

1 **Selection in response to community diversity alters plant performance in**
2 **newly assembled test communities**

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20 *Abstract.* In grassland biodiversity experiments the positive biodiversity–ecosystem
21 functioning relationship generally increases over time. However, there is still a large gap in
22 our understanding of the underlying short-term evolutionary processes. Research has shown
23 that differential selection in monoculture vs. mixed-species communities can lead to rapid
24 evolution. We assessed whether selection history altered productivity, biodiversity effects
25 and species complementarity within newly assembled monocultures and 2-species mixtures
26 using five plant species selected for twelve years in such a biodiversity experiment in
27 mixture or monoculture and plants without such a selection history. Plants without past
28 community selection history produced the lowest community biomass and showed the
29 weakest biodiversity effects. Furthermore, we found that twelve years of selection history in
30 monocultures or species mixtures differentiated plants into monoculture- and mixture-types
31 within species. In newly assembled mixtures, plants with a selection history in mixtures
32 performed better than plants with a monoculture selection history. Biodiversity effects were
33 generally positive but, contrary to expectation, not stronger for mixture types. In addition,
34 biodiversity effects were both influenced by trait differences among plants and community-
35 weighted means, but these relationships were largely independent of selection history. Our
36 findings indicate possible mechanisms underlying the rapid evolution of adapted subtypes
37 within a species in grasslands. Uncovering these mechanisms contributes to our
38 understanding of the biodiversity–ecosystem functioning relationship, which has the
39 potential to influence species conservation practice.

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41 **Key words** biodiversity effects, complementarity effect, ecosystem functioning, grasslands,
42 plant productivity, sampling effect, species selection, trait variation

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INTRODUCTION

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The loss of biodiversity due to species extinctions is a major threat to global

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ecosystems (Steffen et al. 2015) and has led to a large body of research investigating the

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importance of biodiversity to maintain ecosystem functions, such as productivity or nutrient

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cycling (Cardinale et al. 2012). In grasslands, many studies have found a positive

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biodiversity–productivity relationship (e.g. Tilman et al. 2001, Isbell et al. 2011), with

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biodiversity increasing multiple ecosystem functions (Soliveres et al. 2016) and ecosystem

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services (Balvanera et al. 2006). The positive effect of biodiversity has also been shown to

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increase with time (Cardinale et al. 2007, Reich et al. 2012), suggesting that

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complementarity between the co-occurring species can increase over time (Fargione et al.

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2007).

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Despite more than a decade of research on the biodiversity–productivity relationship

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(e.g. Reich et al. 2012), little is known about evolutionary mechanisms potentially affecting

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species interactions (Thorpe et al. 2011). It is conceivable that selection acting on traits

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could increase ecological combining ability (Harper 1977, Aarssen 1983) via niche

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differentiation in plant mixtures (Zuppinge-Dingley et al. 2014). Such adaptation may occur

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when there is either sufficient standing genetic variation in a population and the most

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suitable genotypes are sorted out (Fakheran et al. 2010) or by recombination and novel

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mutations (Anderson et al. 2011). Furthermore, plants may adapt to a novel environment by

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phenotypic plasticity (Price et al. 2003, Turcotte and Levine 2016), thus changing their

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morphology without genotypic changes. Epigenetic mechanisms have been suggested to

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enable adaptation (Bossdorf et al. 2008), especially in short-term evolutionary processes.

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Whereas the influence of environmental factors on adaptive responses of plant

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populations is well studied (e.g. Schmid 1985, Joshi et al. 2001), much less effort has been

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devoted to studying the influence of community diversity on a species' performance (but see

70 Lipowsky et al. 2011, Kleyhans et al. 2016). Based on previous observations in
71 experimental ecosystems suggesting a “division of labor” among species in plant mixtures, it
72 is likely that community diversity plays a role in the evolution of plant functional trait
73 variation. For example, in forests more diverse tree communities have been shown to express
74 greater crown complementarity (Niklaus et al. 2017, Williams et al. 2017). In diverse
75 grassland communities, increased complementarity effects as estimated by the additive
76 partitioning method of Loreau and Hector (2001) have been observed promoting community
77 productivity via a range of mechanisms: diversification of the canopy structure and hence
78 light and space use (Spehn et al. 2000, Allan et al. 2011), soil resource partitioning (Fornara
79 and Tilman 2008, Roscher et al. 2008, von Felten et al. 2009), root depth distribution
80 (Mueller et al. 2013) and distribution of leaf mass (Wacker et al. 2009). It is now timely to
81 ask how and on what time scale selective forces may contribute to the evolution of the
82 observed combining ability.

83 Using the additive partitioning method (Loreau and Hector 2001), net biodiversity
84 effects (NEs) can be partitioned into complementarity (CEs) and sampling effects (SEs).
85 When CEs drive over-yielding, most species are expected to contribute to greater biomass in
86 more diverse communities. In contrast, when SEs are drive over-yielding, a few dominant
87 species increase community productivity in species mixtures. The CE is therefore related to
88 coexistence and trait variation between species, as it inherently suggests a differentiation in
89 functional traits (Cadotte et al. 2009, Flynn et al. 2011). Conversely, the SE should rather be
90 driven by traits of the dominant species and thus by community-weighted trait means
91 (CWMs); an increase in CWMs (e.g. taller plants) should increase biodiversity effects
92 (Roscher et al. 2012).

93 The use of functional traits to define species’ niches has a long history in
94 evolutionary ecology (van Valen 1965, Schoener and Gorman 1968, Roughgarden 1974) but

95 only recently has become a popular approach in functional ecology (Violle et al. 2007)
96 where it is being used to explain mechanisms of species coexistence and ecosystem
97 functioning (Kraft et al. 2015, Hart et al. 2016). However, there is still a large gap in our
98 understanding of how evolutionary mechanisms shape such trait-based niches (Roscher et al.
99 2015) and how they may drive corresponding niche differentiation according to functional
100 traits (Sterck et al. 2011).

101 In particular, the selective power of community diversity on biodiversity effects as
102 well as trait means and variation has received limited attention (but see Lipowsky et al.
103 2011, Zuppinger-Dingley et al. 2014, 2015, 2016, Kleynhans et al. 2016, Rottstock et al.
104 2017). Kleynhans et al. (2016) observed adaptation to new environmental conditions but
105 only when the diversity level of the selection treatment and the assay treatment were the
106 same. Although a selective past of growth in different diversity levels has been shown to
107 have trans-generational influences on productivity for one species (Rottstock et al. 2017), it
108 is unknown whether such an effect may be common to many species in plant communities.

109 In the present study, we tested whether community diversity as a selective
110 environment can influence heritable variation in plant aboveground biomass and functional
111 traits within and between species and how this may relate to biodiversity effects in two-
112 species mixtures. We measured biomass production and traits of individual plants in
113 monocultures and mixtures established with seedlings from either a selection history of
114 experimental monoculture or mixture communities in a biodiversity field experiment (Jena
115 Experiment, see (Roscher et al. (2004) for methods) or in monoculture fields from the
116 commercial seed supplier which provided the original seeds for the biodiversity experiment
117 in 2002. We refer to the plants growing in Jena since 2002 in mixture or monoculture
118 experimental plots as mixture types and monoculture types, respectively. The plants derived
119 from seeds obtained from the commercial supplier in 2014 are referred to as naïve plants.

120 Whereas selection outcomes in an earlier study in the Jena Experiment were assessed
121 after eight years and one controlled sexual reproduction cycle (Zuppinge-Dingley et al.
122 2014), in the present study we continued the selection treatment for another four years and
123 added a second controlled sexual reproduction cycle. We included naïve plants as a control
124 treatment without selection under continuous growth in monoculture or mixture
125 communities. We hypothesized that during the twelve years of selection in the experimental
126 field, mixture-type plants should have evolved high mixture performance (hypothesis 1, see
127 Table 1). This should be related to large NEs, in particular CEs (hypothesis 2), and large
128 between-species trait variation (hypothesis 3). Conversely, we hypothesized that
129 monoculture-type plants should have evolved high monoculture performance (hypothesis 4),
130 which should be related to large within-species trait variation (hypothesis 5). For control
131 plants, we hypothesized intermediate results between monoculture- and mixture-type plants.
132 We therefore aimed to expand on the relationship between biodiversity effects and between-
133 species trait variation, hypothesizing that large CEs should be due to between-species trait
134 variation (hypothesis 6). Finally, we hypothesized that large SEs should be due to large
135 CWMs (hypothesis 7).

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METHODS

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Plant selection histories

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To test whether plant types selected over twelve years in mixtures outperform those types selected in monocultures when assembled in mixture test communities, we chose five species grown in monoculture and mixture plots in the Jena Experiment (Jena, Thuringia, Germany, 51°N, 11°E, 135 m a.s.l., see Roscher et al. (2004) for experimental details): *Plantago lanceolata* L., *Prunella vulgaris* L., *Veronica chamaedrys* L., *Galium mollugo* L. and *Lathyrus pratensis* L. For brevity, we will use the genus names to refer to the species.

