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1 **Multiple facets of diversity effects on plant productivity: species richness,**
2 **functional diversity, species identity and intraspecific competition**

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22 **Abstract**

23 1. Deciphering the mechanisms that drive variation in biomass production across plant
24 communities of contrasting species composition and diversity is a main challenge of
25 biodiversity-ecosystem functioning research. Niche complementarity and selection effect have
26 been widely investigated to address biodiversity-productivity relationships. However, the
27 overlooking of the specific role played by key species have limited so far our capacity to
28 comprehensively assess the relative importance of other potential drivers of biodiversity effects.

29 2. Here, we conducted a grassland diversity-productivity experiment to test how four potential
30 facets of biodiversity effects, namely species richness, functional diversity, species identity and
31 the relaxation of intraspecific competition, account for variations in above and root biomass
32 production.

33 3. We grew six plant species in monoculture, as well as in every combinations of two, three and
34 six species. Plant density was kept constant across the richness gradient but we additionally
35 grew each species in half-density monoculture to estimate the strength of intraspecific
36 competition for each studied species. We characterized eight functional traits, including root
37 traits, related to nutrient and light acquisition and computed both the functional dissimilarity
38 and the community weighted mean (CWM) of each trait. We further partitioned aboveground
39 biodiversity effect into complementarity and selection effects.

40 4. We observed strong positive biodiversity effects on both aboveground and root biomass as
41 well as strong positive complementarity effect. These arose largely from the presence of a
42 particular species (*Plantago lanceolata*) and from CWM trait values more than from a higher
43 functional dissimilarity in plant mixtures. *P. lanceolata* displayed the highest intraspecific
44 competition, which was strongly relaxed in species mixtures. By contrast, the presence of

45 *Sanguisorba minor* negatively affected the productivity of plant mixtures, this species suffering
46 more from interspecific than intraspecific competition.

47 5. This study provides strong evidences that the search for key species is critical to understand
48 the role of species diversity on ecosystem functioning and demonstrates the major role that the
49 balance between intraspecific and interspecific competition plays in biodiversity-ecosystem
50 functioning relationships. Developing more integrative approaches in community and
51 ecosystem ecology can offer opportunities to better understand the role that species diversity
52 plays on ecosystem functioning.

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54 **Key words:** biodiversity-ecosystem functioning, complementarity effect, functional trait,
55 functional distinctiveness, niche difference, roots, selection effect, species coexistence

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66 **Introduction**

67 Although numerous plant diversity-ecosystem functioning experiments have reported
68 positive effects of plant species richness on ecosystem productivity (*e.g.*, Tilman *et al.*, 2001;
69 Cardinale *et al.*, 2012; Lefcsek *et al.*, 2015), the nature of the mechanisms that cause this pattern
70 remains highly controversial. It is widely accepted that niche complementarity can lead to
71 higher productivity in plant mixtures compared to monocultures (*biodiversity effects*; Huston,
72 1997; Loreau & Hector, 2001). Such a complementarity effect may be due to species differences
73 in the way they capture and use resources (so-called resource partitioning), due to species ability
74 to alter their surrounding environment and to subsequently favour the fitness of other species
75 (*e.g.*, abiotic facilitation), or due to plant interactions with other trophic levels (Barry *et al.*,
76 2018). Positive biodiversity effects can also result from an increased probability of selecting a
77 species with a specific property as the size of the community increases, for example a highly
78 productive species (Loreau & Hector, 2001). The *selection effect* describes whether the species
79 that dominate plant mixtures are the most productive species in monoculture (*i.e.* positive
80 selection effect) or the least productive species in monoculture (*i.e.* negative selection effect;
81 Loreau & Hector, 2001). However, the presence of some other species can also exert a
82 disproportionate effect on ecosystem functioning irrespective of their biomass in monoculture
83 (Jaillard, Deleporte, Loreau & Violle 2018). Such a species-specific effect underpins the well-
84 known concept of keystone species, *i.e.* species having 'disproportionately large effects relative
85 to its abundance' (Paine, 1969; see also Violle *et al.* 2017 for a revisiting concept in the light of
86 functional ecology theory). Recently, Maire *et al.* (2018) extended this concept by defining "key
87 species" as those species that are 'consistently and significantly associated to a certain level of
88 ecosystem functioning or services' (Maire *et al.*, 2018). Although the search for key species can
89 reveal unsuspected mechanisms for ecosystem functioning (Huston, 1997; Diaz *et al.*, 2007),
90 their role in biodiversity-ecosystem functioning experiments have been largely neglected.

91 Because ecological niches are theoretically linked to a suite of functional traits (Violle
92 & Jiang 2009), functional traits appear to be a promising tool for understanding diversity-
93 productivity relationships. On the one hand, differences in functional traits (*functional*
94 *dissimilarity*) can reflect differences in the use of resources that allow species to partition the
95 local pool of resources and avoid interspecific competition (Violle *et al.*, 2012). For instance,
96 differences in the vertical distribution of roots among species allow the capture of water and
97 nutrients at different soil depths. On the other hand, the functional traits of dominant species in
98 plant mixtures can be approximated using the community weighted mean (CWM) of functional
99 trait values (Garnier *et al.*, 2004; Diaz *et al.*, 2007). It has been argued that functional
100 dissimilarity can mediate the complementarity effect while CWMs can mediate the selection
101 effect by highlighting the role of the dominant species on ecosystem functioning (Cadotte,
102 2017). Disentangling the respective influence of both processes through a trait-based approach
103 thus requires using a set of traits that are directly linked to species' resource use and competitive
104 ability. For instance belowground, this requires studying root traits that reflect how species
105 develop specialized strategies to explore the soil volume (*e.g.*, deep root fraction, specific root
106 length, root inter-branch distance) and to extract water and nutrients (*e.g.*, root hair length,
107 specific nutrient absorption rate; Freschet, Violle, Bourget, Scherer-Lorenzen & Fort, 2018).

108 Finally, species may exert highly specific effects on the functioning of ecosystems that
109 cannot be captured by metrics of functional diversity computed at the community scale (Diaz
110 *et al.*, 2007). Among others, the fact that every species has a specific density-productivity
111 relationship in monoculture can be an important mechanism for ecosystem functioning. Indeed
112 in most biodiversity-productivity experiments, species relative density - which directly drives
113 the strength of intraspecific competition (Chesson, 2000) - decreases along the gradient of
114 species richness (*i.e.* substitutive experimental design; Hector, 1998; Joliffe, 2000). In parallel,
115 interspecific competition – which by essence is null in monoculture – increases along this

116 gradient, so that weaker competitors can perform better in monoculture where they do not
117 encounter other species (Turnbull, Levine, Loreau & Hector, 2013). The relative importance of
118 intraspecific and interspecific competition on the productivity of each species could therefore
119 be an important driver of biodiversity-ecosystem functioning relationships (Benedetti-Cecchi,
120 2004; Turnbull *et al.*, 2013, 2016). Despite these evidences, previous experimental biodiversity-
121 ecosystem functioning studies have largely neglected the role of species intraspecific
122 competition (but see Polley, Wilsey & Derner, 2003), leaving the question unanswered.

123 In this study, we tested the strength and significance of four drivers of plant biomass
124 production in biodiversity-ecosystem functioning experiment, namely species richness,
125 functional diversity, species identity and intraspecific competition. To do so, we experimentally
126 designed grassland plant communities representing a gradient of species richness (from one to
127 six) and functional diversity. We manipulated three different functional groups (namely
128 ‘grasses’, ‘forbs’ and ‘legumes’), and characterized eight functional traits (three shoot and five
129 root traits) that were directly related to the acquisition of light and nitrogen (Freschet *et al.*,
130 2018). We tested each above-mentioned effect separately by combining the conceptual
131 framework of Diaz *et al.* (2007) and the statistical framework of Maire *et al.* (2018). Briefly, to
132 understand how species diversity affects ecosystem functioning, Diaz *et al.* (2007) suggests to
133 first test for the role of functional diversity and, in a second step, to look for potentially
134 remaining species-specific effects. In parallel, Maire *et al.* (2018) developed a statistical
135 framework that aims at identifying key species that drive ecosystem functioning (Maire *et al.*,
136 2018). In this framework, we separately tested the effect of the presence of a candidate species
137 or the effect of a candidate functional trait by adding species presence or functional diversity as
138 an explanatory variable to a baseline model that previously accounted for the effects of species
139 richness. Finally, we estimated the strength of the effect of intraspecific competition by

140 quantifying for every species the gain of individual biomass when decreasing plant density in
141 monocultures.

142 **Materials and Methods**

143 *Experimental design*

144 The experiment was conducted at the Center for Functional and Evolutionary Ecology,
145 Montpellier, France. We grew six plant species in monoculture (6 combinations), as well as in
146 every combinations of two (15 combinations), three (20 combinations) and six species (1
147 combination) in a greenhouse with three replicate pots for the monoculture, two and three
148 species combinations and six replicates for the six species combination. Plant species were
149 common European herbaceous species (see Table 1): two grasses (*Bromus erectus* Huds.,
150 *Dactylis glomerata* L.), two forbs (*Plantago lanceolata* L., *Sanguisorba minor* Scop.) and two
151 legumes (*Lotus corniculatus* L., *Trifolium repens* L.). We chose this set of species to avoid
152 functional redundancy, these species displaying contrasted functional traits. Seeds were
153 collected from permanent grasslands located in southern France. Plant density was kept
154 constant across the richness gradients (i.e. six individuals per pot with equal species relative
155 abundance) but we additionally grew each species in three replicates of half-density
156 monoculture (i.e. three individuals per pot) to estimate the strength of intraspecific competition
157 for each studied species. Climate conditions in the greenhouse were semi-controlled.
158 Temperature was allowed to fluctuate between 15 and 19°C at night and between 21 and 25°C
159 during the day. Natural light conditions were complemented for the duration of the experiment
160 (with 400W Na-ion lamps) to provide a typical change in photoperiod during the plant growing
161 season from 12 h initially to 14.5 h at the end of the experiment.

162 We used deep pots (depth 60 cm, diameter 15 cm) containing *c.* 17 kg (DW) of soil. Soil
163 density was increased by compaction every 20 cm in depth (from 1.51 to 1.63 and 1.74 g.cm⁻³)

164 to ensure realistic growth conditions for plants. The soil was a calcareous sandy loam (pH =
165 8.5) with rather low organic matter content (9.7 g.kg⁻¹), cation-exchange capacity (0.5 g.kg⁻¹)
166 and total N content (0.5 g.kg⁻¹). At the start of the experiment, in November 2015, a soil leachate
167 solution was added to ensure the presence of symbiotic N₂-fixing bacteria in the pot. Pots were
168 watered three times a week to provide moisture conditions close to field capacity in the soil
169 profiles; this corresponded to 0.1L of water at the start of the experiment and 0.6L at the end in
170 order to account for increasing plant demand. In addition, all pots received three soil
171 enrichments (after 1, 4 and 9 weeks) in phosphorus (P) and potassium (K) in increasing amount
172 over time for a total of 10 g P m⁻² and 24 g K m⁻¹. Note that nitrogen was not supplied so that it
173 remained the main limiting resource for plant growth. We randomly placed pots on wheeled
174 carriages and avoided side effects by rearranging carriages every two weeks.

