Community evolution increases plant productivity at low diversity

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Species extinctions from local communities can negatively affect ecosystem functioning[1]. Ecological mechanisms underlying these impacts are well studied[2–4] but the role of evolutionary processes is rarely assessed[5,6]. Using a long-term field experiment, we tested whether natural selection in plant communities increased the effects of biodiversity on productivity. We re-assembled communities with 8-year co-selection history adjacent to naïve communities with identical species composition but no history of co-selection. Mixtures of two to four co-selected species were more productive than their corresponding naïve communities over four years in soils with or without co-selected microbial communities. At the highest diversity level of eight plant species, no such differences were observed. Our findings suggest that plant community evolution can lead to rapid increases in ecosystem functioning at low diversity but may take longer at high diversity. This effect was not modified by treatments that simulated additional co-evolutionary processes between plants and soil organisms.

A large number of experiments have shown that species richness positively influences ecosystem functioning, in particular plant biomass production[1,3,4,7–10]. These biodiversity effects have been explained by sampling effects that increase the chance of including productive species in diverse communities[2,3] or by complementary effects between species, which allow mixtures to extract resources from the environment more efficiently[11,12]. Furthermore, diversity-dependent reductions in soil fertility[13] or density-dependent accumulations of specialist pathogens over time[14] have been shown to contribute to decreasing productivity at low plant diversity and in plant monocultures.

Complementarity effects between co-occurring species increase over time[8–10,15]. Evidence that this might be due to evolutionary processes in plant communities has been found in a glasshouse experiment comparing the performance of populations selected in monocultures vs. diverse plant communities in newly assembled test monocultures and two-

species mixtures[6]. This suggests that community evolution may shape diversity–productivity relationship more generally, which could be tested if entire communities of co-selected plant species would be compared with communities of the same plant species but without co-selection history. Community evolution has been defined as genetically based changes among species constituting the community, which alter species performances and interactions[16]. Such changes may occur via genetic recombination, mutations[17], or a sorting-out from standing genetic variation through differential survival and growth of individuals[18]. Natural selection can lead not only to changes in gene frequencies in populations within species, but selection at the level of communities can in addition lead to correlated changes in gene frequencies in multiple species[16] in response to one another or to co-varying environmental conditions. But empirical evidence for community evolution so far has only been demonstrated in planktonic and bacterial communities[19–22] and not yet in higher plants. Here we report results from a field experiment where we tested whether plant community evolution influences plant community productivity.

Recent evidence suggests selection of particular genotypes from the total genetic pool of a species may affect ecosystem functioning in field experiments[21,23–27]. We propose that selection of genotypes from the gene pool of entire communities may affect ecosystem functioning if non-random niche or trait changes in response to other phenotypes in the community result in reduced niche overlap and a more complete use of biotope space[28,29], thus leading to increased plant community productivity. We therefore compared the productivity of plant communities assembled from plants which have co-occurred for eight years in a long-term grassland biodiversity experiment (the Jena Experiment[30]) with the productivity of plant communities of identical species composition, but without any co-occurrence history ("naïve communities"). The naïve species were obtained from the seed supplier of the original seeds used to establish the Jena Experiment. We used experimental

plant monocultures and 2-, 4- or 8-species mixtures with twelve different species compositions for each diversity level.

Plant community evolution in the field may also depend on the local environment, such as the soils in which co-evolution with soil microorganisms occurred. For instance, 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[31–33]. To assess whether additional co-evolutionary processes between plants and soil organisms modified plant community evolution, we grew the selected and naïve plant communities in soils with co-selected soil organisms (native soil) and with external soil organisms (neutral soil; see Methods and Extended Data Fig. 1). Community-level plant productivity was measured each year from 2012 to 2015 by collecting species-specific aboveground biomass at the time of peak biomass in spring (see Methods).

Results

Overall, for each doubling of species richness community aboveground biomass increased by 100 $g \cdot m^{-2} \cdot y^{-1}$, a typical value for grassland biodiversity experiments[34]. In general, communities of co-selected plants were more productive than naïve communities of the same species composition. The significant interaction between species richness and community-evolution treatment or in short plant history ($F_{3,191.2} = 2.77$, $P = 0.043$; Extended Data Table 1a) indicated that this was mainly due to increased productivity of 2- and 4-species mixtures and a smaller increase in monocultures of co-selected plants. In contrast, 8-species mixtures of co-selected or naïve plants were equally productive (Fig. 1a). The calculated relative productivity (percentage of the mean productivity of 8-species mixtures for each plant history-by-soil treatment-by-year combination) confirmed that especially 2- and 4-species mixtures of co-selected plants increased productivity relative to 8-species

98 mixtures ($F_{3,191.9}$ = 2.90, P = 0.036; Fig. 1b; Extended Data Table 1b). The positive effect of
99 community evolution on relative productivity was significantly larger in 2- and 4-species
100 mixtures than in monocultures ($F_{1,43.7}$ = 6.37, P = 0.015 for the interaction between plant
101 history and the contrast of "2- or 4- species mixtures vs. others"). The differences in relative
102 productivity between communities of co-selected plants and naïve communities increased
103 over time for these low-diversity mixtures as well as for monocultures in all three soils (Fig.
104 2). For monocultures, this was due to the deteriorating performance of naïve plants, possibly
105 due to the accumulation of soil pathogens, whereas for 2- and 4-species mixtures it was due
106 to an increasing relative performance of communities of co-selected plants.

