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Lucie Mahaut, Florian Fort, Cyrille Violle, Gregoire T. Freschet. Multiple facets of diversity effects on plant productivity: species richness, functional diversity, species identity and intraspecific competition. Functional Ecology, 2019, 10.1111/1365-2435.13473. hal-02321331

HAL Id: hal-02321331 https://hal.science/hal-02321331

Submitted on 21 Oct 2019

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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

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

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

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
well as strong positive complementarity effect. These arose largely from the presence of a
particular species (*Plantago lanceolata*) and from CWM trait values more than from a higher
functional dissimilarity in plant mixtures. *P. lanceolata* displayed the highest intraspecific
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.

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

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

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66 Introduction

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

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

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

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

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

quantifying for every species the gain of individual biomass when decreasing plant density inmonocultures.

142 Materials and Methods

143 Experimental design

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

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

to ensure realistic growth conditions for plants. The soil was a calcareous sandy loam (pH = 164 8.5) with rather low organic matter content (9.7 g.kg⁻¹), cation-exchange capacity (0.5 g.kg⁻¹) 165 and total N content (0.5 g.kg⁻¹). At the start of the experiment, in November 2015, a soil leachate 166 solution was added to ensure the presence of symbiotic N₂-fixing bacteria in the pot. Pots were 167 watered three times a week to provide moisture conditions close to field capacity in the soil 168 profiles; this corresponded to 0.1L of water at the start of the experiment and 0.6L at the end in 169 order to account for increasing plant demand. In addition, all pots received three soil 170 enrichments (after 1, 4 and 9 weeks) in phosphorus (P) and potassium (K) in increasing amount 171 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 172 remained the main limiting resource for plant growth. We randomly placed pots on wheeled 173 carriages and avoided side effects by rearranging carriages every two weeks. 174

175 Biomass measurements

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

182 Trait measurements

We measured three aboveground traits and five belowground traits related to both nitrogen and light acquisition. For each trait, the detailed protocol is presented in Freschet *et al.* (2018). Briefly, three weeks before harvest, we measured light-saturated leaf photosynthetic rate per area (A_{area} , $\mu mol_{CO2} m^{-2} s^{-1}$) - that provides the leaf maximal photosynthesis capacity on one individual per monoculture pot by quantifying the amount of C accumulated in a leaf

exposed to a high light intensity for several minutes (C influx vs efflux). One week before the 188 experiment harvest, we recorded the maximum height (cm) achieved by all plant individuals in 189 all pots. Plant height is a good proxy for light depletion through the canopy (Violle et al. 2009). 190 Specific leaf area (SLA, m².kg⁻¹) was assessed at harvest based on two to four leaves (depending 191 on the species) from each plant individual that we immediately scanned for leaf area 192 measurement. Specific leaf area corresponds to the area of light capture per biomass invested 193 in leaves and is related to the fundamental trade-off existing between species acquisition and 194 195 conservation of resources (Garnier & Laurent 1994).

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

amount of ¹⁵N taken up by plants after injection of different forms of ¹⁵N in the soil, per length of fine root and per h (μ g ¹⁵N m⁻¹ h⁻¹).

215 *Biodiversity effects*

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

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$$\Delta Y_i = N_i \cdot \overline{\Delta RY} \cdot \overline{M} + N_i \cdot COV(\Delta RY_{i,i}, M_i)$$
 Equation 1