175 *Biomass measurements*

176 Plants harvest took place 13 weeks after seedling transplantation after all species had
177 shown first signs of flowering. We cut aboveground parts of plants at the base and separated the
178 six plant individuals to measure aboveground biomass of each individual plant. We evaluated
179 root biomass of each pot after splitting the column of soil in three equal cylinders, each 20 cm
180 long, and careful retrieving and washing roots from each cylinder. Plant material was oven-
181 dried at 60°C for 48 h and weighed.

182 *Trait measurements*

183 We measured three aboveground traits and five belowground traits related to both
184 nitrogen and light acquisition. For each trait, the detailed protocol is presented in Freschet *et al.*
185 (2018). Briefly, three weeks before harvest, we measured light-saturated leaf photosynthetic
186 rate per area (A_{area} , $\mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$) - that provides the leaf maximal photosynthesis capacity -
187 on one individual per monoculture pot by quantifying the amount of C accumulated in a leaf

188 exposed to a high light intensity for several minutes (C influx vs efflux). One week before the
189 experiment harvest, we recorded the maximum height (cm) achieved by all plant individuals in
190 all pots. Plant height is a good proxy for light depletion through the canopy (Violle *et al.* 2009).
191 Specific leaf area (SLA, $\text{m}^2 \cdot \text{kg}^{-1}$) was assessed at harvest based on two to four leaves (depending
192 on the species) from each plant individual that we immediately scanned for leaf area
193 measurement. Specific leaf area corresponds to the area of light capture per biomass invested
194 in leaves and is related to the fundamental trade-off existing between species acquisition and
195 conservation of resources (Garnier & Laurent 1994).

196 Root functional traits were measured from monoculture pots only because of the
197 difficulty and labour associated to separating roots among species in mixture pots. A subsample
198 of roots was used to determine root length, mean root diameter and the proportion of very fine
199 roots (<0.2 mm) using a digital image analysis system (WinRhizo, version 2009, Regent
200 Instrument, Québec, Canada). Deep root fraction (DRF), which reflects the relative investment
201 of species to take up nutrient from the deeper soil horizons, was estimated as the ratio of root
202 biomass deeper than 20 cm to total root biomass. Root inter-branch distance (RID, cm) is a
203 measure of root cost-efficiency to explore large soil volume (rather than exploit soil volume
204 intensively) and was quantified as the average distance between first order roots. Specific root
205 length (SRL, $\text{m} \cdot \text{g}^{-1}$) was estimated as the ratio of root length to root dry mass to represent the
206 cost-efficiency of roots to explore and/or exploit soil volume. A second subsample of roots was
207 stained with methyl violet in order to make root hairs visible and measure root hair length (RHL,
208 mm) on 10 randomly selected first order roots, over stretches of 1 mm roots situated 2 mm away
209 from the root tips, using ImageJ software. Root hair length is a proxy for the soil volume
210 explored around the root. Finally, we used one replicate (pot) from the six species in
211 monoculture to measure specific root nitrogen absorption rate (N_{abs}), which reflects the short-
212 term maximum nitrogen uptake capacity per unit root length. We calculated N_{abs} as the total

213 amount of ^{15}N taken up by plants after injection of different forms of ^{15}N in the soil, per length
214 of fine root and per h ($\mu\text{g } ^{15}\text{N m}^{-1} \text{ h}^{-1}$).

215 *Biodiversity effects*

216 We quantified the biodiversity effect (ΔY), which is the performance of plant mixture
217 relative to that expected from monocultures, separately for aboveground and root biomass
218 production. Then, following the equation proposed by Loreau & Hector (2001):

$$219 \Delta Y_j = N_j \cdot \overline{\Delta RY} \cdot \bar{M} + N_j \cdot \text{COV}(\Delta RY_{i,j}, M_i) \quad \text{Equation 1}$$

220 we computed the two components of ΔY , the complementarity and selection effects, only for
221 aboveground ΔY as we did not measure individual root biomass in plant mixtures. In this
222 equation, N_j is the number of species in pot j . $\Delta RY_{i,j}$ is the deviation from the expected relative
223 yield of species i in pot j calculated as:

$$224 \Delta RY_{i,j} = \frac{Y_{i,j}}{M_i} - \frac{1}{N_j} \quad \text{Equation 2}$$

225 where $Y_{i,j}$ is the biomass measured for species i in pot j and M_i is the average monoculture
226 biomass for species i . As species were sown at constant density of individuals, the expected
227 yield is simply the inverse of the number of species in pot j ($1/N_j$). The first component of the
228 biodiversity effect equation ($N_j \cdot \overline{\Delta RY} \cdot \bar{M}$) is the *complementarity effect*, which quantifies the
229 performance of plant mixtures relative to the performance of the component monocultures. The
230 covariance between species performance in monoculture and in plant mixture,
231 $N_j \cdot \text{COV}(\Delta RY_{i,j}, M_i)$, has been termed the *selection effect*.

232 *Functional diversity*

233 We assessed the effects of species traits on ecosystem functioning by computing two
234 facets of functional diversity, namely functional dissimilarity and community weighted mean

235 (CWM). We quantified functional dissimilarity using the functional dispersion (FDis) index
236 computed separately for each trait using the *fdisp* function of the FD R package (Laliberté,
237 Legendre & Shipley, 2014). For each trait, we computed FDis based on mean species trait
238 values measured in monoculture pots only to insure homogeneity between the different traits
239 that were measured in all pots or in monoculture only (Table 1). Since plant height and SLA
240 were quantified at the individual level, we further tested the role of intraspecific trait variability
241 by computing FDis_{Height} and FDis_{SLA} based on trait values measured on individuals from all
242 pots. CWM were calculated for each trait by multiplying the mean species trait value measured
243 in monoculture pots by the proportional abundance of each species in each community. Finally,
244 we classified the six species into three functional groups (legumes, herbs and forbs).

245 *Data analyses*

246 We investigated the effect of species richness, functional dissimilarity, CWM and
247 species identity on aboveground and root biomass production, aboveground and belowground
248 biodiversity effects as well as aboveground complementarity and selection effects using linear
249 models. Following Maire *et al.* (2018), we first tested the extent to which species richness
250 affected biomass production, biodiversity effects, complementarity effect and selection effect
251 in a baseline model (M0). Next, we built ‘functional group’, ‘functional dissimilarity’, ‘CWM’
252 and ‘species identity’ models to test the extent to which the data support the effect of a particular
253 functional group, functional trait or species identity on these response variables. To do so, we
254 added the presence of each functional group or species (coded as a binary variable) or FDis and
255 CWM of each trait separately as an explanatory variable to M0. The resulting model (M1_i),
256 which is the importance of a candidate species *i*, functional group *i* or functional trait *i* to explain
257 variation in productivity, was then evaluated according to its Akaike information Criterion
258 (AIC). We considered a species, a functional group or a functional trait as important for
259 productivity if ΔAIC ($AIC_{M0} - AIC_{M1i}$) was greater than 4 (Maire *et al.*, 2018). Although a

260 commonly adopted rule of thumb states that a model with $\Delta\text{AIC} < 2$ is likely to be the best model
261 (Burnham & Anderson, 2002; Richards, 2005), here we doubled this threshold to reduce the
262 probability of having false positive. We standardized all variables before analysis to facilitate
263 the interpretation of the regression coefficients (Schielzeth, 2010). Because in the six species
264 mixtures each species and functional group were systematically present, we ran the functional
265 group and species identity models without the six-species mixture pots. The sample size were
266 therefore 128 for the functional trait models and 110 for the functional group and species
267 identity models. We further computed the posterior model probabilities to report the probability
268 that each model $M1_i$ is better than $M0$ using the *bicreg* function of the BMA package (Raftery
269 et al., 2018). Posterior model probabilities were highly consistent with the ΔAIC analysis.
270 Consequently, we presented ΔAIC in the main manuscript and posterior model probabilities in
271 supplementary Table S1.

272 In addition, we tested for the influence of intraspecific competition, i.e. species-specific
273 density-productivity relationships, on biomass production by computing for each species
274 intraspecific competition logarithmic response-ratio (Hedges, Gurevitch & Curtis 1999). To do
275 so, for each species, we compared the biomass of the nine individuals grown in monocultures
276 sown at half-density to the biomass of the 18 individuals grown in monocultures sown at full
277 density. Positive logarithmic response-ratio corresponds to higher biomass for the individual of
278 the monoculture sown at half-density while negative response-ratio corresponds to higher
279 biomass for the individuals of the monoculture sown at full density. Finally, we computed the
280 standardized difference (*effect size*) between individual plant biomass of species grown in
281 monoculture with half density and monoculture and mixtures of two, three and six species
282 grown at full density (six individuals). Since root biomass was not quantified at the level of
283 individual plants in mixtures, such effect sizes were only calculated for aboveground biomass.
284 Confidence intervals ($\alpha=0.05$) were computed to test whether individual plant biomass in full

285 density pots significantly differed from individual plant biomass of the same species grown in
286 monoculture at half-density. All analyses were conducted using R ver. 3.4.4. ([www.r-](http://www.r-project.org)
287 [project.org](http://www.r-project.org)).

288 **Results**

289 *Effects of species richness on plant aboveground and belowground biomass production*

290 Among all mixtures, aboveground productivity was the main fraction of plant biomass
291 production (Fig. 1a, b), accounting for c. 70% of the biomass produced per pot. Aboveground
292 biomass significantly increased with species richness ($P < 0.001$, $r^2 = 0.08$) while root biomass
293 did not ($P = 0.17$, $r^2 = 0.01$; Supplementary Table S2). Most importantly, both mean
294 aboveground and belowground biodiversity effects (ΔY) were positive at all species richness
295 levels (Fig. 1b). However, they did not increase with species richness ($P = 0.09$, $r^2 = 0.02$; $P =$
296 0.70 , $r^2 = 0.01$ for aboveground and belowground net effects, respectively; Table S2).

297 The additive partitioning of aboveground biodiversity effect (ΔY) revealed that among
298 all mixtures, complementarity effect was the main fraction of ΔY (Fig. 1c), accounting for ~
299 83% of aboveground ΔY . Complementarity effect did not increase with species richness ($P =$
300 0.34 , $r^2 = 0.01$; Table S2) while the selection effect did ($P = 0.02$, $r^2 = 0.04$; Table S2).

301 Removing the six species mixtures from the analyses did not change the effects of
302 species richness on aboveground biomass production, aboveground and belowground
303 biodiversity effects and complementarity effects (Table S2). However, root biomass
304 significantly increased with species richness while the positive effect of species richness on
305 selection effect disappeared when the six species mixtures were removed from the analyses
306 (Table S2).