107 To test whether the communities of co-selected plants were particularly productive in
108 2- and 4-species mixtures at the beginning of the Jena Experiment (i.e. when they were
109 "naïve" communities themselves), we compared the productivity data of 2003–2006 with the
110 data of 2012–2015. To standardize for differences in overall productivity between time
111 periods we again used relative productivity (percentage of mean of 8-species mixtures per
112 year). The plant communities were established in neutral soil in 2002 at the beginning of the
113 experiment. We therefore used only data from neutral soil from 2012 to 2015. The
114 communities of co-selected plants were significantly different in their response compared to
115 the two types of naïve communities because of their increased relative productivity in 2- and
116 4- species mixtures ($F_{1,46.5}$ = 5.73, P = 0.021 for the interaction of plant history with the
117 contrast "2- or 4- species mixtures vs. others"; Extended Data Fig. 2). Differences between
118 the communities of the naïve ancestors of the co-selected plants and our current re-assembled
119 naïve plant communities were small and not significant ($F_{1,46.1}$ = 0.23, P = 0.637 for the
120 interaction of the contrast "naïve ancestors vs. current naïve communities" with the contrast
121 "2- or 4- species mixtures vs. others").

122 Plant community productivity was initially greater in inoculated soils, in particular at
123 high diversity, which was reflected in an overall main effect of soil treatment and significant
124 interactions with year, and with year and species richness (Extended Data Table 1). This was
125 probably caused by the nutrient flush associated with gamma-sterilization of the soil[35]. But
126 we found no evidence that our soil treatments modified the differences in biodiversity effects
127 between communities of co-selected plants and naïve communities ($F_{1,183}$= 0.27, P = 0.847
128 and $F_{1,183.8}$= 1.401 P = 0.244 for the three-way interactions of plant history with species
129 richness and the soil-treatment contrasts neutral vs. native and sterilized native vs.
130 unsterilized native, respectively).

131 To explore potential mechanisms for the increased biodiversity effects in 2- and 4-
132 species mixtures of co-selected plants, we calculated the proportional increase (decrease) in
133 plant productivity for each community composition and soil treatment as the log ratio
134 between communities of co-selected plants and naïve communities (Fig. 3). As expected,
135 there was no increase in productivity in 8-species mixtures, but a strong increase in 2-species
136 mixtures followed by 4-species mixtures (which had a higher absolute increase than 2-species
137 mixtures, see Fig. 1a) and monocultures. Using contrasts between the different diversity
138 levels, we could confirm that the three low diversity levels were significantly different form
139 the 8-species mixtures ($F_{1,37.1}$ = 5.34 and P = 0.026). Among the three low diversity levels,
140 the 2-species mixtures had significantly greater log ratios than 4-species mixtures and
141 monocultures ($F_{1,39.2}$ = 4.44, P = 0.042).

142 Next, we tested whether the presence of particular plant functional groups influenced
143 the increase in productivity in communities of co-selected plants at the 2- and 4-species
144 richness levels; especially as legumes are known to drive over-yielding in grasslands[36]. The
145 presence of legumes and other plant functional groups, however, did not provide any further
146 explanation for our results. Species-level productivity within communities was higher for the

147 majority of plant species with a co-selection history, irrespective of functional-group identity
148 (Fig. 4). Naïve communities showed more even species abundance distributions ($F_{1,132.2}$ =
149 4.28, P = 0.041; Extended Data Table 2), mainly due to the lower evenness of communities
150 of co-selected plants in the unsterilized native soil treatment (Extended Data Fig. 3). Over the
151 course of the experiment, evenness decreased similarly in communities of co-selected plants
152 and naïve communities (Extended Data Table 2).

153 Finally, we analysed changes in within-species trait variation along the species
154 richness gradient as a potential mechanism contributing to the difference in productivity
155 between communities of co-selected plants and naïve communities[37]. Within-species
156 variation in specific leaf area (SLA) decreased for communities of co-selected plants and
157 increased for naïve communities with increasing species richness (Fig. 5; $F_{1,69.2}$ = 4.87, P =
158 0.031 for interaction of log species richness with plant history).