145 The study species had previously been classified into the following functional groups
146 (Roscher et al. 2004): *Veronica*, *Prunella* and *Plantago* as small herbs, *Galium* as a tall herb
147 and *Lathyrus* as a legume.

148 Plant progeny from three different selection histories was used for the experiment.
149 Plants without selection history in the Jena Experiment (selection history “naïve”) were
150 obtained from a commercial seed supplier (Rieger Hoffmann GmbH, Blaufelden-
151 Raboldshausen, Germany). Plants with a selection history in the Jena Experiment were
152 grown in either mixtures or monocultures from 2002 (selection history “mixture” and
153 “monoculture”, respectively). In 2010, cuttings of these plants were brought to Zurich and
154 used for seed production for an earlier experiment. The plants were grown in their respective
155 community in an experimental garden in Zurich and seeds were collected from these plants
156 throughout the growing season of 2010. The propagation of seedlings from these seeds is
157 described in Zuppinger-Dingley et al. (2014). These seedlings were then planted back into
158 the experimental plots in Jena in 2011 using the identical parental species composition (for
159 detailed procedure see van Moorsel et al. (2017)).

160 To ensure a second sexual reproductive event and to collect seed material for the
161 present study, entire plant communities from some of the experimental plots replanted in
162 Jena in 2011 were excavated again in March 2014. These plants were used to establish plots
163 with an identical plant composition to the plots in Jena from which the plants were collected,
164 in an experimental garden in slug-exclosure compartments at the University of Zurich,
165 Switzerland (47°33'N, °37'E, 534 m a.s.l.). We added a layer of soil (“Gartenhumus”
166 consisting of 50% agricultural soil and 50% garden compost, Ricoter, Aarberg, Switzerland)
167 to each plot to ensure the plants established well. Mesh fabric netting around each plot
168 minimized the possibility of cross-pollination between the same species from different
169 experimental plots. Seeds were collected throughout the growing season of 2014 from

170 monoculture plots and from 4- and 8-species mixtures. Seeds from different mother plants
171 were pooled together. Seeds were cleaned manually for three species and mechanically for
172 two species (*Plantago* and *Prunella*). The dry seeds were stored at 5° C for cold stratification
173 until germination.

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175 *Experimental set up*

176 Seeds were germinated in germination soil (“Anzuchterde”, Ökohum, Herbertingen,
177 Germany) under constant conditions in the glasshouse without additional light in December
178 2014, each species being sown on the same day. From 25 February to 13 March 2015,
179 seedlings were planted in monocultures of four individuals and 2-species mixtures of four
180 individuals into pots (two liters) filled with neutral agricultural soil (50% agricultural sugar
181 beet soil, 25% perlite, 25% sand; Ricoter AG, Aarberg, Switzerland). Seedlings which died
182 in the first two weeks were replaced with seedlings of the same species and age.

183 These seedlings were used to assemble test communities in six blocks (replicates) with
184 each block consisting of the full experimental design as far as possible. Within each block,
185 pots were placed on three different tables in the glasshouse in a randomized fashion without
186 reference to selection history or assembly treatment. Throughout the experiment, we did not
187 move pots but noted their position in the glasshouse. Single pots always contained four
188 plants of the same selection history. Every selection history × species assembly combination
189 was replicated five to six times depending on plant availability. We planted 30 monoculture
190 and 42 mixture assemblies with mixture selection history, 30 monoculture and 60 mixture
191 assemblies with monoculture selection history and 24 monoculture and 35 mixture
192 assemblies with naïve selection history. There were thus 221 pots and 884 plants (Appendix
193 S2 for monoculture identities and species combinations).

194 During the experiment, we grew the plants initially at day temperatures of 17–20°C
195 and night temperatures of 13–17°C without supplemental light. To compensate for
196 overheating in summer, an adiabatic cooling system (Airwatech; Bern, Switzerland) was
197 used to match inside with outside temperatures. The plants were not fertilized. Due to an
198 infestation of white flies (*Trialeurodes vaporariorum*, Westwood 1856) and spider mites
199 (*Tetranychidae* spp., Donnadieu 1875), we applied the insecticide SanoPlant Neem (1%
200 Azadirachtin A (10 g/l); Maag AG) three times. The fungicide Fenicur (*Oleum foeniculi*,
201 Andermatt Biocontrol) against powdery mildew (*Podosphaera* spp.) was applied twice. Plant
202 height, leaf thickness, specific leaf area (SLA) and individual aboveground biomass were
203 measured after twelve weeks of the experiment from 18 May to 4 June 2015. Leaf thickness
204 was measured for three representative leaves using a thickness gauge. Specific leaf area
205 (SLA) of up to 20 representative leaves (depending on the leaf size of the species) of each
206 species in a pot was measured by scanning fresh leaves with a Li-3100 Area Meter (Li-cor
207 Inc., Lincoln, Nebraska, USA) immediately after harvest and determining the mass of the
208 same leaves after drying. Plant height and individual aboveground biomass were measured a
209 second time after 24 weeks, the end of the experiment, from 18–25 August 2015. All four
210 individuals in a pot were sampled. Research assistants, who were not informed of the
211 specific experimental treatments, assisted in the regular measurements and harvesting of
212 plants at the end of the experiment.

213

214 *Data analyses*

215 SLA outliers (> 99% percentile) were replaced with a maximum value (the 99%
216 percentile, n = 6). We calculated pot-wise aboveground community biomass (plant
217 community production) as the sum of the biomass of the four individual plants. Relative
218 between-species differences (RDs, absolute difference between two species divided by the

219 mean of the two) in plant height (first and second harvest), leaf thickness (first harvest) and
220 SLA (first harvest) were calculated for mixture assemblies. Relative differences within
221 species were calculated for both mixture and monoculture assemblies taking the relative
222 difference between two individuals of the same species per pot. Furthermore, we calculated
223 community-weighted means (CWMs) and pot standard deviation (SDs) for the same traits.
224 Pots with dead plant individuals were excluded from the calculation of community-weighted
225 means, but were included for the other data analyses. Net biodiversity effects (NEs) were
226 calculated by comparing the 2-species mixtures with the average monoculture and
227 partitioned according to Loreau and Hector (2001) into complementary (CEs) and sampling
228 (selection) effects (SEs). This partitioning approach allows assessing how CEs and SEs
229 contribute to the observed NEs (Loreau and Hector 2001). To avoid confusion with the term
230 selection used for the selection-history treatment, we here use the term “sampling effect” for
231 the SE (as in Zupping-Dingley et al. (2014)). Additive partitioning calculations were based
232 on the difference between the observed yield of each species in the mixture and the
233 monoculture yield for that species and selection history averaged across blocks. Absolute
234 values of CE and SE were square root-transformed and the original signs put back on the
235 transformed values for analysis (Loreau and Hector 2001). Differences in these measures
236 between mixtures assembled from plants with monoculture selection history and mixtures
237 assembled from plants with mixture selection history would suggest differential evolution of
238 trait-based niches between species as a potential mechanism underlying biodiversity effects.

239 All statistical analyses were done in R (Version 3.2.3, R Core team 2016). Mixed-
240 model analysis was done using the R-package *asreml* (VSNI international, 2016) and results
241 assembled in ANOVA tables. Fixed-effects terms were selection-history treatment (naïve,
242 monoculture, mixture), assembly treatment (monoculture vs. 2-species mixture assemblies),
243 species identity of monoculture assemblies and of mixture assemblies (in short “species

244 assembly”) and interactions of these. Table (including blocks) was used as random-effects
245 term. CWMs, RDs, within species differences and SDs of plant height, SLA and leaf
246 thickness were added as covariates to models to investigate the influence of these covariates
247 on community biomass and biodiversity effects.

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RESULTS

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Plant selection history and community productivity

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We compared the community productivity of plants from different selection histories (naïve, monoculture, mixture) grown in newly assembled monocultures and 2-species mixtures by harvesting aboveground biomass twice, once after twelve weeks and a second time after 24 weeks. Because the first measure assessed growth and the second regrowth, the harvests were analyzed separately. Communities consisting of plants with naïve selection history produced the lowest community biomass at both the first and the second harvest (Fig. 1, Table 2). At the second harvest, this contrast between plants with and without selection history was stronger in mixture than in monoculture assemblies (Fig 1; interaction monoculture vs. mixture \times naïve vs. monoculture or mixture in Table 2). Hence, both plants with monoculture- (unexpected) and with mixture- (expected) selection history in the Jena Experiment benefitted more from growing in mixtures (see also analysis of biodiversity effects in the next section).

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At the second harvest the mixture-selection-history communities outperformed the monoculture-selection-history communities and this effect was marginally more pronounced in mixture assemblies (see Fig.1 and main effect mono types vs. mix types and the two-way interaction monoculture vs. mixture assembly \times mono vs. mix types in Table 2). This partly confirms hypothesis 1 but not hypothesis 4 (see hypotheses listed in Table 1).