307 *Stronger effects of CWMs compared to functional dissimilarity and functional group diversity*

308 Δ AIC values revealed that the main facet of functional diversity affecting biomass
309 production was the CWM of the studied traits (Table 2). After controlling for species richness
310 effect, CWM_{SLA} and CWM_{Amax} exerted a strong influence on all the components of biomass
311 production - except the selection effect (Table 2). Productivity, biodiversity effects and
312 complementarity effect consistently decreased with CWM_{SLA} and CWM_{Amax} (Table 2; Figs. S1,
313 S2 and S3). In addition, aboveground productivity, root productivity and belowground net effect
314 increased with CWM_{Height} (Table 2; Figs. S1 and S2). Aboveground net effect, belowground net
315 effect and complementarity effect also increased with CWM_{Nabs} and CWM_{DRF} and decreased
316 with CWM_{RHL} (Table 2; Figs. S2 and S3). By contrast, plant functional group identity poorly
317 affected plant productivity and biodiversity effects beyond the overall effect of species richness
318 (Table 2). The only exception was the presence of leguminous species that exerted a negative
319 effect on root productivity in plant mixtures ($P < 0.001$). The Δ AIC analysis also revealed that
320 functional dissimilarity slightly affected plant productivity and biodiversity effects (Table 2).
321 After controlling for species richness effect, root productivity significantly increased with
322 $FDis_{Height}$, $FDis_{SSL}$ and $FDis_{Nabs}$ (Table 2; Fig. S4). Finally, aboveground net effect,
323 belowground net effect and complementarity effect significantly decreased with $FDis_{RID}$ (Table
324 2; Figs. S5 and S6).

325 *Key species associated to changes in productivity*

326 The presence of *P. lanceolata* in the mixture was the principal driver of change in
327 productivity (for aboveground and root productivity: Δ AIC = 20.307, $r^2 = 0.225$ and Δ AIC =
328 69.211, $r^2 = 0.471$, respectively), net effects (for aboveground and belowground net effects:
329 Δ AIC = 26.224, $r^2 = 0.229$ and Δ AIC = 45.967, $r^2 = 0.366$, respectively) and complementarity
330 effect (Δ AIC = 26.578, $r^2 = 0.230$; Table 2). All these components of biomass production were
331 significantly higher when *P. lanceolata* was in the plant mixtures (Fig. 2). The presence of *S.*
332 *minor* and *T. repens* in plant mixtures also markedly affected biomass production. Aboveground

333 and root productivity, net effects and complementarity effects were lower in presence of *S.*
334 *minor* while the selection effect was higher. Aboveground productivity was higher in the
335 presence of *T. repens* while root productivity and selection effects were lower (Fig. 2).
336 Nevertheless their influence on net effects, complementarity and selection effects were
337 substantially (from two to ten times) lower than to those of *P. lanceolata* (Table 2).

338 *Species-specific effect and intraspecific competition*

339 Species' logarithmic response-ratio calculated based on aboveground biomass
340 production was positive for all species (Fig. 3), meaning that biomass production was in average
341 higher in half-density plots for all species. However, we found significant differences between
342 species (ANOVA, $F=41.3$, $P < 0.001$), mean logarithmic response-ratio being the highest for *P.*
343 *lanceolata* (1.36 ± 0.45) and the lowest for *S. minor* (0.41 ± 0.69 ; Fig. 3). In other words, the
344 biomass of *P. lanceolata* individual plants was four times lower in the full-density monoculture
345 than in the half-density monoculture. In addition, we found that the biomass of individual plants
346 of *P. lanceolata* in the three and six species mixtures did not significantly differ from their
347 biomass in the half-density monoculture (Fig. 4). Similarly, the biomass of individual plants of
348 *T. repens* in the six species mixture was equivalent to their biomass in the half-density
349 monoculture, whereas it was otherwise lower (Fig. 4). By contrast, the biomass of individual
350 plants of *S. minor* in full-density monoculture, two, three and six species mixtures was lower
351 than in half-density monoculture but the lowest difference was observed between full-density
352 monoculture and half-density monoculture (Fig. 4).

353 **Discussion**

354 Our study revealed contrasting influences of the four studied facets of biodiversity
355 effects on ecosystem biomass production. Species richness and functional dissimilarity showed
356 only moderate influence, whereas community weighted trait means (CWM), species identity

357 and the relaxation of intraspecific competition accounted for a large part of observed
358 biodiversity effects.

359 The significantly higher aboveground and root biomass production observed here in
360 plant mixtures compared to monoculture is a common pattern in biodiversity-ecosystem
361 functioning studies (e.g., Tilman *et al.*, 2001; Cardinale *et al.*, 2012; Lefcheck *et al.*, 2015). We
362 also reported a strong dominance of the complementarity effect over the selection effect, which
363 has been frequently observed, at least in long-term experiments (Cardinale *et al.*, 2007; Reich
364 *et al.*, 2012). Furthermore, the selection effect increased with species richness, confirming that
365 the probability of selecting a highly productive species that over-produce in mixture increases
366 with the size of the community (Huston, 1997). However, species richness *per se* did not affect
367 aboveground and belowground biodiversity effects nor complementarity effect (Fig. 1). This
368 reveals the limited value of species number *per se* to predict biodiversity-ecosystem functioning
369 relationships, and emphasizes the importance of considering other biodiversity facets.

370 Since niche complementarity theoretically relies on functional trait differences (Violle
371 & Jiang, 2009), we expected that biodiversity and complementarity effects would increase with
372 functional dissimilarity (Cadotte, 2017). Surprisingly, we found weak effects of functional
373 dissimilarity, except for a decrease of the biodiversity and complementarity effects with the
374 dissimilarity in root inter-branch distance. The use of trait-by-trait dispersion indices to compute
375 functional dissimilarity can explain the weakness of such relationships. However, while the
376 combinations of traits may better describe species differentiation along the multiple ecological
377 dimensions of species niche (Kraft *et al.*, 2015), using a multi-dimensional functional
378 dispersion index did not improve the observed relationship between functional dissimilarity and
379 biodiversity effects (See Supplementary Table S3). Another reason may be that we computed
380 functional dissimilarity in plant mixtures based on mean species trait values in monoculture.
381 Doing so, we did not account for intraspecific trait variations, which can vary in conditions of

382 competition and affect resource uptake (e.g., belowground, Mommer, van Ruijven, Jansen, van
383 de Steeg & de Kroon, 2012; Schenk, 2006). However, aboveground, accounting for
384 intraspecific trait variations in plant height and specific leaf area, both traits being measured at
385 the individual level, did not change the results (see Supplementary Table S3). Overall, given
386 our targeted choice of traits capturing multiple facets of light and nutrient acquisition above and
387 belowground (Freschet *et al.*, 2018), the weak relationship between functional dissimilarity and
388 the complementarity effect confirms that the complementarity effect does not only reflect
389 resources partitioning but a larger set of biotic interactions in species mixtures (Loreau &
390 Hector, 2001; Carroll, Cardinale & Nisbet, 2011; Niklaus, Baruffol, He, Ma & Schmid, 2017;
391 Garry *et al.*, 2018).

392 By contrast, we reported strong influence of five out of eight community weighed trait
393 means on the complementarity effect – and by extent on biodiversity effects. Species ability to
394 take up nitrogen resources was a main driver of biomass productivity, as suggested by the
395 positive relationships between the community weighted mean of both nitrogen absorption rate
396 and deep root fraction and biodiversity effects. Furthermore, biodiversity and complementary
397 effects increased with decreasing the community weighted mean of specific leaf area and
398 maximum photosynthetic rate, implying that biomass production was maximum when plant
399 communities were dominated by slow-growing, resource conservative species (Wright *et al.*,
400 2004). Although such a result might be surprising given the short-term nature of our experiment,
401 it may reflect the fact that low nutrient availability in this experiment have favored plants with
402 the more conservative resource strategies (Wright *et al.*, 2004; Carmona *et al.*, 2019). More
403 globally, the importance of functional trait values gives evidence that in this experiment,
404 ecosystem functioning is strongly driven by the identity of the dominant species (*mass-ratio*
405 *hypothesis*, Grime, 1998). However, we did not find significant relationship between the CWMs
406 and the selection effect while this is a main expectation under the mass-ratio hypothesis

407 (Cadotte, 2017). This shows that the effect of the dominant species on ecosystem functioning
408 differs from the selection effect *sensu* Loreau & Hector (2001) and calls for a more mechanistic
409 approach to understand the relationships between biodiversity and ecosystem functioning.

410 We found a disproportionate contribution of one species, *Plantago lanceolata*, on the
411 production of biomass and biodiversity effects in plant mixtures. Among the six species of this
412 experiment, *P. lanceolata* displayed the lowest biomass in monoculture but the highest biomass
413 in the 6x6-plant mixtures (Figure 4). Consequently, the specific effect of selecting *P. lanceolata*
414 in mixture differs conceptually from the selection effect, which can be positive only when the
415 most productive species in monoculture produce even more biomass in mixture (Loreau &
416 Hector, 2001). Despite this, the selection of *P. lanceolata* in mixture was the major determinant
417 of positive biodiversity effect on productivity. Its low biomass in monoculture was due to high
418 intraspecific competition, which was relieved in half-density monocultures and even more in
419 species mixtures (Figure 3). Consequently, the much lower level of interspecific competition as
420 compared to intraspecific competition for this particular species, appeared as the most critical
421 driver of biodiversity effects in our experiment. Since the strength of intraspecific competition
422 may be generally stronger than the strength of interspecific competition in plant communities
423 (Adler *et al.*, 2018), we expect that such a mechanism may be widespread in biodiversity –
424 biomass production relationships. The same pattern, although much less strong, was also
425 observed here for *T. repens*, and the reverse pattern was recorded for *S. minor*, which suffered
426 more from interspecific competition than from intraspecific competition (see also Turnbull *et*
427 *al.*, 2013). Interestingly, we observed that, across our six species, the effect of intraspecific
428 competition on species production was inversely related to the effect of interspecific
429 competition (Figure 4), suggesting that *a priori* knowledge of species-specific density-
430 dependence production may be particularly useful to explain (and potentially predict) biomass
431 gains in mixtures. An increasing number of biodiversity-productivity studies already accounts

432 for the effect of negative density-dependence mechanisms such as density-dependence plant
433 disease (e.g., Schnitzer et al., 2011; Mommer et al., 2018). By contrast, the role of intraspecific
434 competition has received less attention (but see Polley et al., 2003). Our study shows that
435 accounting for the balance between interspecific and intraspecific competition in experimental
436 studies is essential to better predict the effect of species diversity on ecosystem functioning.

437 Since the relative strength of intraspecific compared to interspecific competition should
438 increase with niche differences (Chesson, 2000; Kraft *et al.*, 2015), we might have expected
439 that *P. lanceolata* occupied a functional niche that is highly different from the one of the other
440 species. However, computing species functional distinctiveness (*sensu* Violle *et al.*, 2017) based
441 on the traits used in this study (Supplementary Table S4) revealed that *P. lanceolata* is not
442 particularly different from the other species. This suggests that other aspects of plant eco-
443 physiology (e.g., three-dimensional architecture, Schenk, 2006) may drive the response of *P.*
444 *lanceolata* to intraspecific and interspecific competition.

445 Finally, we found that the presence of legume species in plant mixtures negatively
446 affects belowground biomass production. By improving the availability of nitrogen in the
447 mixture (relief of competition and transfer to neighboring plants; Temperton, Mwangi, Scherer-
448 Lorenzen, Schmid & Buchmann, 2007) legumes may lower the typical balance between root
449 versus shoot biomass investments (Freschet, Swart & Cornelissen, 2015). Indeed, legumes
450 generally exert a positive effect on aboveground biomass production (Temperton *et al.*, 2007;
451 Marquard *et al.*, 2009). Taking together, these results highlight the importance of considering
452 both aboveground and belowground biomass production in biodiversity-ecosystem functioning
453 analyses as both compartments can differentially respond to species diversity.