159

160 Discussion

161 Our results show that eight years of community evolution in a biodiversity experiment
162 can increase biodiversity effects on community productivity, suggesting that this may at least
163 in part explain why biodiversity effects commonly increase over time in such experiments[8–
164 10,15]. The greater productivity in communities consisting of co-selected plants compared to
165 communities consisting of naïve plants was particularly evident in communities comprised of
166 two or four species. One might claim that these effects were because we purchased the plant
167 material of co-selected and naïve plants at two different points in time. We argue that this is
168 not the case for the following reasons. First, co-selected and naïve plants were obtained for
169 52 different species and for each of them there were different community-specific co-
170 selection histories. Second, 8-species mixtures with and without co-selection history showed
171 the same productivity. In other words, because the positive effect of the community-evolution

172 treatment was not statistically evident in the 8-species mixtures but strong in 2- and 4-
173 species mixtures, this effect was unlikely simply due to initial differences in plant material.

174 Why was the community-evolution treatment not effective at the highest richness
175 level tested? It is conceivable that selection pressure was dampened in communities where
176 more than four species co-occurred. For instance, during initial establishment in a diverse
177 community, each individual can have a very different set of immediate neighbours that could
178 constrain the consistency in the selection pressure on individuals within a community. With
179 fewer species in a mixture, the potential for the evolution of increased complementarity
180 between plant species should be greater, given the relative constancy of the neighbours any
181 given plant experiences. The greater proportional (but not absolute) increase of productivity
182 in communities of co-selected plant species at the 2-species level than at the 4-species
183 richness level, and the absence of such an increase at the 8-species richness level, are
184 compatible with the idea that evolution for co-adaptation is stronger at low than at high
185 diversity. At low diversity, intraspecific densities are higher and thus the chance for a
186 uniform selection pressure across all intraspecific individuals is greater. As a consequence,
187 there might be an upper limit of species richness beyond which selection is unlikely to
188 strengthen biodiversity effects[1]. Additionally, community evolution leading to increased plant
189 growth and productivity in diverse mixtures may be at the expense of reduced pathogen
190 defence[38]. This may explain why 8-species mixtures were initially much more productive in
191 neutral than in native soil.

192 The performance of the naïve communities in the current study over the four years
193 was comparable to the initial performance of the ancestral community of the co-selected
194 plants (2003–2006). This similarity supports the view that the observed results at 2- and 4-
195 species richness levels in communities of co-selected compared with communities of naïve
196 plants are likely due to diversity-dependent community evolution. Indeed, the naïve

197 communities did not catch up with the communities of co-selected plants during the course of
198 the current experiment and differences in productivity from 2012 to 2015 even increased
199 between the two community-evolution treatments (Fig. 2). With regard to underlying
200 evolutionary mechanisms, this suggests that in our study community evolution was not or at
201 least not solely due to an immediate sorting out of genotypes from standing variation[17] during
202 seedling establishment and initial growth.

203 The driving force behind community evolution for greater productivity at low
204 diversity could have been related to particular species compositions[6]. There was, however, no
205 evidence for any plant functional-group specific effect typically found in other contexts of
206 biodiversity–ecosystem functioning research[36,39]. In fact, the majority of species produced
207 greater biomass in communities of co-selected plants and evenness was only slightly reduced
208 in these communities compared with communities of naïve plants.

209 Intraspecific variation in SLA decreased in communities of co-selected plants and
210 increased in naïve communities with increasing species richness (Fig. 5), a result in line with
211 previous findings for SLA in grassland species[40]. The increased within-species variation in
212 monocultures suggests an evolutionary broadening of niches to benefit from a wider range of
213 light conditions. In contrast, within-species trait variation may be less important in mixtures,
214 due to the inherently lower intraspecific density at greater richness. The narrowing of within-
215 species variation with increasing diversity in communities of co-selected plants could be an
216 expected consequence of character displacement between species[6]. In relative terms, it
217 seemed that species in naïve communities had not yet responded to different diversity
218 treatments with an adjustment of within-species variation in the four years of this study. A
219 more heterogeneous biotic environment may have caused their higher variation at high
220 diversity.

221 Selected plants also had greater productivity than naïve plants in monoculture. The
222 adaptation of selected plants to monoculture environments could have been due to the
223 evolution of increased (belowground) pathogen defence[41] or greater niche width[42]. Assuming
224 soil-borne plant pathogens accumulated over time[14], in particular in the initially sterilized
225 treatments, the decrease in monoculture productivity in naïve communities (Fig. 2) would be
226 consistent with the hypothesis of increased pathogen defence in selected communities[41].
227 Assuming a correlation between resource-uptake and trait-based niches[43], the increase in
228 within-species variation in SLA in monocultures of selected plants (Fig. 5) would be
229 consistent with the second explanation related to niche width.