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

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

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

232 Functional diversity

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

(CWM). We quantified functional dissimilarity using the functional dispersion (FDis) index 235 236 computed separately for each trait using the *fdisp* function of the FD R package (Laliberté, Legendre & Shipley, 2014). For each trait, we computed FDis based on mean species trait 237 values measured in monoculture pots only to insure homogeneity between the different traits 238 that were measured in all pots or in monoculture only (Table 1). Since plant height and SLA 239 240 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 pots. CWM were calculated for each trait by multiplying the mean species trait value measured 242 in monoculture pots by the proportional abundance of each species in each community. Finally, 243 244 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 species identity on aboveground and root biomass production, aboveground and belowground 247 248 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 affected biomass production, biodiversity effects, complementarity effect and selection effect 250 in a baseline model (M0). Next, we built 'functional group', 'functional dissimilarity', 'CWM' 251 252 and 'species identity' models to test the extent to which the data support the effect of a particular functional group, functional trait or species identity on these response variables. To do so, we 253 added the presence of each functional group or species (coded as a binary variable) or FDis and 254 CWM of each trait separately as an explanatory variable to M0. The resulting model (M1_i), 255 which is the importance of a candidate species i, functional group i or functional trait i to explain 256 257 variation in productivity, was then evaluated according to its Akaike information Criterion (AIC). We considered a species, a functional group or a functional trait as important for 258 productivity if ΔAIC (AIC_{M0} – AIC_{M1i}) was greater than 4 (Maire *et al.*, 2018). Although a 259

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

In addition, we tested for the influence of intraspecific competition, i.e. species-specific 272 density-productivity relationships, on biomass production by computing for each species 273 274 intraspecific competition logarithmic response-ratio (Hedges, Gurevitch & Curtis 1999). To do so, for each species, we compared the biomass of the nine individuals grown in monocultures 275 sown at half-density to the biomass of the 18 individuals grown in monocultures sown at full 276 277 density. Positive logarithmic response-ratio corresponds to higher biomass for the individual of the monoculture sown at half-density while negative response-ratio corresponds to higher 278 279 biomass for the individuals of the monoculture sown at full density. Finally, we computed the standardized difference (effect size) between individual plant biomass of species grown in 280 281 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 individual plants in mixtures, such effect sizes were only calculated for aboveground biomass. 283 Confidence intervals (α =0.05) were computed to test whether individual plant biomass in full 284

density pots significantly differed from individual plant biomass of the same species grown in
monoculture at half-density. All analyses were conducted using R ver. 3.4.4. (www.rproject.org).

288 **Results**

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

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

The additive partitioning of aboveground biodiversity effect (Δ Y) revealed that among all mixtures, complementarity effect was the main fraction of Δ Y (Fig. 1c), accounting for ~ 83% of aboveground Δ Y. Complementarity effect did not increase with species richness (P =0.34, r² = 0.01; Table S2) while the selection effect did (P = 0.02, r² = 0.04; Table S2).

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

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

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

325 *Key species associated to changes in productivity*

The presence of *P. lanceolata* in the mixture was the principal driver of change in productivity (for aboveground and root productivity: $\Delta AIC = 20.307$, $r^2 = 0.225$ and $\Delta AIC =$ 69.211, $r^2 = 0.471$, respectively), net effects (for aboveground and belowground net effects: $\Delta AIC = 26.224$, $r^2 = 0.229$ and $\Delta AIC = 45.967$, $r^2 = 0.366$, respectively) and complementarity effect ($\Delta AIC = 26.578$, $r^2 = 0.230$; Table 2). All these components of biomass production were significantly higher when *P. lanceolata* was in the plant mixtures (Fig. 2). The presence of *S. minor* and *T. repens* in plant mixtures also markedly affected biomass production. Aboveground and root productivity, net effects and complementarity effects were lower in presence of *S. minor* while the selection effect was higher. Aboveground productivity was higher in the
presence of *T. repens* while root productivity and selection effects were lower (Fig. 2).
Nevertheless their influence on net effects, complementarity and selection effects were
substantially (from two to ten times) lower than to those of *P. lanceolata* (Table 2).

338 Species-specific effect and intraspecific competition

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

353 **Discussion**

Our study revealed contrasting influences of the four studied facets of biodiversity effects on ecosystem biomass production. Species richness and functional dissimilarity showed only moderate influence, whereas community weighted trait means (CWM), species identity and the relaxation of intraspecific competition accounted for a large part of observedbiodiversity effects.