454 To conclude, our study brings novel evidence that species do not equally contribute to
455 ecosystem functioning and that the search for key species (*sensu* Maire *et al.*, 2018) is a critical
456 issue to understand the effects of species diversity on ecosystem functioning (Diaz *et al.*, 2007).

457 More precisely, by looking for a species-specific effect, we highlight the important role that
458 intraspecific competition plays in shaping biodiversity-ecosystem functioning relationships,
459 although the traits underlying species intraspecific competitive ability remain unknown. The
460 fact that intraspecific competition also plays a dominant role for species coexistence (Adler *et*
461 *al.*, 2018) claims for a more integrative approach in community and ecosystem ecology to better
462 understand biodiversity-ecosystem functioning relationships (Turnbull *et al.*, 2013, 2016).
463 Accounting for non-linear species-specific density-productivity relationships will be critical to
464 predict the effect of species diversity on ecosystem functioning (Baert, Jaspers, Janssen, De
465 Laender & Aert, 2017).

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476 **Author contributions**

477 G.T.F., F.F. and C.V. planned and designed the research. G.T.F. and F.F. performed the
478 experiments. L.M. analysed the data and wrote the manuscript. G.T.F., C.V., F.F. and L.M.
479 contributed substantially to revisions.

480

481 **Data Availability Statement**

482 Data deposited in the Dryad Digital Repository: DOI <https://doi.org/10.5061/dryad.1jwstqjgh>
483 (Mahaut et al., 2019)

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629 **Figure 1:** Effect of species richness on mean (A) aboveground and root productivity and (B)
630 aboveground and belowground biodiversity effects and (C) aboveground complementarity and
631 selection effects. Differences across the richness gradients are tested using linear models. ***:
632 $p < 0.001$; **: $p < 0.01$; * < 0.05 ; ns: non-significant. Barplots represent the 1st, 2nd and 3rd quartiles.

633 **Figure 2:** Species-specific effect on aboveground (red) and belowground (blue) productivity
634 (a), net effects (b) and complementarity (light grey) and selection (dark grey) effects on
635 aboveground productivity (c). Arrows represent significant effect of the presence of a species
636 and its direction ($p < 0.05$). Barplots represent the 1st, 2nd and 3rd quartiles.

637 **Figure 3:** Variation of the intraspecific competition log-response ratio between species. We
638 computed log-response ratio between individual plant aboveground biomass in monoculture
639 sown at half-density ($Biomass_{Hdens}$) and individual plant aboveground biomass in monoculture
640 sown at full-density ($Biomass_{Fdens}$). Positive log-response ratio corresponded to higher
641 aboveground biomass for the individual of the monoculture sown at half-density. Barplots

642 represent the 1st, 2nd and 3rd quartiles.

643 **Figure 4:** Standardized difference between individual plant biomass of species grown in
644 monoculture with half density (three individuals) and monoculture and mixtures of two, three
645 and six species grown at full density (six individuals). Whiskers are confidence intervals
646 ($\alpha=0.05$): if confidence interval crossed 0, then individual plant biomass in full density pot does
647 not significantly differ from the individual plant biomass of the same species grown in
648 monoculture at half-density. A negative value means that individual plant biomass in full density
649 pot is lower than in half density pot, suggesting the influence of negative-density dependence
650 mechanisms.

651 **Tables**652 **Table 1:** Species list and average trait values (\pm sd) as grown in monoculture conditions. g: grass; f: forb; l: legume.

	Specific leaf area ($\text{m}^2 \text{kg}^{-1}$)	Max photo-synthetic capacity ($\mu\text{mol-CO}_2 \text{m}^{-2} \text{s}^{-1}$)	Plant height (cm)	Specific root length (m g^{-1})	Deep root (< 20 cm) fraction	Specific N absorption rate ($\mu\text{g m}^{-1} \text{h}^{-1}$)	Root inter-branch distance (cm)	Root hair length (mm)
<i>B. erectus</i> (g)	26.63 \pm 2.5	14.64 \pm 1.0	24.50 \pm 4.2	150.12 \pm 53.7	0.38 \pm 0.02	0.06 \pm 0.01	0.35 \pm 0.04	0.24 \pm 0.03
<i>D. glomerata</i> (g)	29.23 \pm 0.8	5.70 \pm 0.7	41.89 \pm 3.7	275.50 \pm 27.6	0.41 \pm 0.03	0.04 \pm 0.01	0.46 \pm 0.04	0.24 \pm 0.04
<i>P. lanceolata</i> (f)	18.58 \pm 1.0	9.97 \pm 1.7	27.78 \pm 1.4	151.54 \pm 15.6	0.55 \pm 0.03	0.08 \pm 0.06	0.17 \pm 0.01	0.18 \pm 0.01
<i>S. minor</i> (f)	24.83 \pm 0.3	24.85 \pm 0.9	15.44 \pm 0.9	130.26 \pm 45.8	0.61 \pm 0.03	0.06 \pm 0.02	0.14 \pm 0.01	0.13 \pm 0.01
<i>L. corniculatus</i> (l)	42.75 \pm 5.1	14.53 \pm 2.1	15.33 \pm 1.1	87.52 \pm 19.1	0.38 \pm 0.11	0.09 \pm 0.03	0.36 \pm 0.09	0.20 \pm 0.01
<i>T. repens</i> (l)	31.26 \pm 2.3	20.60 \pm 7.5	22.89 \pm 0.9	140.19 \pm 24.8	0.28 \pm 0.03	0.08 \pm 0.04	0.20 \pm 0.01	0.16 \pm 0.02

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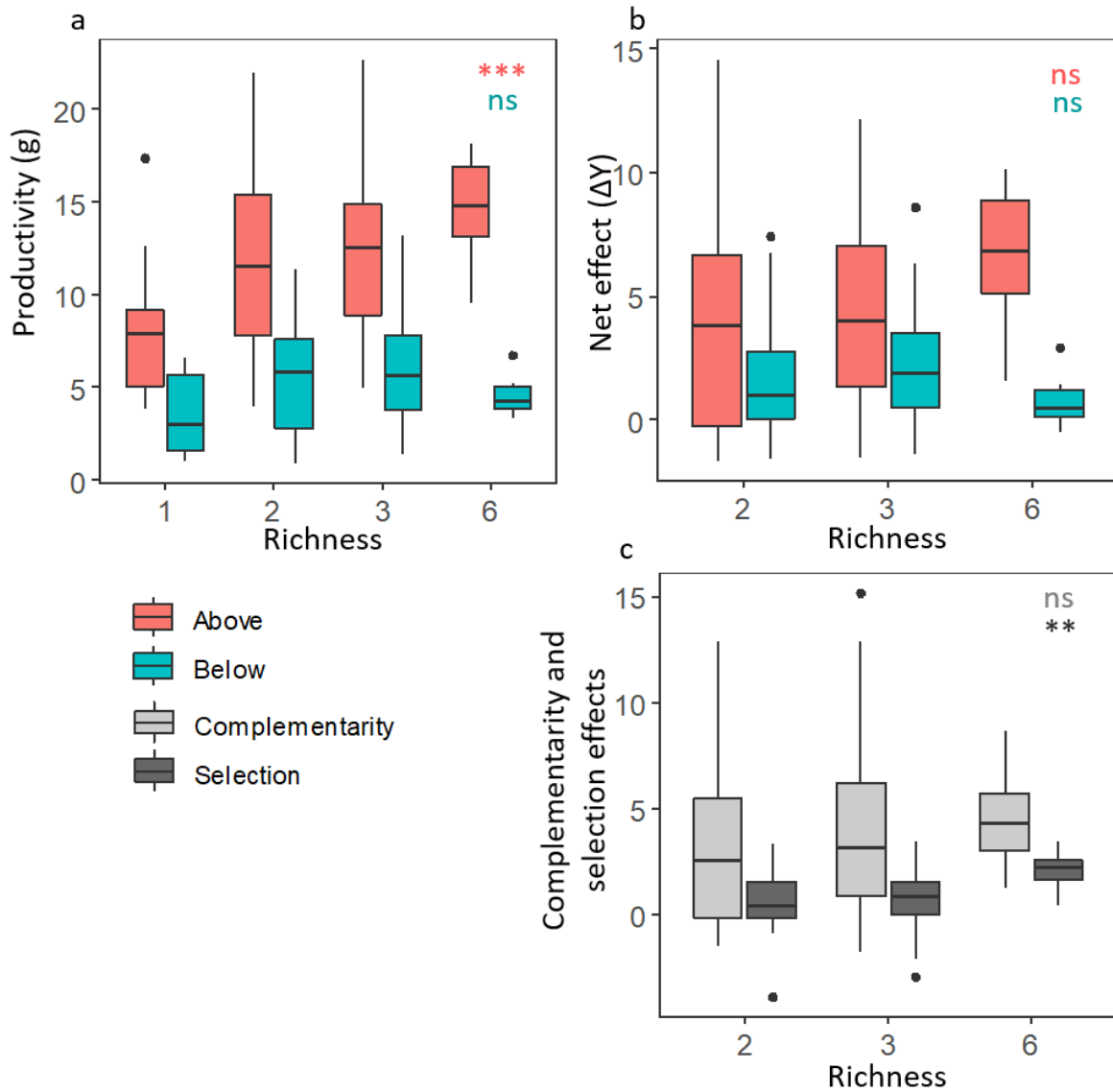
663 **Table 2:** Effects of functional group, functional dissimilarity, community weighted mean of trait (CWM) and species identity on biomass production
 664 (productivity), biodiversity effects (net effect), complementarity effect and selection effect.