230 Positive plant diversity–productivity relationships may not only be driven by
231 complementary resource use, and thus increased performance at high diversity[11,12], but also
232 by pathogen accumulation in the soil and thus reduced performance at low diversity[14].
233 Previous studies in the context of biodiversity–ecosystem functioning research have reported
234 negative plant–soil feedbacks in native as opposed to neutral soils[32,44,45]. Consequently, an
235 increase of biodiversity effects during community evolution could also be due to the presence
236 of co-selected soil biota. In our study, however, the outcome of the community-evolution
237 treatment in mixtures was largely independent of the presence of co-selected soil biota. The
238 generally lower productivity for both communities of co-selected plants and naïve
239 communities in native soil, and with time in neutral soil, may have occurred through nutrient
240 depletion or pathogen accumulation in all soil treatments. It is conceivable that co-evolution
241 of plants with soil biota in our experimental systems was not effective because the large
242 population sizes and short generation times of most soil organisms contributed to the re-
243 assembly and fast evolution of soil communities[24]. Another explanation could be that
244 microbes were dispersed via wind-blown particles to adjacent plots thereby potentially

245 making the microbial communities less different in composition than if the plots would have
246 been separated more in space.

247 Changes in the performance of individual species selected in different species
248 diversity levels and tested under experimental abiotic or biotic conditions have been observed
249 in previous studies[6,25–27]. In our study, we demonstrated for the first time that changes in the
250 performance of entire plant communities over time depend on a history of co-selection
251 among the plants species of the assembled mixtures. We suggest that these changes are the
252 result of community evolution because they were maintained through seed production in an
253 experimental garden and propagation of seedlings in a glasshouse to the replanting of
254 communities in the field. However, we cannot exclude maternal carry-over and epigenetic
255 changes[46] as additional potential evolutionary mechanisms. Independent of the mechanism,
256 an ecosystem with individuals adapted to optimize the use of the local resources by reducing
257 interspecific competition will be a well-functioning and sustainable system. Our new findings
258 suggest that it is not sufficient to preserve species outside a community context for the
259 conservation of biodiversity and its beneficial influence on ecosystem functioning and
260 services. To protect species interactions and ecosystem functioning more efficiently, novel
261 strategies should consider the conservation of entire communities or at least subsets of these.
262 Our results emphasize that this is especially critical for less diverse communities, which may
263 already suffer from the loss of some of their constituents.

264

265 Methods

266 **Study site.** The present study was conducted at the Jena Experiment field site (Jena,
267 Thuringia, Germany, 51˚N, 11˚E, 135m a.s.l.) from 2011 to 2015. The Jena Experiment is a
268 long-term biodiversity field experiment located in the floodplain of the river Saale where 60

269 Central European grassland species have been grown in a number of species combinations
270 since 2002[25].

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

289 The seeds of communities of co-selected plants and naïve communities were
290 germinated in potting soil (BF4, De Baat; Holland) in mid-January 2011 in a glasshouse in
291 Zurich. In March 2011, the seedlings were transported back to the field site of the Jena
292 Experiment and planted within 2 x 2 m subplots of the original plots (Extended Data Fig. 1).
293 There were four 1 x 1 m quadrats with different soil treatments in each (see next section).

294 Each quadrat was further divided into two 1 x 0.5 m halves. The seedlings of communities of
295 co-selected plants were transplanted into one half and seedlings of naïve communities into
296 the other half of each quadrat at a density of 210 plants per m^2 with a 6-cm distance between
297 individuals in a hexagonal pattern (Extended Data Fig. 1). Species were planted in equal
298 proportions, but if a species was no longer present in an original plot of the Jena Experiment
299 it was excluded from both communities of co-selected plants and naïve communities. Five
300 plant species were excluded in total. The seedlings received water every second day for six
301 weeks after transplanting to ensure the plants established.

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

319 filled back into one quadrat of the corresponding plot ("native soil"). The other half of the
320 unsterilized soil was mixed among all plots and filled into the remaining quadrats. This fourth
321 soil treatment was abandoned after two years because the plant community was excavated for
322 another experiment. Therefore, this treatment is not included in the present study.

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

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

333 **SLA measurements.** At the end of the experiment, in May 2015, we measured specific leaf
334 area (SLA) for 30 species in neutral soil. For each species, we collected up to 20
335 representative leaves (depending on the leaf size of the species) from four individuals and
336 measured the leaf area by scanning fresh leaves with a Li-3100 Area Meter (Li-cor Inc.,
337 Lincoln, Nebraska, USA) immediately after harvest and determining the mass of the same
338 leaves after drying.

339 **T-RFLP assay.** Terminal restricted fragment length polymorphism (T-RFLP) targeting the
340 16S RNA was used to characterize the composition of the soil bacterial communities[47]. In
341 April 2011, four soil samples per quadrat were extracted and pooled to assess the
342 establishment of soil microbial communities and to test whether soil treatments were distinct.