268 Species identity in monoculture or mixture assemblies strongly influenced community
269 productivity and, especially at the first harvest, the interaction terms with selection history
270 were significant (main effect monoculture identity or species assembly of mixture and two-
271 way interactions species assembly \times naïve vs. mono or mix types and species assembly \times
272 mono types vs. mix types in Table 2). For example, at the first harvest, mixture-type plants
273 performed better than monoculture-type plants in newly assembled monocultures of *Prunella*
274 (rejecting hypothesis 4) and in mixtures of *Galium* and *Prunella* (confirming hypothesis 1)
275 (Fig. 1a). However, in the two mixtures with the small herbs *Veronica* and *Prunella* and
276 *Plantago* and *Prunella*, monoculture-type plants performed better than mixture-type plants
277 (rejecting hypothesis 1; see Fig. 1a).

278

279 *Plant selection history and biodiversity effects*

280 Overall, biodiversity effects were positive at both harvests (First harvest: NE: $F_{1,15.9} =$
281 26.67, $P < 0.001$, CE: $F_{1,15.8} = 8.214$, $P = 0.011$, SE: $F_{1,14.2} = 97.07$, $P < 0.001$, second
282 harvest: NE: $F_{1,15.1} = 14.35$, $P = 0.002$, CE: $F_{1,14.5} = 4.108$, $P = 0.061$, SE: $F_{1,15.1} = 11.66$, $P =$
283 0.004, Fig. 2, Appendix S3 and S4). At the first harvest, communities of naïve plants on
284 average showed larger SEs than communities of selected plants ($F_{1,104.2} = 12.66$, $P = 0.001$,
285 Appendix S3). At the second harvest, however, NEs and CEs were significantly lower for
286 naïve plant communities (NE: $F_{1,96.1} = 11.54$, $P < 0.001$, CE: $F_{1,96.6} = 5.668$, $P = 0.019$,
287 Appendix S4). These results are in line with the results obtained for community productivity:
288 plant communities consisting of plants without selection history had the lowest average
289 productivity mainly because they could profit the least from growing in 2-species mixtures
290 rather than in monocultures. We had expected naïve plants to have intermediate biodiversity
291 effects between monoculture- and mixture-type plants.

292 Contrary to our expectation (hypothesis 2), at the first harvest NEs, CEs and SEs were
293 significantly larger for communities assembled from monoculture-type plants than for
294 communities assembled from mixture-type plants (NE: $F_{1,93.9} = 21.01$, $P < 0.001$; CE: $F_{1,94.4}$
295 $= 14.2$, $P < 0.001$; SE: $F_{1,101.2} = 10.28$, $P = 0.002$; Appendix S3; Fig. 2a–c, upper panels).
296 This difference was reversed for most species assemblages at the second harvest (Fig. 2a–c,
297 lower panels), when NE, CE and SE were non-significantly larger for communities
298 assembled from mixture-type plants (Appendix S4). In line with the results obtained for
299 community productivity, the influence of selection history on biodiversity effects also
300 additionally depended on the specific species combination in mixture assemblies as follows
301 (interactions species assembly \times naïve vs. mono or mix types and species assembly \times mono
302 types vs. mix types in Appendix S3 and S4). At the first harvest, we found the expected
303 result (hypothesis 2), i.e. a larger NE for mixtures types, for the combinations of *Galium*
304 with either *Prunella* or *Plantago* (Fig. 2a, upper panel). At the second harvest, NEs and CEs
305 were generally more similar between selection histories across different combinations and
306 variation between the specific community compositions was mainly due to different SEs. An
307 exception was the combination *Galium* + *Prunella*, which similarly to the first harvest
308 showed a much larger NE for mixture-type plants, as expected under hypothesis 2. When
309 both harvests were considered, communities including the legume *Lathyrus* or the small herb
310 *Plantago* showed positive biodiversity effects (Fig. 2; effects of species assembly in
311 Appendix S3 and S4). When comparing the CEs between the first and the second harvest, we
312 found that four species combinations shifted from stronger biodiversity effects for
313 monoculture types (rejecting hypothesis 2) to stronger biodiversity effects for mixture types
314 (supporting hypothesis 2) (Fig. 2b). The *Galium* + *Prunella* species combination showed a
315 consistently larger CE for mixture-type plants (supporting hypothesis 3). At the second
316 harvest the different species combinations varied strongly in SEs, but not in CEs (CE: $F_{9,98.4}$

317 = 1.121, $P = 0.356$, SE: $F_{9,100.8} = 11.53$, $P < 0.001$, Appendix S4). SEs were often larger for
318 mixture than for monoculture types (Fig. 2c).

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320 *Plant selection history and within- and between-species trait variance*

321 For SLA, plant height (at the first and at the second harvest) and leaf thickness we
322 calculated relative differences within and between species as well as the total pot standard
323 deviation (SD) and tested for differences between two of the three selection-history
324 treatments (contrast between mixture- and monoculture-type plants, Fig. 3). The difference
325 in plant height at the first harvest was marginally greater interspecifically for plants selected
326 in mixtures, in accordance with hypothesis 3. In contrast to this hypothesis, the interspecific
327 relative difference in leaf thickness was greater for plants selected in monocultures.
328 Monoculture types showed greater intraspecific relative difference in SLA, in accordance
329 with hypothesis 5. Furthermore, pot-level SDs in monocultures (were it was expected under
330 hypothesis 5) or mixture assemblies were non-significantly larger for communities
331 assembled with monoculture than with mixture types (see left two columns in Fig. 3).

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334 *Relationship between biodiversity effects and plant functional traits*

335 We tested how the biodiversity effects were related to the measured functional trait
336 variation (hypothesis 6; Fig. 4 and Fig. 5) and their means (hypothesis 7; Fig. 6 and Fig. 7).
337 We calculated community-weighted means (CWMs) for plant height, SLA and leaf thickness
338 at the first harvest and for plant height at the second harvest. We then related these CWMs to
339 the partitioned biodiversity effects and analyzed if and how selection history could influence
340 this relationship.

341 First, we looked at the relationship of biodiversity effects with between-species
342 differences (RDs) for SLA, plant height and leaf thickness in mixture pots (Fig. 4). The NE
343 was negatively correlated with the RD of plant height and positively correlated with the RD
344 of leaf thickness (see Fig. 4). Thus, while biodiversity effects decreased with increasing
345 variation in plant height, they increased with increasing variation in leaf thickness. Contrary
346 to our expectations under hypothesis 6, this was mainly driven by the SE, whereas the CE
347 was less influenced by the RDs. Selection history had an effect on the relationship between
348 biodiversity effects and RDs marginally or significantly. SEs were more negatively
349 correlated with the RDs of plant height for mixture- than the RDs of monoculture-type and
350 naïve plants. In contrast, the RD of leaf thickness was positively correlated with NEs and
351 CEs for both monoculture and mixture types, but not for naïve plants (Fig. 4c). At the second
352 harvest, NEs and SEs were significantly negatively correlated with the RD of plant height
353 (Fig. 5). CEs were not influenced by interspecific variation in plant height, again not
354 supporting hypothesis 6. SLA and leaf thickness were not measured at the second harvest.

355 Next, we looked at the relationship of biodiversity effects with community-weighted
356 trait means CWMs). Whereas CEs were negatively correlated with the CWM of SLA (Fig.
357 6b), the SE was positively correlated with SLA (Fig. 6b, right panel). Consequently, NEs,
358 driven by CEs, decreased with increasing SLA. Leaf thickness had a marginally significant
359 effect on SEs, but the directionality depended on selection history. Plant height did not have
360 a significant effect on any of the biodiversity effects at the first harvest. However, the
361 interaction between trait means and selection history was significant for the relationship
362 between the CWM of plant height and the SE at the first harvest. Thus, even though the trait
363 mean did not have a direct impact on biodiversity effects, selection history influenced the
364 trait means, which in turn influenced biodiversity effects. Selection history did not
365 significantly impact the relationship between biodiversity effects and CWMs for the other

366 two traits. At the second harvest, CWM of plant height had a significantly positive effect on
367 NE, CE and SE (Fig. 7), hence the biodiversity effects were stronger for overall taller plants.
368 However, when compared to the first harvest, the effect of selection history on the
369 relationship between the CWM of plant height and the SE disappeared at the second harvest
370 (Fig. 7). Overall, these results provided mixed evidence for hypothesis 7, which predicted a
371 positive relationship between SEs and CWMs but no relationship between CEs and CWMs.