		Above ground productivity			Belowground productivity			Aboveground net effect			Belowground net effect			Complementarity effect			Selection effect		
		Estimate	ΔAIC	r ²	Estimate	ΔAIC	r ²	Estimate	ΔAIC	r ²	Estimate	ΔAIC	r ²	Estimate	ΔAIC	r ²	Estimate	ΔAIC	r ²
<i>Functional group</i>	Legume	1.82 *	2.07	0.10	-2.27 ***	17.27	0.19	0.24	-1.92	0.01	-0.30	-1.58	0.00	0.87	-0.88	0.00	-0.63 *	3.42	0.03
	Herbs	-1.43	0.51	0.09	1.25 *	3.48	0.09	-1.42	0.85	0.02	-0.52	-0.73	0.01	-0.99	-0.55	0.00	-0.43	0.46	0.01
	Forbs	-0.53	-1.67	0.07	1.21 *	3.03	0.09	0.85	-0.99	0.00	0.94 *	2.24	0.04	0.73	-1.23	0.01	0.13	-1.79	0.02
<i>Functional dissimilarity</i>	Height	0.37	-1.27	0.08	0.87 ***	9.57	0.09	-0.21	-1.66	0.01	0.27	-0.07	0.00	-0.30	-1.29	0.00	0.09	-1.49	0.04
	SLA	0.47	-0.80	0.08	0.46	1.22	0.02	0.33	-1.20	0.02	0.44 *	3.12	0.03	0.30	-1.29	0.00	0.03	-1.94	0.04
	Amax	0.20	-1.80	0.07	0.48	1.35	0.03	-0.44	-0.53	0.02	0.10	-1.76	0.02	-0.38	-0.84	0.00	-0.06	-1.73	0.04
	SRL	0.20	-1.77	0.07	0.71 **	6.18	0.06	-0.43	-0.62	0.02	0.18	-1.21	0.00	-0.31	-1.22	0.00	-0.12	-1.04	0.04
	Nabs	0.60	-0.17	0.08	-0.090	-1.89	0.00	0.06	-1.98	0.01	-0.10	-1.74	0.02	0.15	-1.82	0.01	-0.10	-1.37	0.04
	RHL	0.06	-2.52	0.07	0.350 *	3.68	0.04	-0.57	0.40	0.03	0.03	-1.97	0.02	-0.43	-0.55	0.00	-0.14	-0.67	0.05
	DRF	0.54	-0.52	0.08	0.79 **	7.04	0.07	-0.26	-1.50	0.01	0.14	-1.54	0.01	-0.07	-1.96	0.01	-0.19	0.51	0.06
	RID	-0.918 *	2.23	0.10	-0.214	-1.38	0.00	-1.29 ***	11.17	0.12	-0.60 **	7.49	0.07	-1.17 ***	9.43	0.09	-0.12	-0.99	0.04
<i>CWM</i>	Height	1.20 **	7.47	0.14	1.46 ***	42.16	0.29	0.63	1.06	0.04	0.67 ***	10.35	0.90	0.61	1.08	0.02	0.02	-1.98	0.03
	SLA	-1.39 ***	10.74	0.16	-1.82 ***	73.88	0.45	-1.72 ***	23.53	0.21	-1.21 ***	43.58	0.33	-1.62 ***	21.73	0.19	-0.11	-1.19	0.04
	Amax	-1.02 *	4.78	0.12	-1.94 ***	90.60	0.52	-1.01 **	6.13	0.08	-1.09 ***	33.99	0.27	-1.01 **	6.64	0.07	-0.01	-1.99	0.03
	SRL	0.47	-0.60	0.08	0.79 ***	9.40	0.09	-1.19	-1.73	0.01	0.19	-1.11	0.00	-0.13	-1.87	0.00	-0.06	-1.75	0.04
	Nabs	0.31	-1.39	0.07	1.28 ***	29.91	0.22	1.17 **	8.80	0.10	1.06 ***	31.22	0.25	1.19 ***	10.11	0.10	-0.03	-1.95	0.04
	RHL	-0.88 *	3.04	0.11	-0.26	-0.76	0.01	-1.20 ***	9.53	0.11	-0.57 **	6.72	0.06	-1.05 **	7.38	0.07	-0.15	-0.49	0.05
	DRF	0.92 *	3.52	0.11	0.03	-1.99	0.01	1.18 **	9.12	0.10	0.50 *	4.48	0.04	1.03 **	7.02	0.07	0.14	-0.51	0.05
	RID	-0.41	0.92	0.08	0.42	1.17	0.02	-0.66	1.45	0.04	-0.26	-0.31	0.00	-0.47	-0.17	0.01	-0.19	0.76	0.06
<i>Species identity</i>	<i>B. erectus</i>	-2.31 **	5.64	0.13	-0.186	-1.86	0.05	-1.07	-0.02	0.01	-1.10 **	5.26	0.06	-1.11	0.26	0.01	0.04	-1.97	0.02
	<i>D. glomerata</i>	0.46	-1.71	0.07	1.53 **	7.44	0.12	-0.59	-1.41	0.01	0.27	-1.57	0.00	-0.21	-1.92	0.01	-0.38	0.33	0.00
	<i>P. lanceolata</i>	3.89 ***	20.31	0.23	3.76 ***	69.21	0.47	3.79 ***	26.22	0.23	2.57 ***	45.97	0.37	3.71 ***	26.58	0.23	0.08	-1.89	0.17
	<i>S. minor</i>	-3.74 ***	19.03	0.22	-1.78 ***	11.04	0.15	-1.95 *	4.77	0.05	-1.05 *	4.61	0.06	-2.60 ***	11.00	0.11	0.64 **	4.94	0.05
	<i>L. corniculatus</i>	-2.031 *	3.77	0.11	-1.58 **	7.98	0.12	-1.19	0.41	0.01	-0.35	-1.28	0.00	-1.49 *	2.02	0.03	0.30	-0.55	0.00
	<i>T. repens</i>	3.31 ***	19.93	0.22	-1.66 ***	9.27	0.13	0.98	-0.34	0.00	-0.35	-1.31	0.00	1.67 *	3.16	0.00	-0.69 **	5.99	0.06

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666 ΔAIC is the difference in AIC between M0 that accounts for the effect of species richness and models that further accounts for the effect of species functional

667 group, functional dissimilarity, CWM of traits or species identity. Data significantly supported the model if ΔAIC (i.e. difference in AIC value between baseline
668 model and a model accounting for either functional group, functional dissimilarity or species identity) >4 (bold values). *: p-value <0.05 ; **: p-value <0.01 ;
669 ***: p-value <0.001 . For the functional group and species identity models, estimates represent the effect of the presence of each functional group and species in
670 the mixture, respectively, while for the functional dissimilarity and CWM models, estimates represent the slope of the effect of increasing functional
671 dissimilarity (CWM) in the mixture.



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673 **Figure 1:** Effect of species richness on mean (A) aboveground and root productivity and (B)

674 aboveground and belowground biodiversity effects and (C) aboveground complementarity and

675 selection effects. Differences across the richness gradients are tested using linear models. ***:

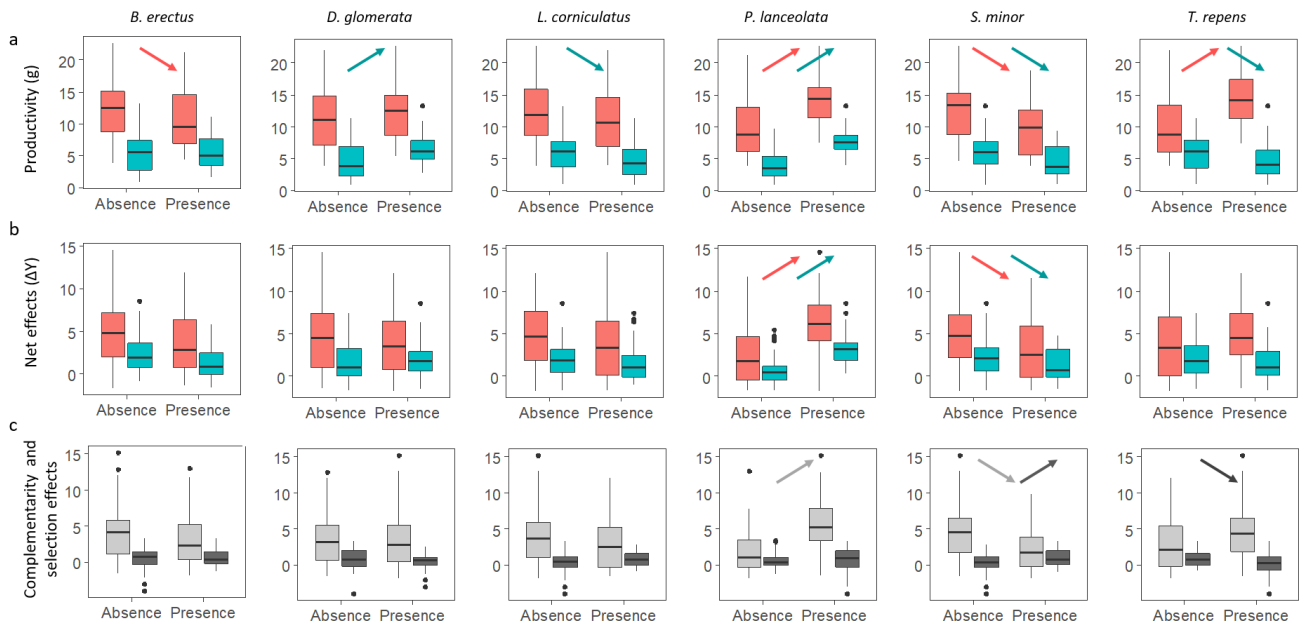
676 $p < 0.001$; **: $p < 0.01$; * < 0.05 ; ns: non-significant. Barplots represent the 1st, 2nd and 3rd quartiles.

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682 **Figure 2:** Species-specific effect on aboveground (red) and belowground (blue) productivity
 683 (a), net effects (b) and complementarity (light grey) and selection (dark grey) effects on
 684 aboveground productivity (c). Arrows represent significant effect of the presence of a species
 685 and its direction ($p < 0.05$). Barplots represent the 1st, 2nd and 3rd quartiles.

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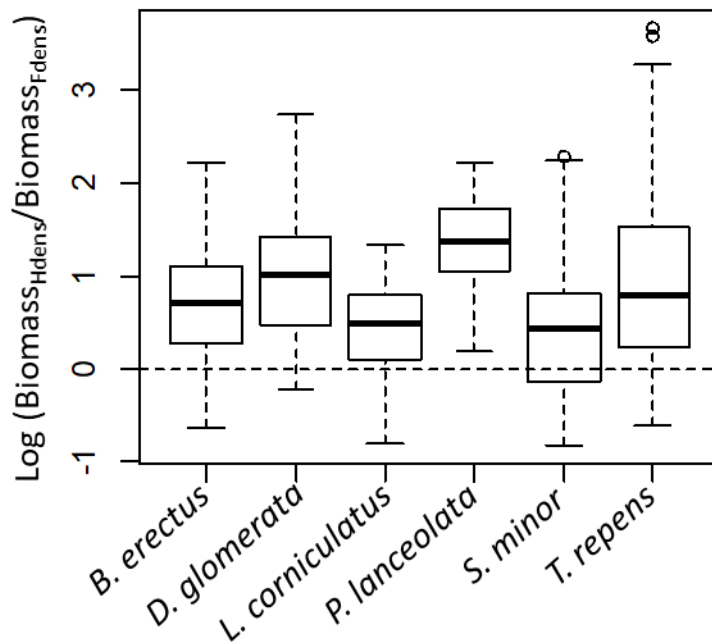
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698 **Figure 3:** Variation of the intraspecific competition log-response ratio between species. We
 699 computed log-response ratio between individual plant aboveground biomass in monoculture
 700 sown at half-density ($Biomass_{Hdens}$) and individual plant aboveground biomass in monoculture
 701 sown at full-density ($Biomass_{Fdens}$). Positive log-response ratio corresponded to higher
 702 aboveground biomass for the individual of the monoculture sown at half-density. Barplots
 703 represent the 1st, 2nd and 3rd quartiles.