343 In 2012, a further set of soil samples was taken and analysed to confirm the establishment of
344 different soil biotic treatments. T-RFLP soil analyses revealed that bacterial communities of
345 the soil treatments remained distinct: each soil treatment had a characteristic bacterial
346 composition both one and two years after planting, with some overlap (Extended Data Table
347 3).

348 **Statistical analysis.** We analysed the data from the four spring harvests 2012, 2013, 2014
349 and 2015, which corresponded to peak aboveground plant biomass values. We analysed plant
350 biomass (g/m^2) as a function of the design variables using mixed models and summarized
351 results in analyses of variance (ANOVA) tables (e.g. Extended Data Table 1). Significance
352 tests were based on approximate F-tests using appropriate error terms and denominator
353 degrees of freedom.

354 The fixed terms in the model were species richness of the original plots of the Jena
355 Experiment (factor with 4 levels: facSR), year of harvest (factor with 4 levels: Har), soil
356 treatment (factor with 3 levels: SH), community-evolution treatment (communities of co-
357 selected plants vs. naïve communities: PH) and interactions of these. The random terms were
358 plot, quadrat, half-quadrat and their interactions with year of harvest. Statistical analyses
359 were conducted using the software R, version 3.2.3[48]. Mixed models using residual maximum
360 likelihood (REML) were fitted using the package ASReml for R[49].

361 Within-species variation in SLA was calculated as the within-species variance
362 component for each community (residual mean square after fitting species). We had
363 insufficient trait data to test for increased between-species variation in communities of co-
364 selected plants containing a mixture of species.

365 The calculation of operational taxonomic units (OTUs) from the T-RFLP raw data
366 (restriction enzyme products) was done using the T-RFLP processing software T-REX[50] for

each soil treatment and year separately and the soil-specific outputs were then compared with an analysis of similarities (anosim() function of the vegan package[51]).

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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.

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. set up the experiment; S.J.V.M., T.H. and D.Z.-D. 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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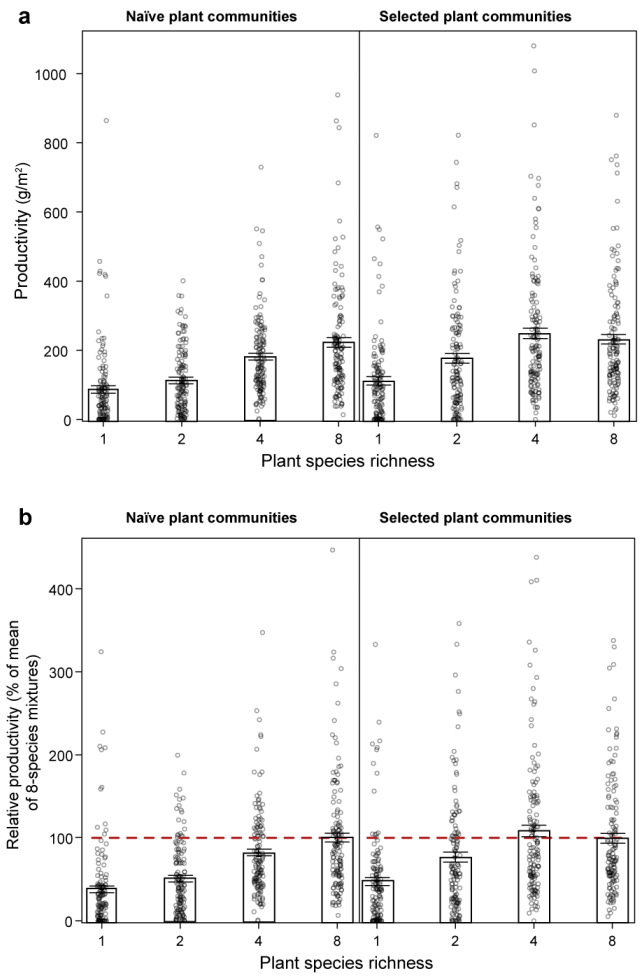

521

522 **Figure 1 | Community productivity for naïve communities and communities of co-**
523 **selected plants at different species-richness levels. a,** Peak community aboveground
524 biomass (g/m^2). Communities of co-selected plants (right panel) had slightly increased
525 productivity in monocultures, more strongly increased productivity in 2- and 4-species
526 mixtures, but similar productivity in 8-species mixtures as naïve communities (left panel). **b,**
527 as in (a) but showing relative productivity (% of mean productivity of 8-species mixtures per
528 plant history-by-soil treatment-by-year combination). Means and standard errors are shown.
529 Raw data plotted as points.