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DISCUSSION

374 *Influence of plant selection history on community productivity (hypotheses 1 and 4)*

375 Previous research has shown that plant community productivity can be influenced by
376 plant selection history, especially by the selection for increased niche differentiation in plants
377 that had been grown for eight years in mixtures (mixture-type plants) compared to plants that
378 had been grown in monoculture (monoculture-type plants, Zuppinger-Dingley et al. 2014).
379 The present study included naïve plants without selection history in a biodiversity
380 experiment. For plants with a selection history in the Jena biodiversity experiment (Roscher
381 et al. 2004), we hypothesized that 2-species mixtures newly assembled with mixture-type
382 plants should have greater community productivity than similar mixtures newly assembled
383 with monoculture-type plants (hypothesis 1) and, conversely, that monocultures newly
384 assembled with monoculture-type plants should have greater community productivity than
385 similar monocultures newly assembled with mixture-type plants (hypothesis 4). For naïve
386 plants, we expected intermediate community productivity in both monocultures and
387 mixtures.

388 Our results provide mixed evidence for these hypotheses, in part depending on the
389 particular species and species combinations. Thus, plant communities consisting of naïve
390 plants without a selection history in the Jena Experiment often produced the lowest

391 community biomass, especially in 2-species mixtures (see Fig. 1). It is conceivable that
392 evolutionary processes in the field plots, where plants were grown for a longer time without
393 re-sowing than was the case for the naïve plants in the propagation cultures of the
394 commercial supplier, led to the increased performance of selected plants.

395 Comparing test communities consisting of either monoculture-type plants or mixture-
396 type plants, we observed that mixture-type plants did have higher community productivity
397 than monoculture-type plants in 2-species mixtures, as expected under hypothesis 1. But
398 contrary to our expectation (hypothesis 4), mixture-type plants also produced more biomass
399 than monoculture-type plants when grown in monoculture, thereby reducing biodiversity
400 effects as discussed below. The generally lower performance of monoculture-type plants
401 could have been due to selection for increased defense, trading off with reduced growth
402 (Coley et al. 1985, Herms and Mattson 1992). The increased defense may not have become
403 effective during the 24 weeks of growth in the present experiment. In a parallel glasshouse
404 experiment with single individuals per pot, we indeed found greater pathogen damage on
405 mixture- than on monoculture-type plants (Terhi Hahl et al., personal observation).

406 Within these main effects of selection history, we found large variation in selection-
407 history effects among species in monocultures and among species compositions in 2-species
408 mixtures. These findings emphasized the importance of conducting such studies with
409 multiple species but at the same time sufficient replication for each in monoculture and for
410 their combinations in mixture. High replication can more easily be achieved in experiments
411 with one focal species (e.g. Kleynhans et al. 2016, Rottstock et al. 2017), but extrapolating
412 results from such experiments might under- or overestimate overall effects of selection on
413 the response of plants to different biotic conditions. In the present study, we used five focal
414 species and already found strong differences regarding their selection response to community
415 diversity.

416

417 *Influence of plant selection history on biodiversity effects (hypothesis 2)*

418 Net biodiversity effects (NEs) can be partitioned into CEs and SEs. When CEs drive
419 over-yielding, most species should contribute equally contribute to greater community
420 productivity in mixtures, due to niche differentiation among them. Conversely, SEs are large
421 when few dominant species are driving positive diversity–productivity relationships, because
422 they benefit from growing in mixtures (Loreau and Hector 2001).

423 Naïve plants exhibited weak biodiversity effects, confirming findings from a field
424 experiment (van Moorsel et al. 2017), where we found biodiversity effects to be weaker for
425 communities assembled with naïve plants, especially when comparing monocultures with 2-
426 and 4-species mixtures. As mentioned above, naïve plants in contrast to selected plants had
427 not experienced the continued selection in field plots without re-sowing. Furthermore, they
428 had not experienced interspecific competition before, which was at least the case for the
429 monoculture types among the selected plants. Comparing the monoculture and mixture
430 types, we found that at the first harvest NEs, CEs and SEs were larger for communities
431 consisting of monoculture-type plants, which for the NEs and CEs was in contrast with our
432 expectation (hypothesis 2). The lower CE for mixture-type plants was due to the good
433 performance of mixture types in newly assembled monocultures and not because mixture
434 types performed poorly in newly assembled mixtures. At the second harvest, NEs, CEs and
435 SEs were rather similar for the two selection histories, thus no longer contradicting
436 expectations, but also not supporting them (hypothesis 2). Nevertheless, at least in four 2-
437 species combinations — *Lathyrus + Veronica*, *Galium + Veronica*, *Veronica + Prunella* and
438 *Plantago + Prunella* — the directionality changed from the unexpected to the expected
439 result, i.e. CEs at the second harvest were larger for mixture- than monoculture-type plants
440 (see Fig. 2b). Over longer timespans, CEs often increase and SEs often decrease (van

441 Ruijven and Berendse 2005, Fargione et al. 2007, Montès et al. 2008, Isbell et al. 2009,
442 Marquard et al. 2009). It is conceivable that this would also have occurred in our experiment
443 if it had continued beyond the 24-weeks timespan.

444

445 *Influence of plant selection history on trait variation (hypotheses 3 and 5)*

446 Because community-level trait variation can reflect niche differentiation (Violle et al.
447 2012, Roscher et al. 2015), we measured intra- and interspecific trait variation among
448 individual plants in all communities. We hypothesized that mixture-type plants should
449 exhibit larger trait variation between species as they underwent selection for increased
450 complementarity during twelve years in the experimental field plots (hypothesis 3).
451 Conversely, we expected stronger within-species trait variation in monoculture-type plants,
452 due to 12 years of strong intraspecific competition in the experimental field plots (hypothesis
453 5). Overall we found that variation tended to be larger both within and between species for
454 monoculture-type plants (see Fig. 3), thus not confirming hypothesis 3, but weakly
455 confirming hypothesis 5. Several studies have investigated the relationship between species
456 richness and community-level trait variation (Hulshof et al. 2013, Le Bagousse-Pinguet et al.
457 2014, Lamanna et al. 2014, Siefert et al. 2015) and found that the relative extent of
458 intraspecific trait variation depended on species richness. In monocultures, a large
459 intraspecific variation is advantageous for a more efficient use of resources, leading to our
460 hypothesis 5. Thus, the observed trend for increased trait variation in monoculture types (see
461 Fig. 3) is consistent with potential selection for within-species niche differentiation and
462 character displacement in monocultures.

463 The lack of increased between species trait differences in mixture- compared with
464 monoculture-type plants was in accordance with a lack of increased CEs for mixture-type
465 plants. This contrasts with the results of an earlier study in which increased CEs of mixture-

466 type plants were associated with increased between-species trait differences (Zuppinger et al.
467 2014). A potential explanation for the different results is that the earlier study used species
468 which were more different among each other, namely grasses, legumes, small herbs and tall
469 herbs, whereas species in the present study were more similar and therefore perhaps less
470 likely to further increase their differences by short-term evolution than species which were
471 more different to begin with. The species in the present study may have evolved “parallel”
472 character displacement in response to species of the other functional groups also present in
473 the mixtures in which they were selected in the Jena Experiment.

474

475

476 *Influence of trait variation and community-weighted means on biodiversity effects*

477 *(hypotheses 6 and 7)*

478 One potential underlying mechanism for increased biodiversity effects observed in
479 field experiments (Cardinale et al. 2007, Reich et al. 2012), could be selection for niche
480 differentiation (Zuppinger-Dingley et al. 2014). Not all trait variation, however, corresponds
481 to niche differentiation (Turcotte and Levine 2016). In particular, traits related to light
482 availability may behave differently because of the asymmetric nature of competition for
483 light, i.e. being tall is generally better than being small. Thus, variation in plant height could
484 be expected to decrease when species are grown in mixtures rather than monocultures
485 (Vermeulen et al. 2008, Roscher et al. 2015). Given the absence of increased CEs and
486 between-species trait variation in mixture-type plants, the relationship between functional
487 traits in our 2-species mixtures and biodiversity effects should not have differed according to
488 plant selection history. Nevertheless, we could still test how trait variation and means were
489 correlated with biodiversity effects. Specifically, we predicted that relative trait differences

490 (RDs) should be positively related to CEs (hypothesis 6) and community-weighted trait
491 means (CWMs) should be positively related to SEs (hypothesis 7).

492 In opposition to hypothesis 6, RDs in plant height were negatively rather than
493 positively correlated with CEs and consequently NEs (see Fig. 4a, 5). This discrepancy of
494 observation and expectation suggests that RDs in plant height may reflect competitive
495 hierarchies rather than complementary of plants with respect to light use, as discussed above
496 with regard to the asymmetry of light competition. At the second harvest, CWMs of plant
497 height had a positive impact on all biodiversity effects (Fig. 7), i.e. not only on SEs — which
498 we had expected under hypothesis 7 —, but in accordance with findings of previous studies
499 (Vermeulen et al. 2008, Roscher et al. 2015).