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

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

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

By contrast, we reported strong influence of five out of eight community weighed trait 392 means on the complementarity effect – and by extent on biodiversity effects. Species ability to 393 take up nitrogen resources was a main driver of biomass productivity, as suggested by the 394 positive relationships between the community weighted mean of both nitrogen absorption rate 395 396 and deep root fraction and biodiversity effects. Furthermore, biodiversity and complementary effects increased with decreasing the community weighted mean of specific leaf area and 397 maximum photosynthetic rate, implying that biomass production was maximum when plant 398 399 communities were dominated by slow-growing, resource conservative species (Wright et al., 2004). Although such a result might be surprising given the short-term nature of our experiment, 400 it may reflect the fact that low nutrient availability in this experiment have favored plants with 401 the more conservative resource strategies (Wright et al., 2004; Carmona et al., 2019). More 402 globally, the importance of functional trait values gives evidence that in this experiment, 403 404 ecosystem functioning is strongly driven by the identity of the dominant species (mass-ratio hypothesis, Grime, 1998). However, we did not find significant relationship between the CWMs 405 406 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 production of biomass and biodiversity effects in plant mixtures. Among the six species of this 411 experiment, P. lanceolata displayed the lowest biomass in monoculture but the highest biomass 412 413 in the 6x6-plant mixtures (Figure 4). Consequently, the specific effect of selecting P. lanceolata in mixture differs conceptually from the selection effect, which can be positive only when the 414 most productive species in monoculture produce even more biomass in mixture (Loreau & 415 416 Hector, 2001). Despite this, the selection of *P. lanceolata* in mixture was the major determinant of positive biodiversity effect on productivity. Its low biomass in monoculture was due to high 417 intraspecific competition, which was relieved in half-density monocultures and even more in 418 species mixtures (Figure 3). Consequently, the much lower level of interspecific competition as 419 compared to intraspecific competition for this particular species, appeared as the most critical 420 421 driver of biodiversity effects in our experiment. Since the strength of intraspecific competition may be generally stronger than the strength of interspecific competition in plant communities 422 (Adler et al., 2018), we expect that such a mechanism may be widespread in biodiversity -423 424 biomass production relationships. The same pattern, although much less strong, was also observed here for T. repens, and the reverse pattern was recorded for S. minor, which suffered 425 426 more from interspecific competition than from intraspecific competition (see also Turnbull et al., 2013). Interestingly, we observed that, across our six species, the effect of intraspecific 427 competition on species production was inversely related to the effect of interspecific 428 429 competition (Figure 4), suggesting that a priori knowledge of species-specific densitydependence production may be particularly useful to explain (and potentially predict) biomass 430 gains in mixtures. An increasing number of biodiversity-productivity studies already accounts 431

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

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

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

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

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

466 Acknowledgements

This study was supported by the EC2CO grant 'MULTIVERS' to G.T.F. and by the European 467 468 Research Council (ERC) Starting Grant Project 'Ecophysiological and biophysical constraints on domestication of crop plants' (Grant-ERC-StG-2014-639706-CONSTRAINTS) to CV. We 469 470 are grateful to Pascal Chapon, Annick Lucas, Malick Diao, Océane Cobelli, David Degueldre, 471 Pauline Durbin, Jérémy Devaux, Pierrick Aury and Elodie Renaut for their proficient help with the experimental setup, harvest and plant measurements. This experiment was supported by 472 Thierry Matthieu and the CEFE 'terrain d'expériences' (TE) team, Nicolas Barthès, Bruno 473 474 Buatois and Raphaëlle Leclerc within the 'plateforme d'analyses chimiques' (PACE) and by the CEFE 'plateforme long-terme' (PLT). 475

476 Author contributions

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

481 Data Availability Statement

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

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- Figure 1: Effect of species richness on mean (A) aboveground and root productivity and (B)
 aboveground and belowground biodiversity effects and (C) aboveground complementarity and
 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.

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

Figure 3: Variation of the intraspecific competition log-response ratio between species. We computed log-response ratio between individual plant aboveground biomass in monoculture sown at half-density (Biomass_{Hdens}) and individual plant aboveground biomass in monoculture sown at full-density (Biomass_{Fdens}). Positive log-response ratio corresponded to higher aboveground biomass for the individual of the monoculture sown at half-density. Barplots 642 represent the 1^{st} , 2^{nd} and 3^{rd} quartiles.