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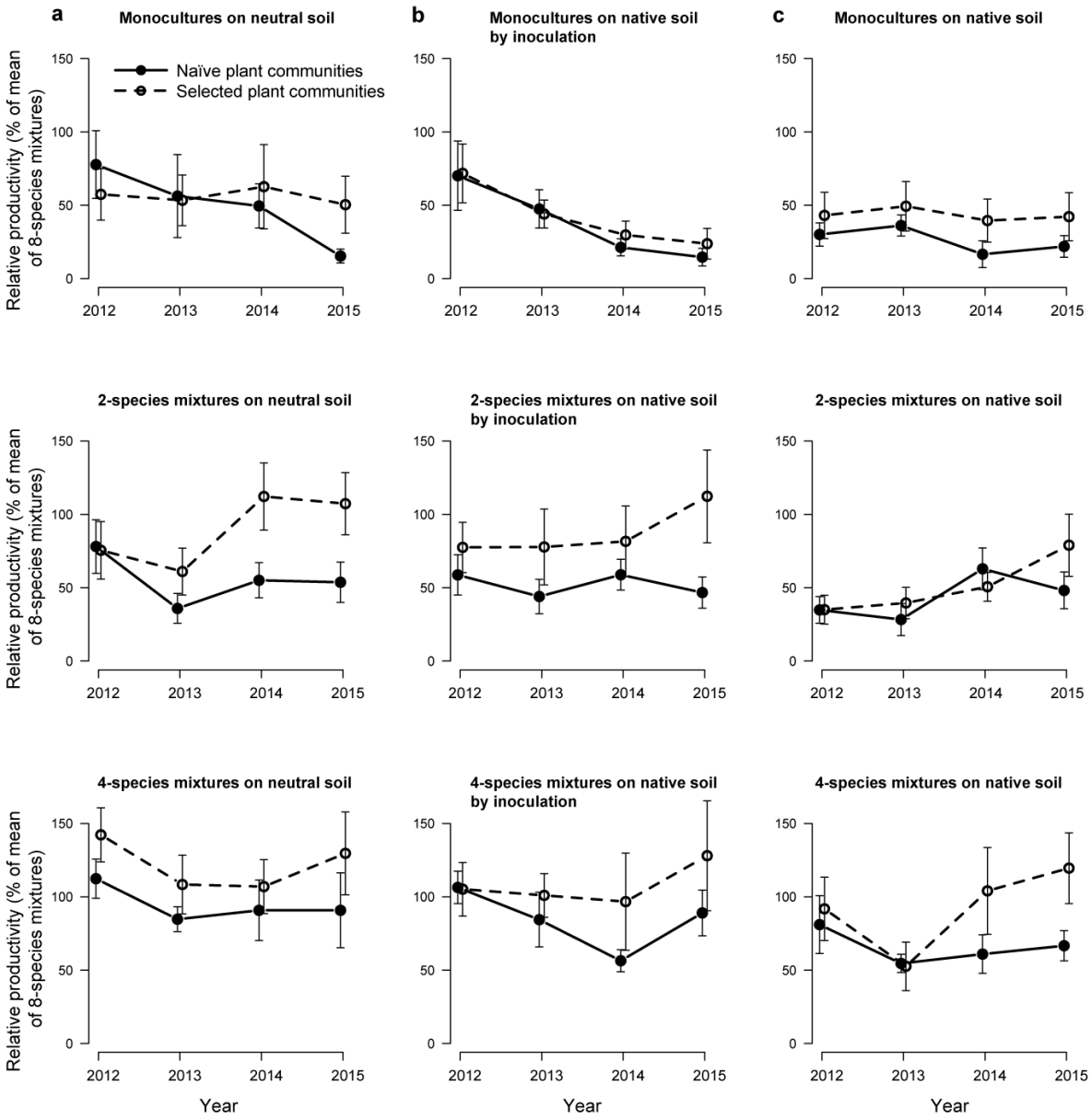
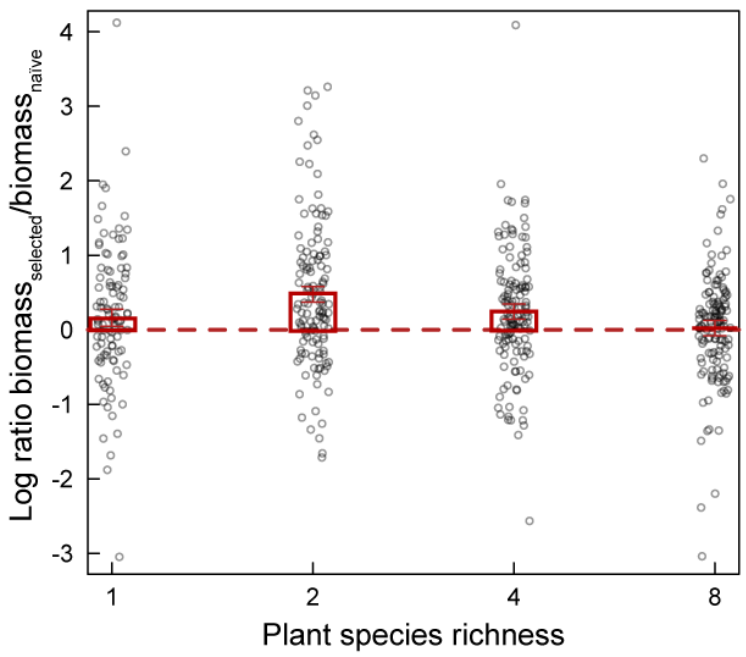