500 Functional diversity in SLA within a community should increase complementary light
501 use (Roscher et al. 2011). Leaf thickness is inherently related to SLA (White and Montes-R
502 2005) and might act similarly to SLA. In our study, RDs in leaf thickness, but not RDs in
503 SLA, were positively correlated with all biodiversity effects, especially for mixture-type
504 plants (see Fig. 4c). Hence, trait plasticity in leaf thickness was advantageous for species
505 growing in mixtures. However, SEs was as much increased as CEs, whereas according to our
506 expectation (hypothesis 6) positive correlations between trait differences should mainly
507 involve CEs. Additionally, CWMs of SLA did have a positive effect on SEs, consistent with
508 hypotheses 7, but also a negative effect on CEs, adding up to a negative effect on NEs (see
509 Fig. 6b), suggesting that overall a smaller leaf area per unit mass for species growing in
510 mixtures has a positive effect on productivity.

511

512 CONCLUSIONS

513 Here, we demonstrated that community diversity had the selective potential to alter
514 species performances, which may in part explain the strengthening biodiversity–ecosystem

539 experiment and S.J. van Moorsel, M.W. Schmid and B. Schmid analyzed the data. S.J. van
540 Moorsel and B. Schmid wrote the manuscript with all other authors contributing to revisions.

541

542

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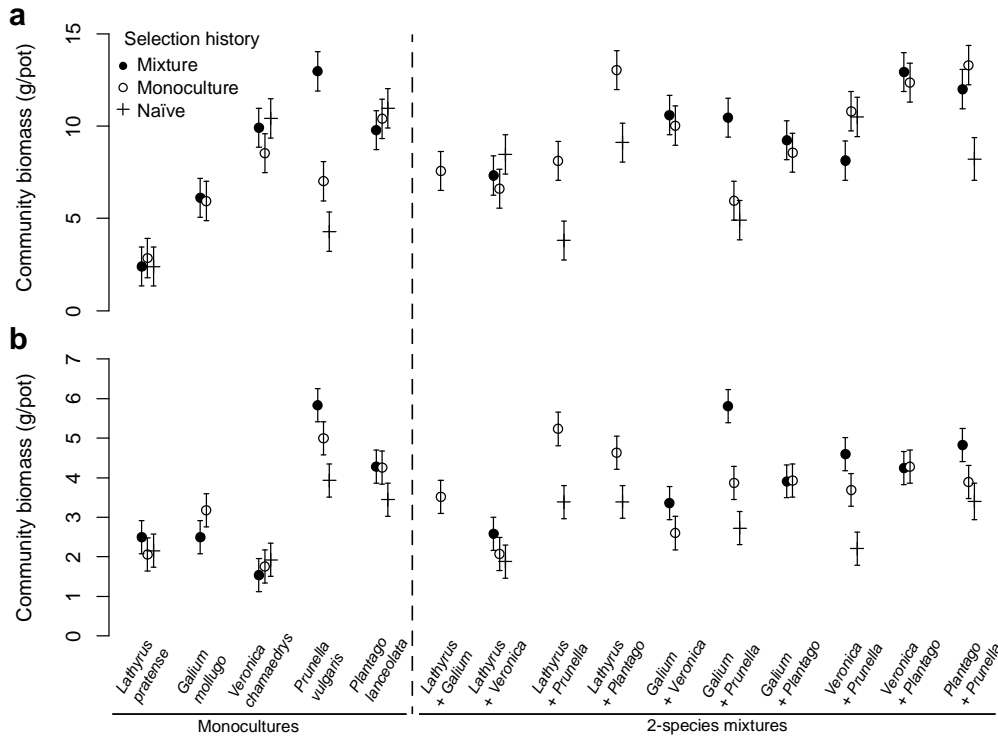
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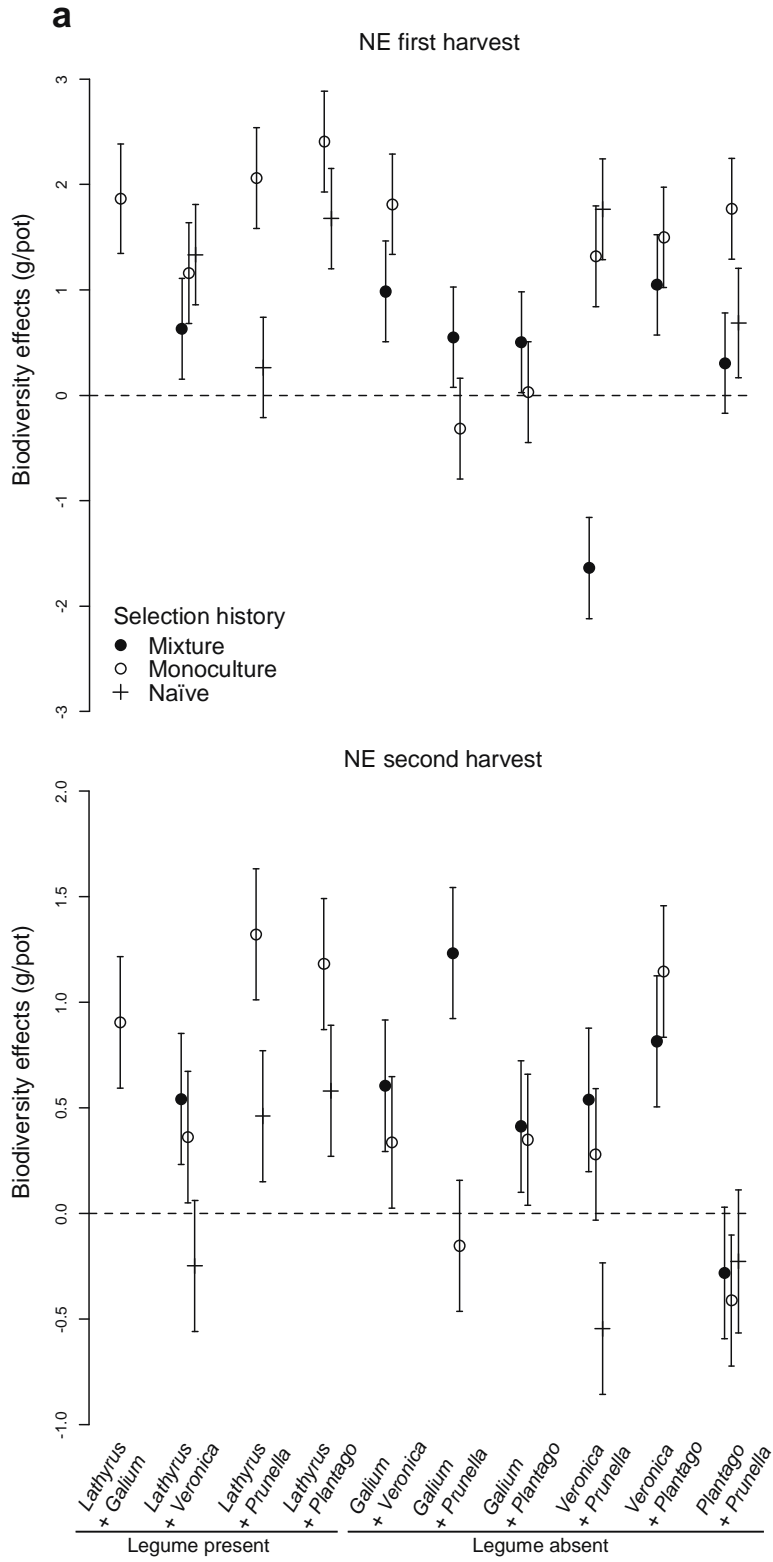
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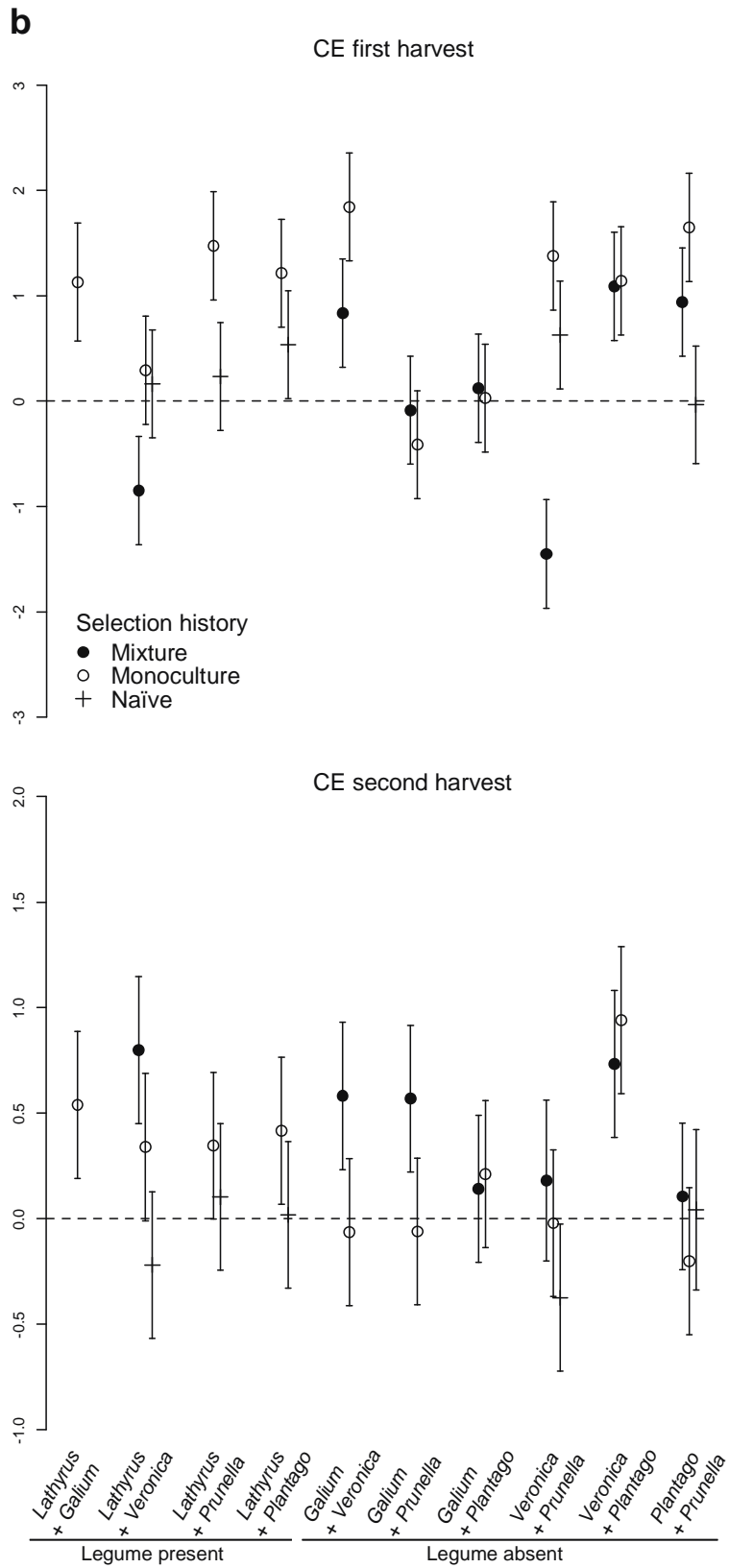