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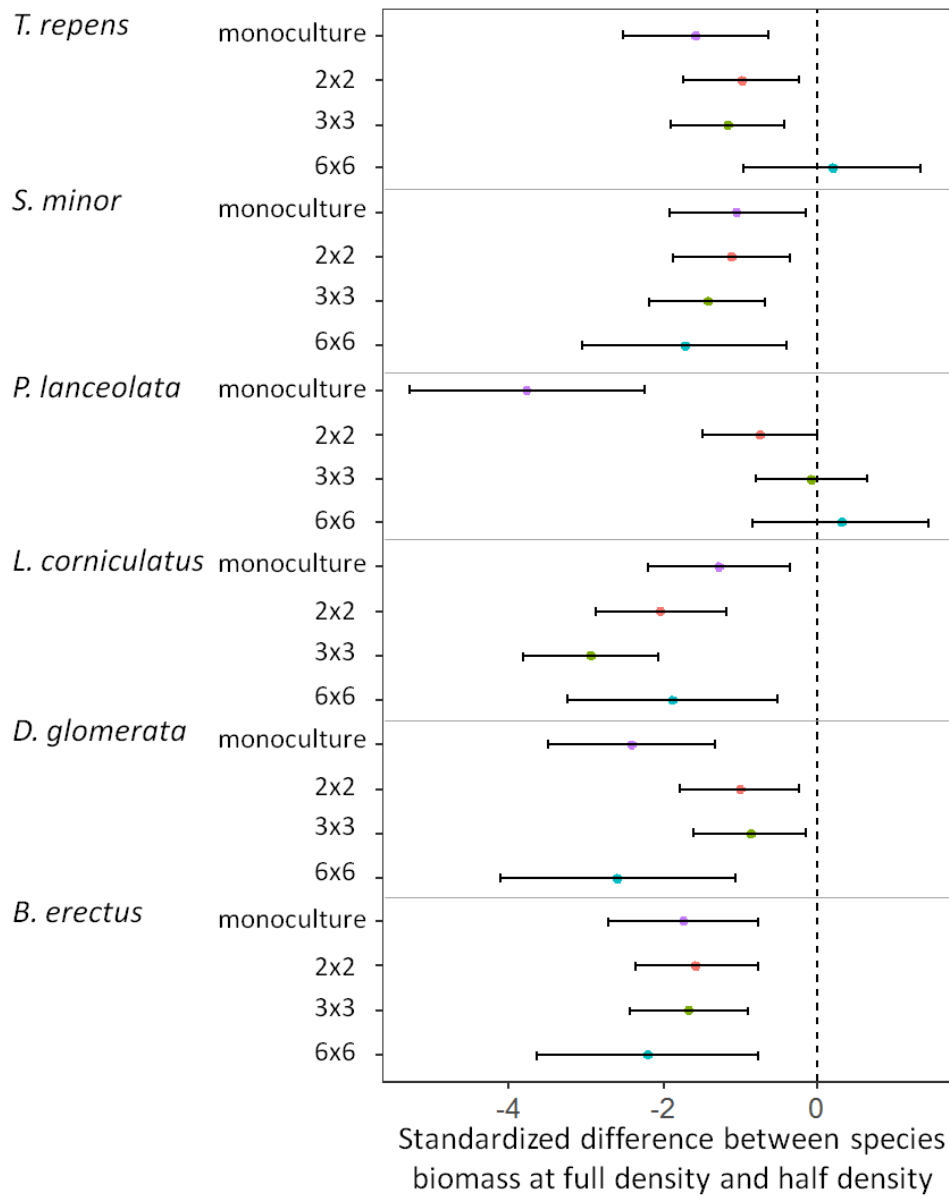
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713 **Figure 4:** Standardized difference between individual plant biomass of species grown in
 714 monoculture with half density (three individuals) and monoculture and mixtures of two, three
 715 and six species grown at full density (six individuals). Whiskers are confidence intervals
 716 ($\alpha=0.05$): if confidence interval crossed 0, then individual plant biomass in full density pot does
 717 not significantly differ from the individual plant biomass of the same species grown in
 718 monoculture at half-density. A negative value means that individual plant biomass in full density
 719 pot is lower than in half density pot, suggesting the influence of negative-density dependence
 720 mechanisms.

722 **Table S1:** Posterior model probabilities computed for the functional group, functional dissimilarity, CWM and species identity models.

		Above ground productivity	Belowground productivity	Aboveground net effect	Belowground net effect	Complementarity effect	Selection effect
<i>Functional group</i>	Legume	0.41	0.76	0.09	0.25	0.15	0.58
	Herbs	0.183	0.08	0.17	0.06	0.10	0.24
	Forbs	0.09	0.08	0.19	0.09	0.14	0.09
<i>Functional dissimilarity</i>	Height	0.11	0.92	0.10	0.08	0.08	0.10
	SLA	0.14	0.04	0.41	0.08	0.25	0.09
	Amax	0.09	0.04	0.09	0.07	0.08	0.08
	SRL	0.09	0.85	0.08	0.07	0.07	0.11
	Nabs	0.16	0.07	0.22	0.23	0.02	0.09
	RHL	0.06	0.71	0.08	0.47	0.11	0.11
	DRF	0.14	0.92	0.10	0.06	0.08	0.16
	RID	0.42	0.07	0.24	0.03	0.18	0.10
<i>CWM</i>	Height	0.85	0.89	0.32	0.81	0.28	0.08
	SLA	0.86	0.92	1.00	0.89	0.67	0.12
	Amax	0.69	0.90	0.80	0.84	0.70	0.08
	SRL	0.15	0.85	0.08	0.04	0.10	0.09
	Nabs	0.11	0.91	0.87	0.89	0.66	0.08
	RHL	0.51	0.13	0.90	0.62	0.69	0.15
	DRF	0.58	0.07	0.82	0.68	0.60	0.14
	RID	0.13	0.06	0.18	0.34	0.11	0.20
<i>Species identity</i>	<i>B. erectus</i>	0.81	0.07	0.19	0.37	0.20	0.08
	<i>D. glomerata</i>	0.09	0.92	0.11	0.11	0.08	0.24
	<i>P. lanceolata</i>	0.75	0.67	0.52	0.88	0.86	0.09
	<i>S. minor</i>	1.00	0.69	0.71	0.31	1.00	0.56
	<i>L. corniculatus</i>	0.62	0.50	0.24	0.06	0.39	0.27
	<i>T. repens</i>	0.69	0.60	0.83	0.06	0.32	0.86

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724 Posterior model probability report the probability that each functional group, functional dissimilarity, CWM and species identity models (M1_i) is

725 better than the baseline model that only accounts for species richness (M0). Bold values correspond to models that have been selected according
726 to the difference in AIC between M0 and M1_i (i.e. ΔAIC , see Table 2).

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740 **Table S2:** Model outputs of the baseline models (M0) that account for the effect of species richness on aboveground and root biomass production,
 741 aboveground and root biodiversity effects as well as aboveground complementarity and selection effects in every treatment (from monoculture to
 742 six-species mixtures for biomass; from two-species to six-species mixtures for biodiversity effects). In addition, we tested for the effect of species
 743 richness without the six-species plant mixtures.

		<i>Above ground productivity</i>			<i>Root productivity</i>			<i>Aboveground ΔY</i>			<i>Belowground ΔY</i>			<i>Complementarity effect</i>			<i>Selection effect</i>		
		Estimate	r ²	AIC	Estimate	r ²	AIC	Estimate	r ²	AIC	Estimate	r ²	AIC	Estimate	r ²	AIC	Estimate	r ²	AIC
Baseline models (M0)	With 6x6	1.29 ***	0.08	744.04	0.31	0.01	615.36	0.68	0.01	609.60	-0.09	0.01	476.59	0.37	0.01	602.84	0.32 *	0.04	363.83
	Without 6x6	1.88 **	0.08	710.60	0.97 **	0.06	584.84	0.68	0.01	579.10	0.51	0.01	452.22	0.59	0.01	573.49	0.09	0.01	345.50

744 *: p-value <0.05; **: p-value <0.01; ***: p-value <0.001.

Table S3: Model outputs of the model accounting for the addition effect of species richness and functional dispersion indices ($M1_k$) based on eight traits (multi-traits) or on single traits for Height and SLA measure at the individual plant levels thus accounting for intraspecific variability (Height ISV and SLA ISV). ΔAIC is the difference in AIC between $M0$ that accounts for the effect of species richness and $M1_k$ that further accounts for the effect of functional dispersion. Data significantly supported the model if delta AIC >4 (bold values).

	Above ground productivity			Belowground productivity			Aboveground ΔY			Belowground ΔY			Complementarity effect			Selection effect		
	Estimate	r^2	ΔAIC	Estimate	r^2	ΔAIC	Estimate	r^2	ΔAIC	Estimate	r^2	ΔAIC	Estimate	r^2	ΔAIC	Estimate	r^2	ΔAIC
Multitraits	0.75	0.08	0.08	0.76 *	0.04	3.93	-0.64	0.03	0.73	0.08	0.01	-1.85	-0.32	0.01	-4.27	-0.32	0.90	4.38
Height (ISV)	-0.02	0.07	-2.00	0.93 ***	0.10	11.64	0.02	0.01	-1.99	0.50 *	0.04	4.33	-0.12	0.01	-1.89	0.13	0.05	-0.78
SLA (ISV)	0.11	0.07	-1.94	0.2	0.01	-1.43	0.17	0.01	-1.79	0.27	0.01	-0.23	0.08	0.01	-1.94	0.08	0.04	-1.51

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746 *: p-value <0.05; **: p-value <0.01; ***: p-value <0.001

Table S4: Species functional distinctiveness. Functional distinctiveness is the average functional distance from a species to all other in a given community using the *distinctiveness* function of *funrar* R library (Grenié *et al.*, 2018). Functional distinctiveness varies from 0 when a species is, on average, functionally close to the other species to 1 when a species is highly distant from others.

	Functional distinctiveness
<i>B. erectus</i>	0.25
<i>D. glomerata</i>	0.77
<i>P. lanceolata</i>	0.27
<i>S. minor</i>	0.28
<i>L. corniculatus</i>	0.45
<i>T. repens</i>	0.25