a
Monocultures on neutral soil
b
Monocultures on native soil by inoculation
c
Monocultures on native soil
Naïve plant communities
Selected plant communities
2-species mixtures on neutral soil
2-species mixtures on native soil by inoculation
2-species mixtures on native soil
4-species mixtures on neutral soil
4-species mixtures on native soil by inoculation
4-species mixtures on native soil
Relative productivity (% of mean of 8-species mixtures)
Year
0
50
100
150
2012
2013
2014
2015

534 **Figure 2 | Relative productivity (% of mean of 8-species mixture) for naïve communities**
535 **and communities of co-selected plants in neutral soil without or in native soil with co-**
536 **selected soil biota.**
537 Relative productivity of communities of co-selected plants (dashed lines, open circles) and
538 naïve communities (solid lines, closed circles) in monocultures and 2- and 4-species mixtures
539 in **a,** neutral soil (sterilized soil with neutral inoculum) **b**, native soil obtained by inoculation
540 (sterilized soil with neutral inoculum and inoculum of co-selected soil biota from original
541 plots) and **c,** native soil (unsterilized soil with co-selected soil biota from original plots). Raw
542 means and standard errors are shown (for significances see Extended Data Table 1b).
543



544

545 **Figure 3 | Log ratio of productivity in communities of co-selected plants (bm$_{selected}$) and**
546 **productivity in naïve communities (bm$_{naïve}$) across years and soil treatments.** In 8-species
547 mixtures, productivity did not differ between communities of co-selected and naïve plants
548 (ratio=0). Especially in 2- and 4-species mixtures, but also in monocultures, communities of
549 co-selected plants produced more biomass than naïve communities. Means and standard
550 errors are shown. Raw data are plotted in the background.