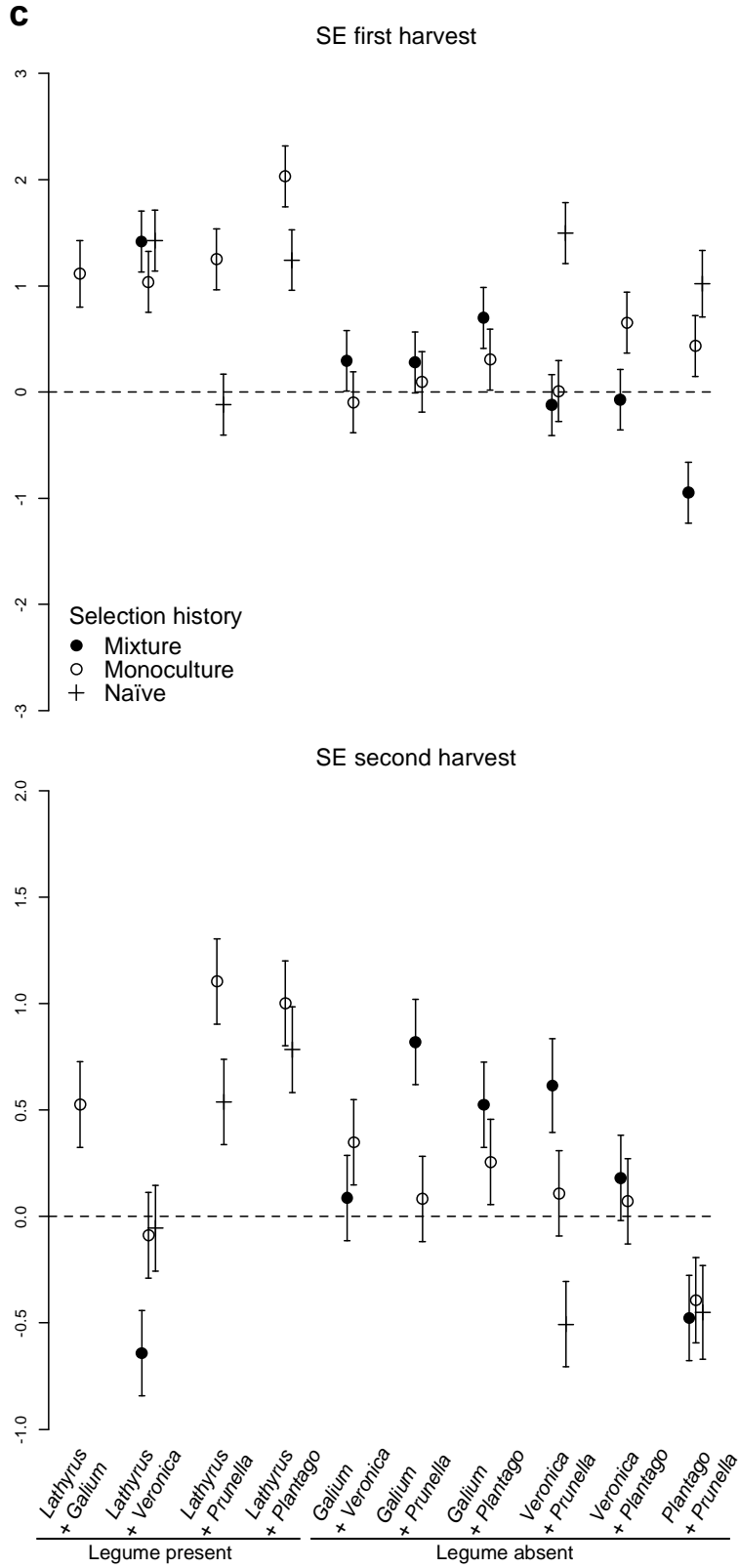
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714 **FIG. 1.** Mean community biomass for monocultures and 2-species mixtures. Shown are
715 means and standard errors from a linear mixed-effects model with selection history, species
716 combination and the interaction between selection history and species assembly as fixed-
717 effects terms and table (including the block) as random-effects term. **a**, first harvest. **b**,
718 second harvest.