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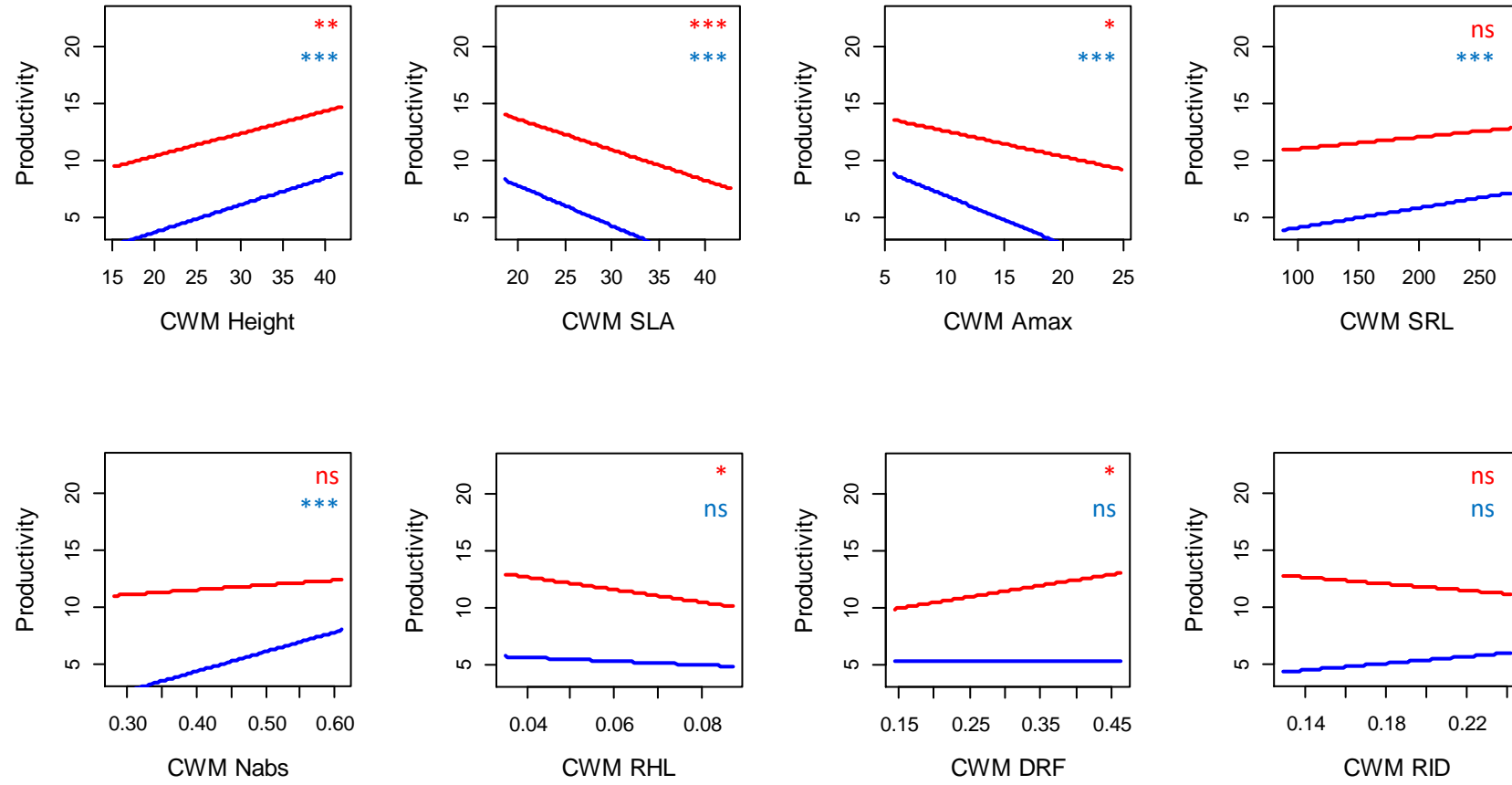


Figure S1: Effects of community weighted mean trait value (CWM) on aboveground (red) and root (blue) productivity. ***: $p < 0.001$; **: $p < 0.01$; * < 0.05 ; ns: non-significant

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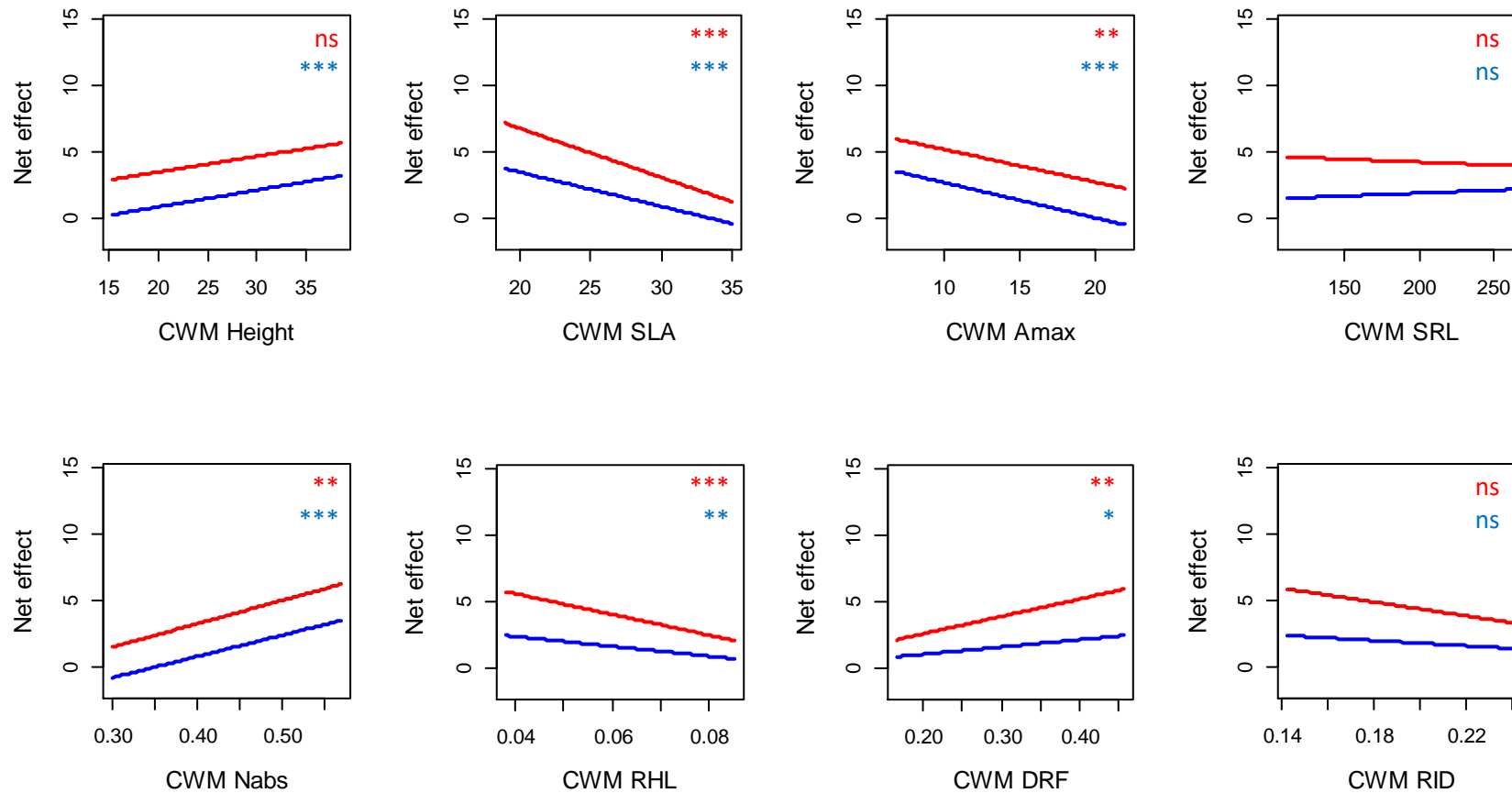


Figure S2: Effects of community weighted mean trait value (CWM) on aboveground (red) and root (blue) net biodiversity effects. ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: non-significant

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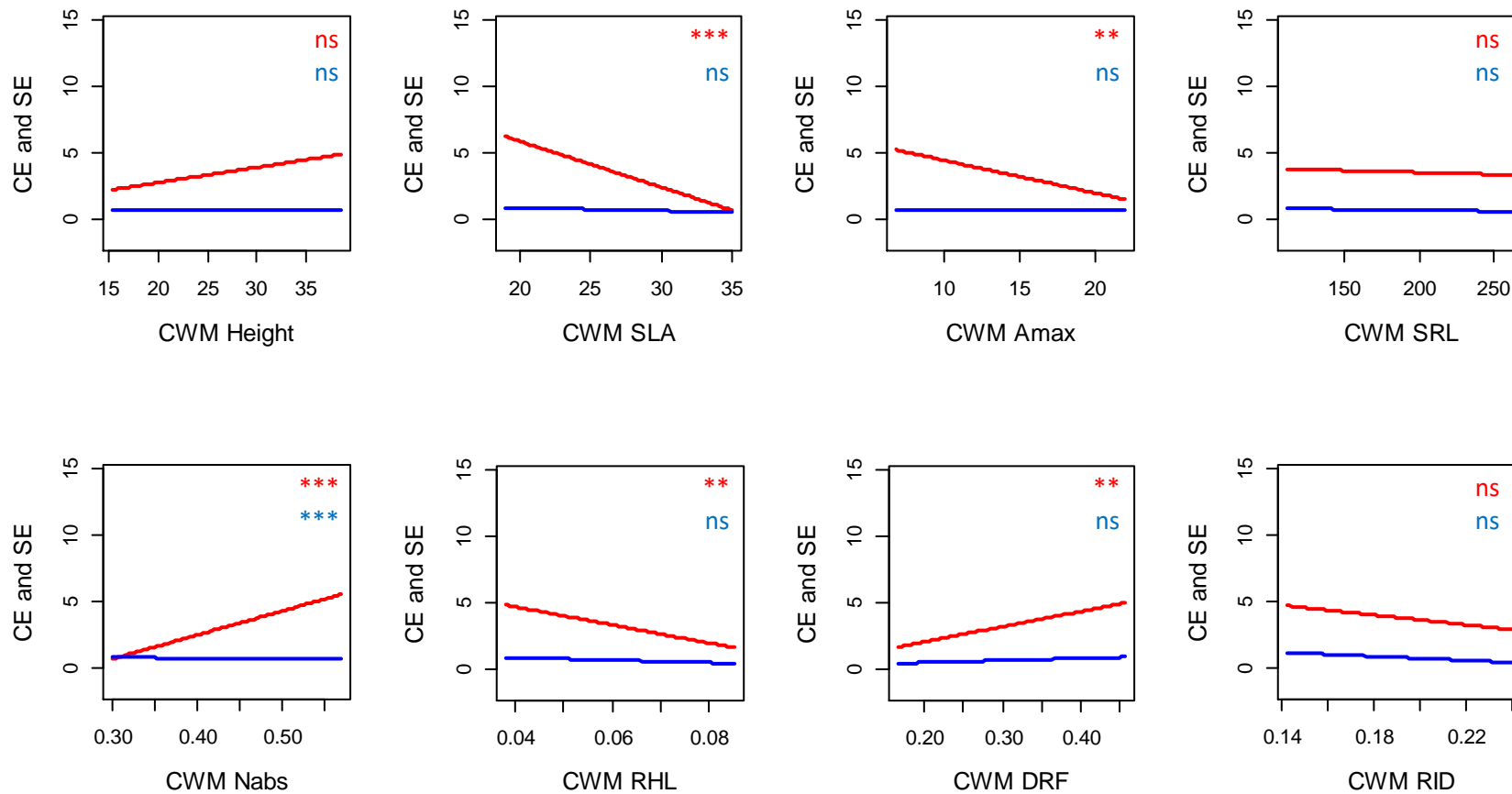


Figure S3: Effects of community weighted mean trait value (CWM) on complementarity (red) and selection (blue) effects. ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: non-significant