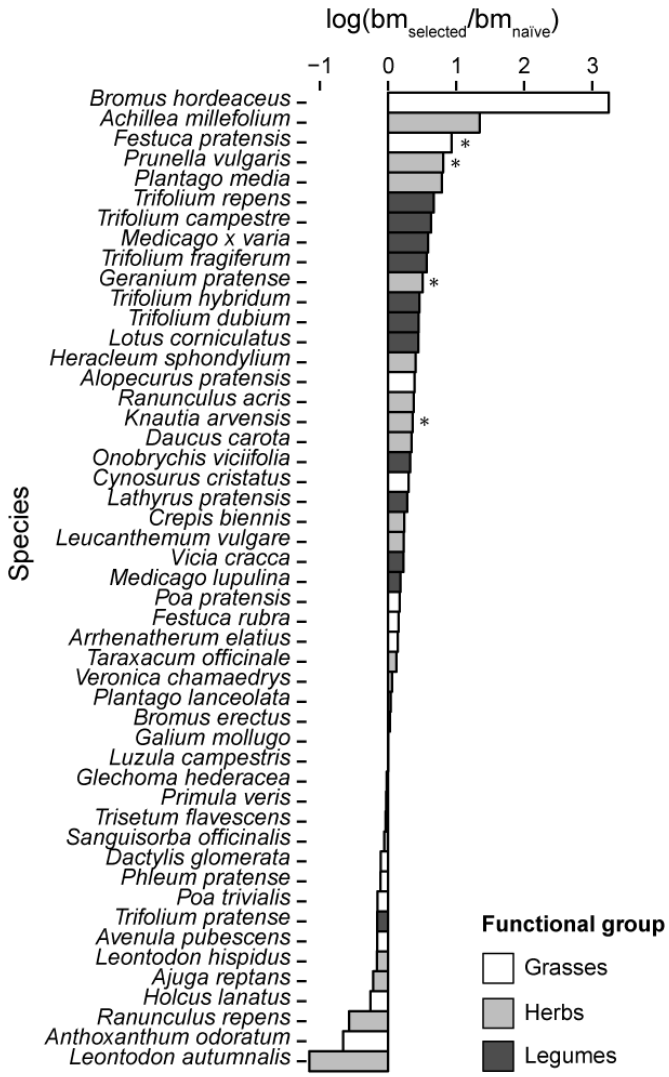
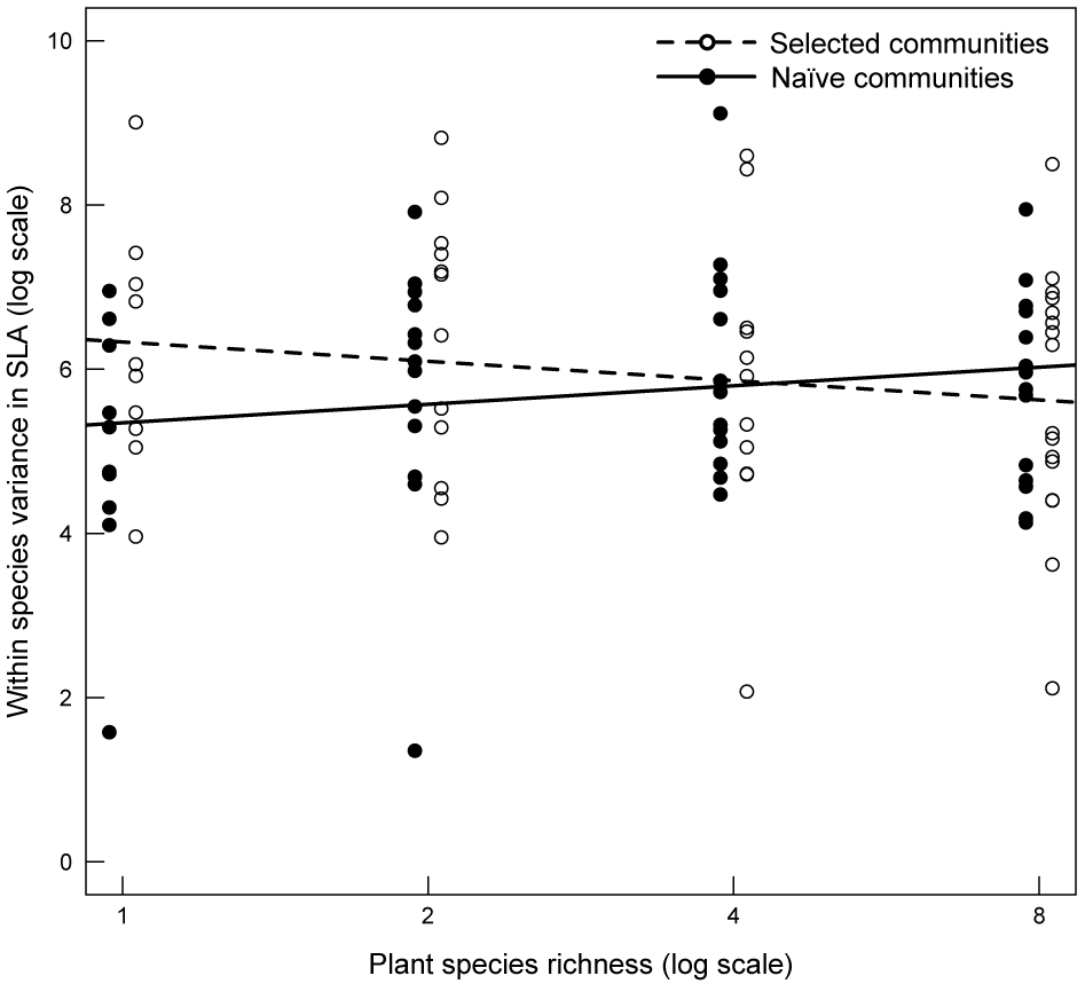


Figure 4 | Log-transformed species biomass ratios between co-selected and naïve plants. The majority of plant species attained greater aboveground biomass in communities of co-selected plants compared with naïve communities. The studied plant species belong to three different functional groups: grasses (white bars), herbs (light grey bars) and legumes (dark grey bars). Data are for each species across the four experimental years, across soil treatments and across species richness levels and species compositions of communities (n = 32–352). Three species with n < 32 were excluded from the analysis (*Anthriscus sylvestris*, *Campanula patula* and *Cardamine pratensis*). The stars represent P-values < 0.05 for species tested separately.



562

563 **Figure 5 | Within-species variation in specific leaf area (SLA) for communities of co-**
564 **selected plants and naïve communities at the end of the experiment in 2015 in neutral**
565 **soil.** In monocultures within-species variation in SLA (measured as the within-species
566 variance component in analysis of variance) was greater for co-selected than for naïve plants
567 and this difference decreased with increasing species richness. Open circles and dashed line
568 refer to communities of co-selected plants, closed circles and solid line refer to naïve
569 communities. The interaction of log(species richness) and plant history was significant ($F_{1,69.2}$
570 $= 4.87$, $P = 0.031$).