719



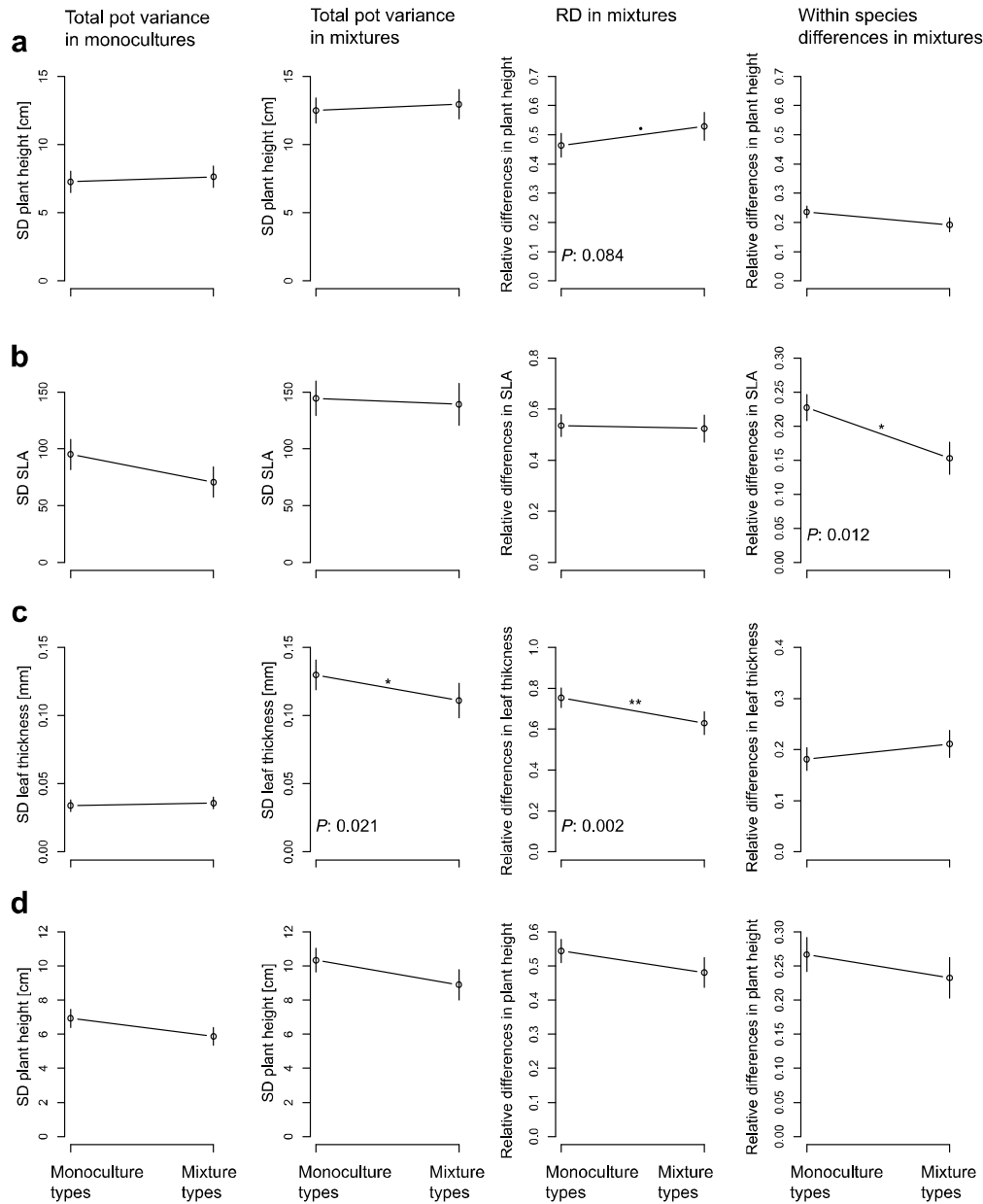




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724 **FIG. 2.** Biodiversity effects were assessed for both biomass harvests by additive partitioning
725 of the net effect (**a**, NE) into complementarity effect (**b**, CE) and sampling effect (**c**, SE) for
726 plants with different selection histories (naïve, monoculture, mixture). Shown are means and
727 standard errors from a linear mixed-effects model, with selection history, species assembly
728 and the interaction between selection history and species assembly as fixed-effects terms and
729 table (including block) as random-effects term.

730



731

732 **FIG. 3.** Trait variance in monoculture and mixture assemblies in response to selection

733 history (monoculture- vs. mixture-type plants). **a)** plant height at the first harvest, **b)** SLA at

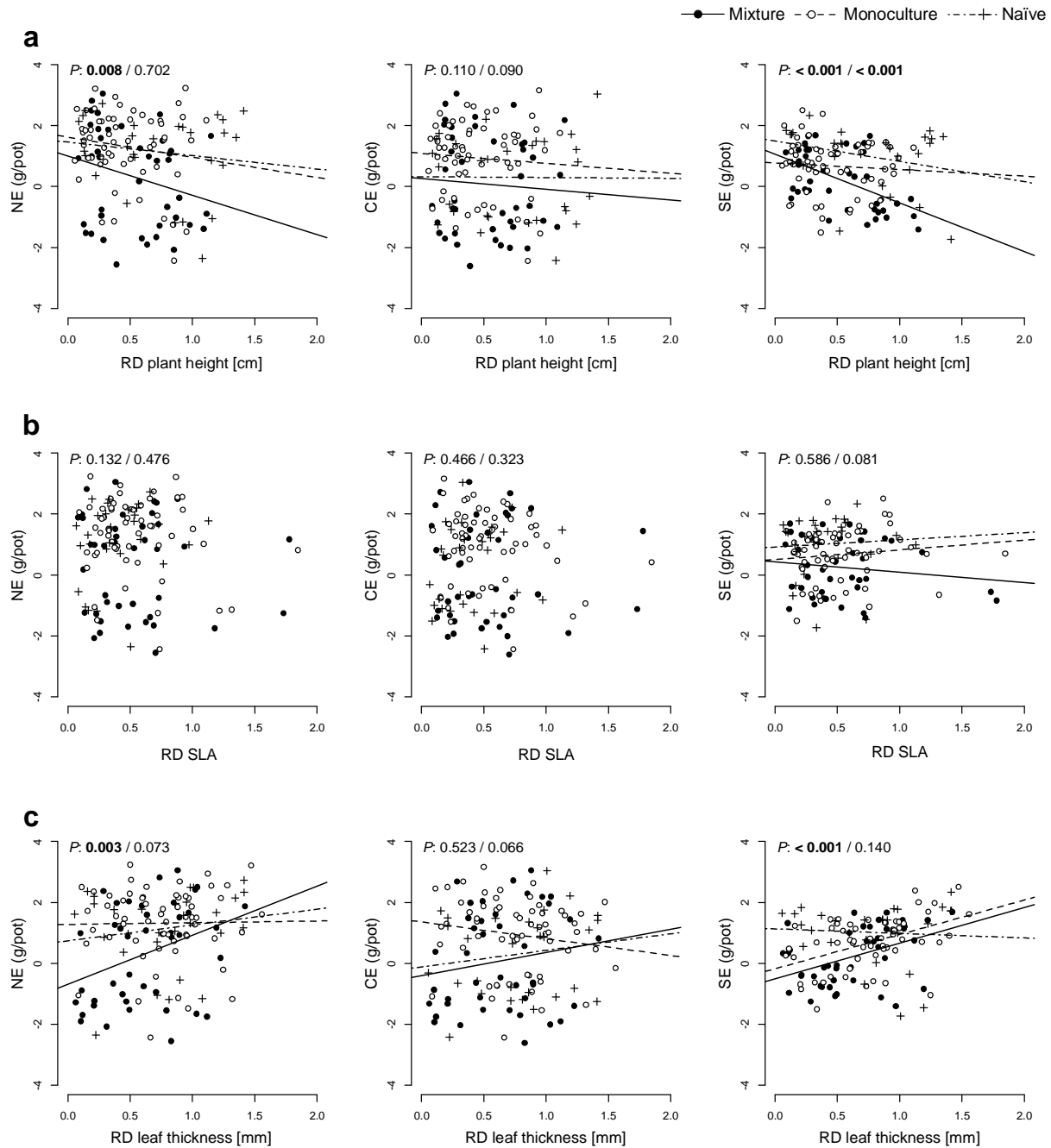
734 the first harvest, **c)** leaf thickness at the first harvest, **d)** plant height at the second harvest.

735 Shown are means and standard errors from a mixed-effects model with selection history,

736 species assembly and the two-way interaction of these as fixed-effects terms and table

737 (including block) as random term. Significant and marginally significant *P*-values are

738 indicated in the respective plot.

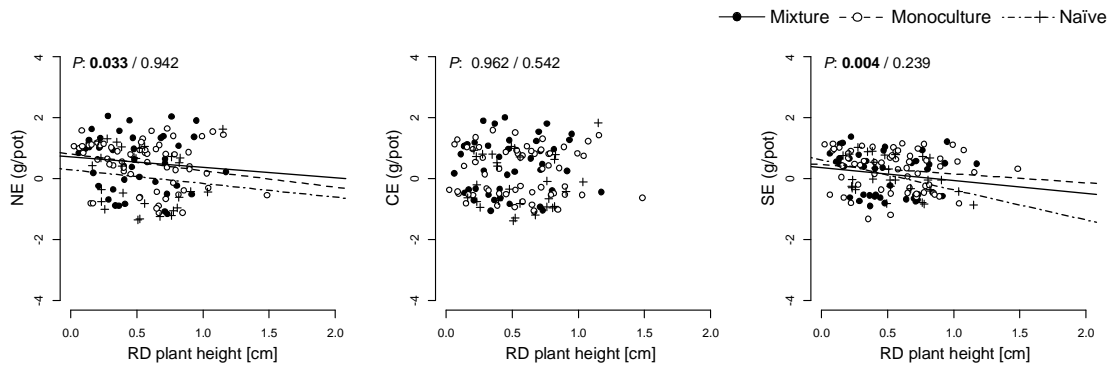


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740 **FIG. 4.** Biodiversity effects at the first harvest in response to relative differences between
741 species (RDs) for three traits: **a**, plant height (in cm), **b**, specific leaf area (SLA) and
742 leaf thickness (in mm). Indicated *P*-values refer to ANOVA results for fixed-effects terms from a
743 mixed-effects model with RD, species assembly, selection history and interactions of these

744 as fixed-effects terms and table (including block) as random-effects term: RD / interaction
745 RD \times selection history (naïve plants vs. mixture types vs. monoculture types). Regression
746 lines are plotted in cases for which at least one *P*-value was significant. Left column: NE,
747 middle column: CE, right column: SE.
748

749



750

751 **FIG. 5.** Biodiversity effects at the second harvest in response to relative differences between

752 species for plant height (in cm). Indicated *P*-values refer to ANOVA results for fixed-effects

753 terms from a mixed-effects model with RD, species assembly, selection history and

