. Main panel: Quadratic response curves are derived from a mixed model. Points are predicted means and standard errors derived from a mixed model including fixed-effects terms for species richness and community selection history and random-effects terms for plot, quadrat and half-quadrat (see Methods). Data are across four consecutive years. Inset panel: separate regression lines for years, with darker colours representing later years.

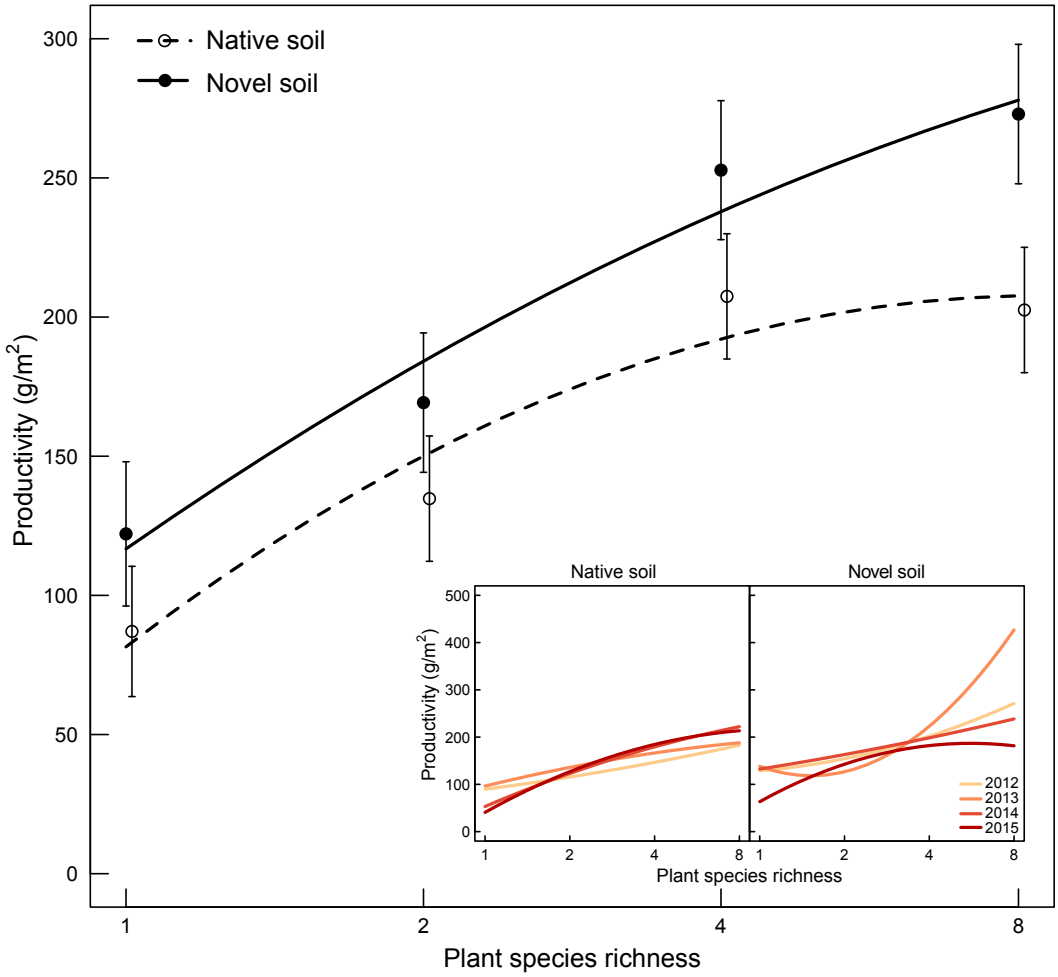

Figure 2 | Diversity–productivity relationships are initially enhanced in novel soil but over time approach those in native soil. In native soil, community productivity was lower in comparison to novel soil but the diversity–productivity relationships remained stable over time. Over time, the relationships in novel soil approached those in native soil (see inset panel). Main panel: Quadratic response curves are derived from a mixed model. Points are predicted means and standard errors derived from a mixed model including fixed-effects terms for species richness and soil treatment and random-effects terms for plot, quadrat and half-quadrat (see Methods). Data are across four consecutive years. Inset panel: separate regression lines for years, with darker colours representing later years.

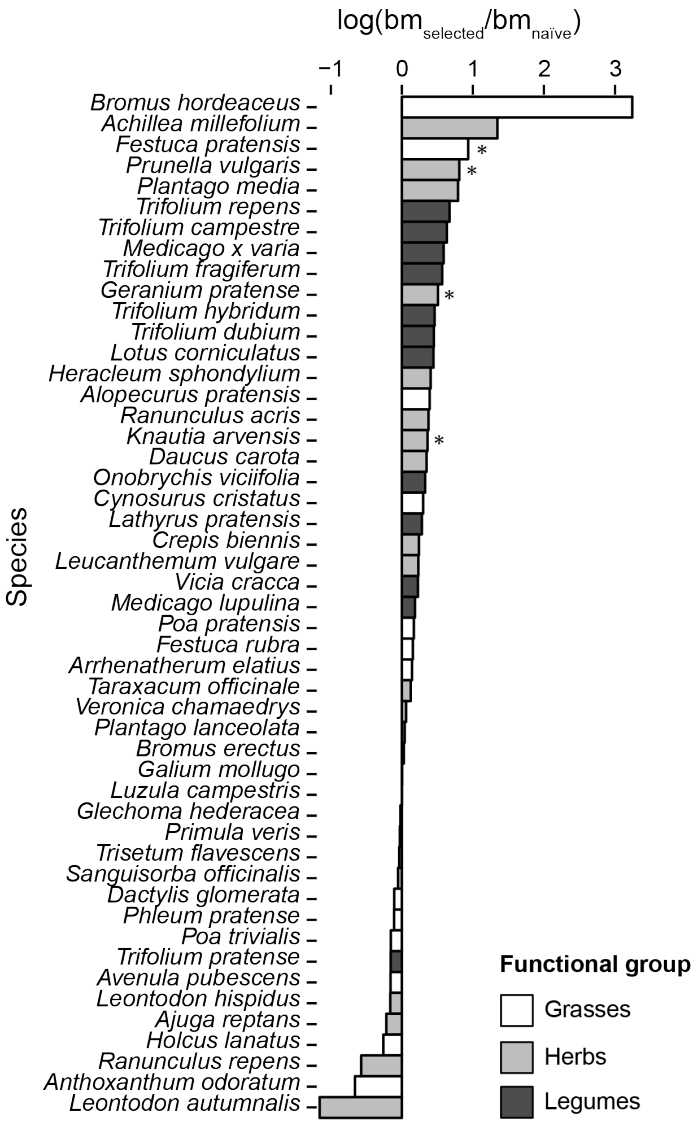

Figure 3 | Log-transformed species biomass ratios between selected and naïve plant communities. The majority of plant species attained greater aboveground biomass in selected plant communities compared to naïve plant communities. The studied plant species belong to three different functional groups: grasses (white bars), herbs (light grey bars) and legumes (dark grey bars). Data are for each species across all four experimental years, across soil treatments and across species richness levels (n = 32–352). Four species with n < 32 were excluded from the analysis. The stars represent P-values < 0.05 for species tested separately.