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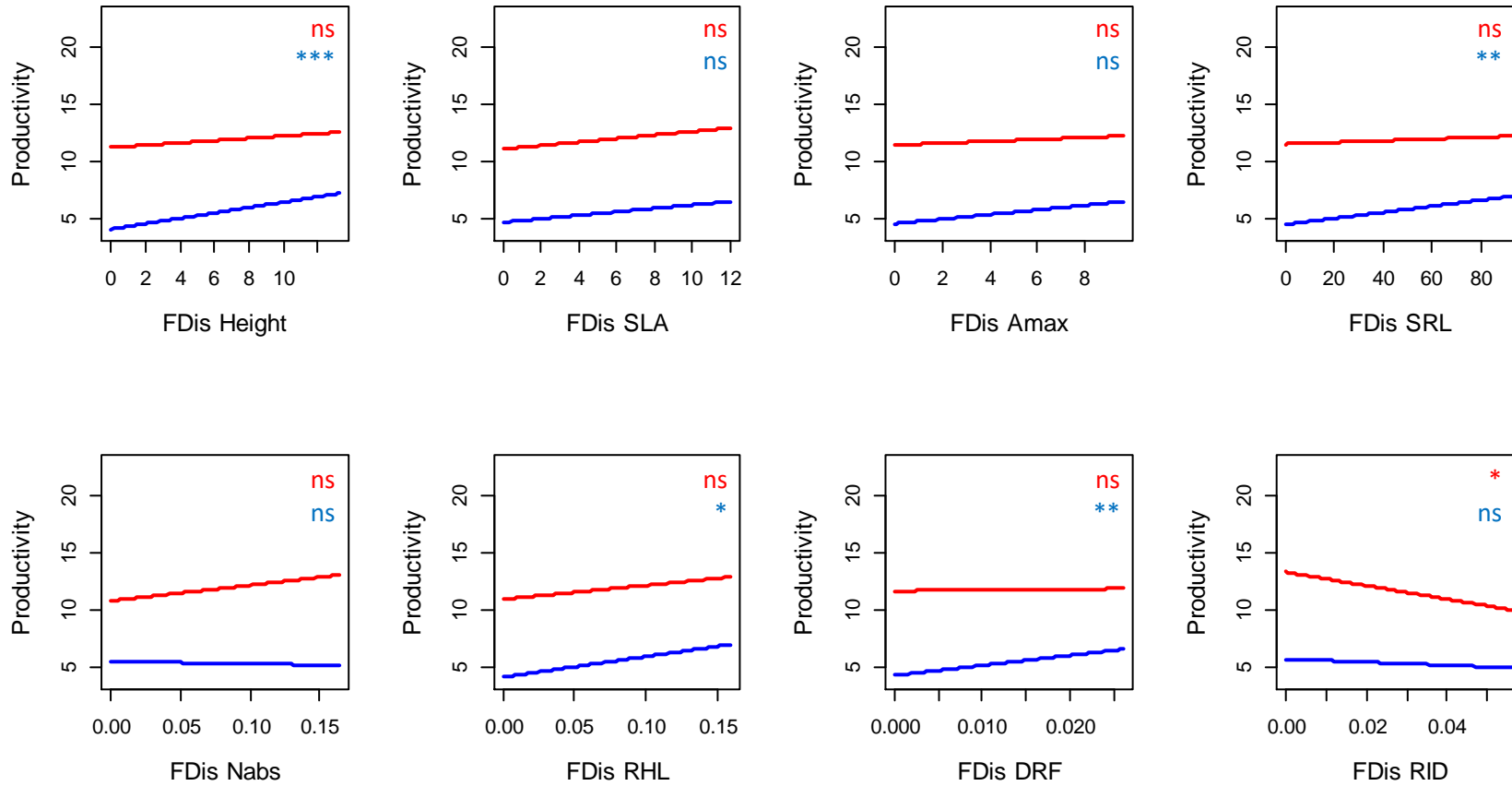
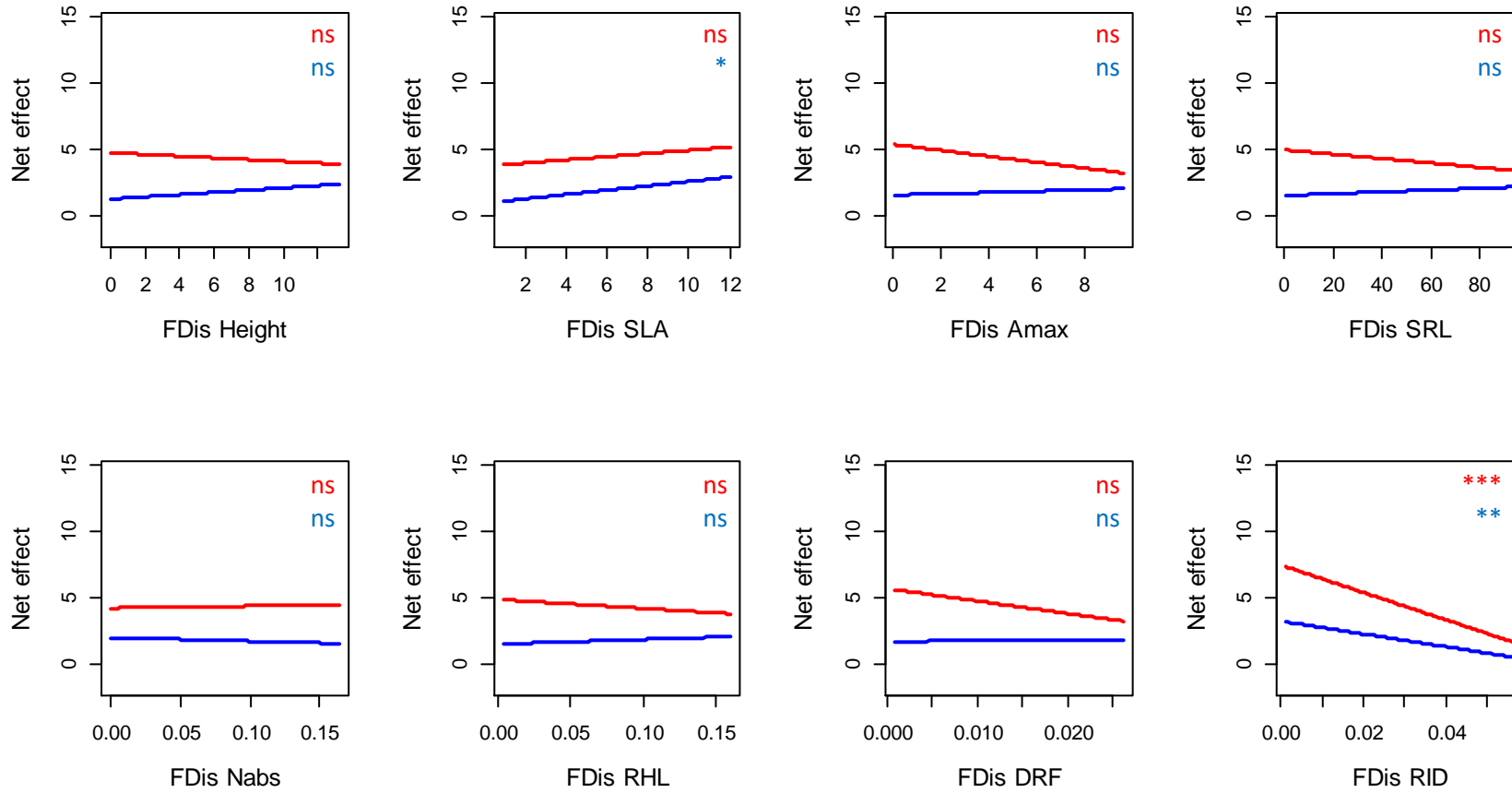


Figure S4: Effects of trait-by-trait functional dissimilarity (FDis) on aboveground (red) and root (blue) productivity. ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: non-significant



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Figure S5: Effects of trait-by-trait functional dissimilarity (FDis) on aboveground (red) and root (blue) net biodiversity effects. ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: non-significant

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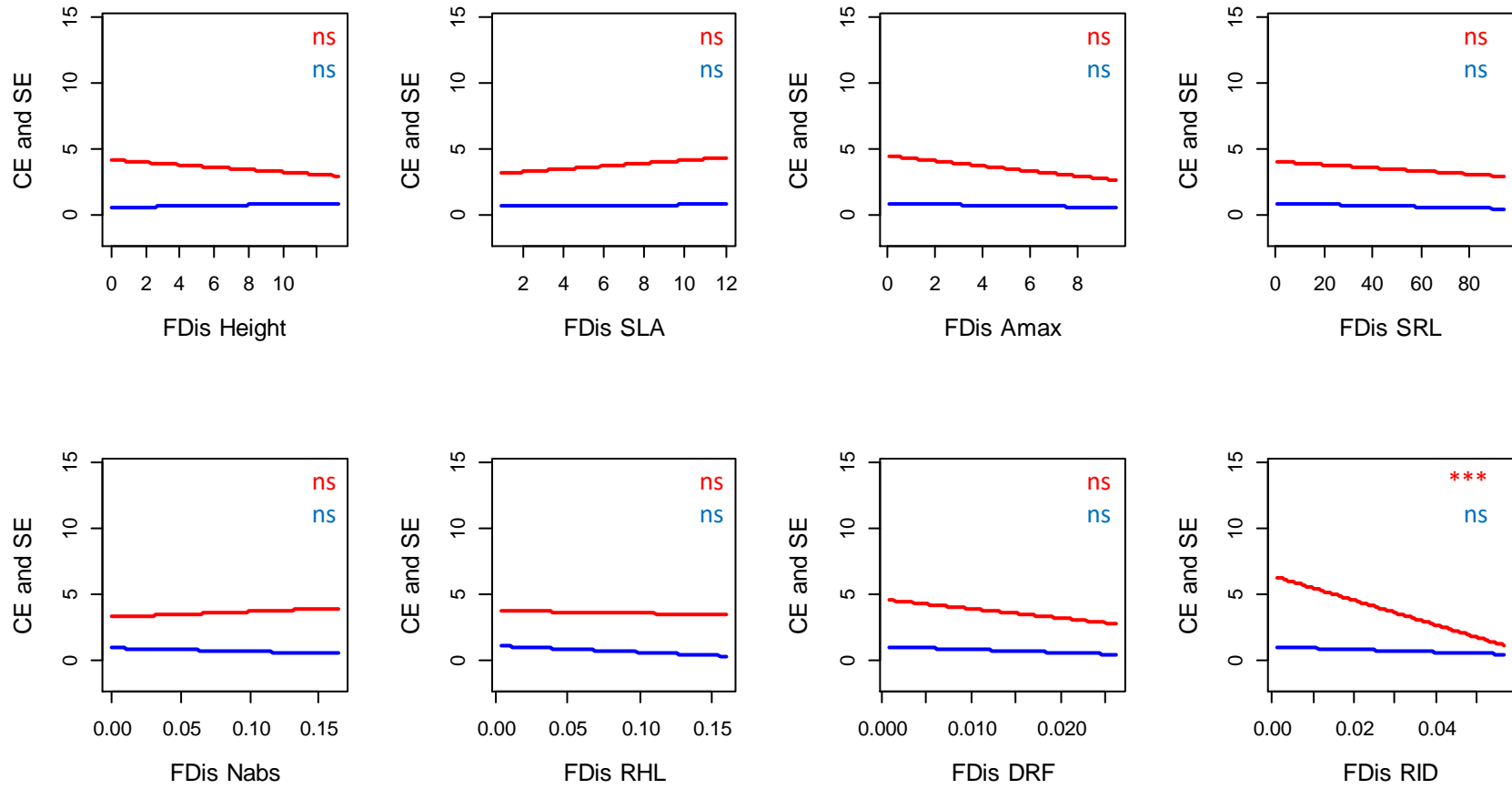


Figure S6: Effects of trait-by-trait functional dissimilarity (FDis) on complementarity (red) and selection (blue) effects. ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: non-significant