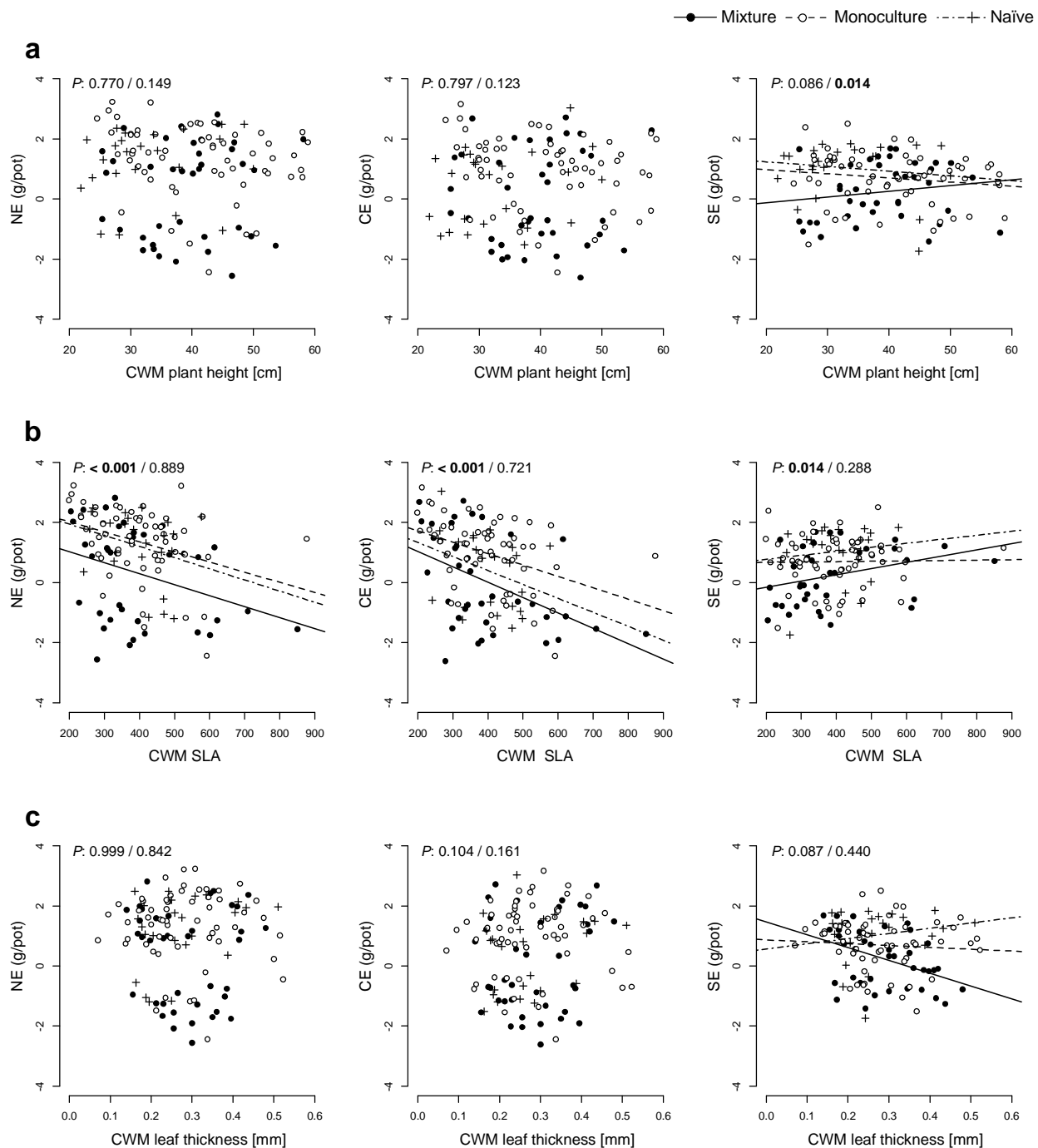
754 interactions of these as fixed-effects terms and table (including block) as random-effects

755 term: RD / interaction RD × selection history (naïve plants vs. mixture types vs. monoculture

756 types). Regression lines are plotted in cases for which at least one *P*-value was significant.

757 Left column: NE, middle column: CE, right column: SE.

758



759

760

761 **FIG. 6.** Biodiversity effects at the first harvest in response to the community-weighted mean

762 (CWM) of three traits: **a**, plant height (in cm), **b**, specific leaf area (SLA) and **c**, leaf

763 thickness (in mm). Indicated *P*-values refer to ANOVA results for fixed-effects terms from a

764 mixed-effects model with CWM, species assembly, selection history and interactions of

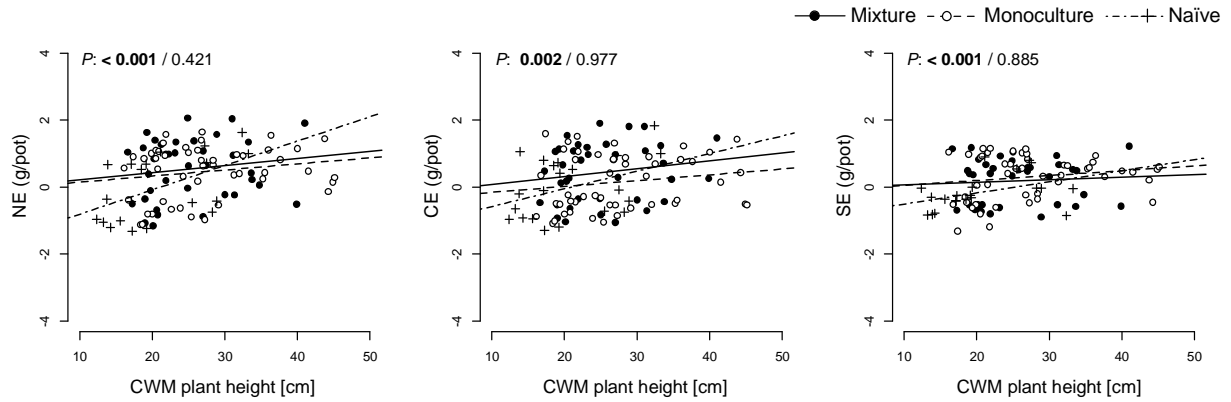
765 these as fixed-effects terms and table (including block) as random-effects term: CWM /

766 interaction CWM \times selection history (naïve plants vs. mixture types vs. monoculture types).

767 Regression lines are plotted in cases for which at least one *P*-value was significant. Left

768 column: NE, middle column: CE, right column: SE.

769



770

771

FIG. 7. Biodiversity effects at the second harvest in response to the community-weighted

772

mean (CWM) of plant height (in cm). Indicated *P*-values refer to ANOVA results for fixed-

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effects terms from a mixed-effects model with CWM, species assembly, selection history

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and interactions of these as fixed-effects terms and table (including block) as random-effects

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term: CWM / interaction CWM × selection history (naïve plants vs. mixture types vs.

776

monoculture types). Regression lines are plotted in cases for which at least one *P*-value was

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significant. Left column: NE, middle column: CE, right column: SE.

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779 **TABLE 1.** Summary of hypotheses.

Hypothesis

- 1) Mixture-type plants produce high biomass in mixtures.
- 2) Mixture-type plants have large NEs and CEs.
- 3) Mixture-type plants show large interspecific trait variation.
- 4) Monoculture-type plants produce high biomass in monocultures.
- 5) Monoculture-type plants show large intraspecific trait variation.
- 6) Large CEs are due to between-species trait variation.
- 7) Large SEs are due to large CWMs.

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782 **TABLE 2.** Results of mixed-effects ANOVA for the aboveground biomass of the test
 783 communities.

Source of variation		Harvest 1			
		nDf	dDF	F	P
Species assembly:					
	Monoculture vs. mixture	1	173.3	29.09	< 0.001
	Monoculture identity or species combination of mixture	13	171.2	16.53	< 0.001
Selection history:					
	Naïve vs. mono or mix types	1	173	16.63	< 0.001
	Mono vs. mix types	1	169.6	1.78	0.184
Assembly × history:					
	Monoculture vs. mixture × naïve vs. mono or mix types	1	168.4	1.72	0.191
	Monoculture vs. mixture × Mono or mix types	1	172.2	1.69	0.195
	Species assembly × naïve vs. mono or mix types	8	171.7	5.35	< 0.001
	Species assembly × mono types vs. mix types	10	172.3	2.91	0.002
Variance components		n	Var	SE	
	Table (including blocks)	18	1.7512	0.8010	
	Residual (pots)	221	5.8403	0.6395	

Source of variation		Harvest 2			
		nDf	dDF	F	P
Species assembly:					
	Monoculture vs. mixture	1	174	10.78	0.001
	Monoculture identity or species combination of mixture	13	171.8	15.47	< 0.001
Selection history:					
	Naïve vs. mono or mix types	1	173.7	42.72	< 0.001
	Mono vs. mix types	1	170.1	5.71	0.018
Assembly × history:					
	Monoculture vs. mixture × naïve vs. mono or mix types	1	168.8	8.56	0.004
	Monoculture vs. mixture × Mono or mix types	1	172.9	3.52	0.062
	Species assembly × naïve vs. mono or mix types	8	172.3	2.15	0.033
	Species assembly × mono types vs. mix types	10	172.9	1.23	0.275
Variance components		n	Var	SE	
	Table (including blocks)	18	0.2451	0.1145	
	Residual (pots)	221	0.9225	0.1009	

Note: nDF = numerator degrees of freedom, dDF = denominator degrees of freedom, F = variance ratio, P = probability of type-I error. Variance components (Var) and associated standard errors (SE) for the random effects are provided together with the number of replicates.

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