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

651 Tables

Table 1: Species list and average trait values (± sd) as grown in monoculture conditions. g: grass; f: forb; l: legume.

	Specific leaf area $(m^2 kg^{-1})$	Max photo- synthetic capacity $(\mu mol-CO_2 m^{-2} s^{-1})$	Plant height (cm)	Specific root length (m g^{-1})	Deep root (< 20 cm) fraction	Specific N absorption rate $(\mu g m^{-1} h^{-1})$	Root inter- branch distance (cm)	Root hair length (mm)
B. erectus (g)	26.63 ±2.5	14.64 ± 1.0	24.50 ± 4.2	150.12 ± 53.7	0.38 ± 0.02	0.06 ± 0.01	0.35 ± 0.04	0.24 ±0.03
D. glomerata (g)	$29.23 \pm \! 0.8$	5.70 ± 0.7	41.89 ± 3.7	275.50 ± 27.6	0.41 ± 0.03	0.04 ± 0.01	0.46 ± 0.04	0.24 ± 0.04
P. lanceolata (f)	18.58 ± 1.0	9.97 ± 1.7	27.78 ± 1.4	151.54 ± 15.6	0.55 ± 0.03	0.08 ± 0.06	0.17 ± 0.01	0.18 ± 0.01
S. minor (f)	24.83 ± 0.3	24.85 ± 0.9	15.44 ± 0.9	130.26 ± 45.8	0.61 ± 0.03	0.06 ± 0.02	0.14 ± 0.01	0.13 ± 0.01
L. corniculatus (l)	42.75 ± 5.1	14.53 ±2.1	15.33 ± 1.1	87.52 ± 19.1	0.38 ± 0.11	0.09 ± 0.03	0.36 ± 0.09	0.20 ± 0.01
T. repens (l)	31.26 ±2.3	20.60 ± 7.5	22.89 ± 0.9	140.19 ± 24.8	0.28 ± 0.03	0.08 ± 0.04	0.20 ± 0.01	0.16 ±0.02

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 gro	ound proc	luctivity	Belowgro	und prod	luctivity	Abovegr	ound net	teffect	Belowgr	ound net	effect	Compler	nentarity	effect	Sele	ction eff	ect
		Estimate	ΔAIC	r ²	Estimate	ΔAIC	r ²	Estimate	ΔAIC	r ²	Estimate	ΔAIC	r ²	Estimate	ΔAIC	r ²	Estimate	ΔAIC	r ²
	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
F unctional group	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
group	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
	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
Functional	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
dissimilarity	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
	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
CWM	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
CWM	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
	B. erectus	-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
	D. glomerata	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
Spacios idantity	P. lanceolata	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
species identity	S. minor	-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
	L. corniculatus	-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
	T. repens	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

⁶⁶⁵

 Δ AIC 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

- $figure{1}$ group, functional dissimilarity, CWM of traits or species identity. Data significantly supported the model if ΔAIC (i.e. difference in AIC value between baseline
- 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.





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



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



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





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

Supplementary informations

		Above ground productivity	Belowground productivity	Aboveground net effect	Belowground net effect	Complementarity effect	Selection effect
	Legume	0.41	0.76	0.09	0.25	0.15	0.58
Functional group	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
	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
Functional	SRL	0.09	0.85	0.08	0.07	0.07	0.11
dissimilarity	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
	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
CWM	SRL	0.15	0.85	0.08	0.04	0.10	0.09
CWM	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
	B. erectus	0.81	0.07	0.19	0.37	0.20	0.08
	D. glomerata	0.09	0.92	0.11	0.11	0.08	0.24
Spacios identity	P. lanceolata	0.75	0.67	0.52	0.88	0.86	0.09
species identity	S. minor	1.00	0.69	0.71	0.31	1.00	0.56
	L. corniculatus	0.62	0.50	0.24	0.06	0.39	0.27
	T. repens	0.69	0.60	0.83	0.06	0.32	0.86

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

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. Δ AIC, 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 biodiversity effects as well as aboveground complementarity and selection effects in every treatment (from monoculture to six-species mixtures for biodiversity effects to six-species mixtures for biodiversity effects). In addition, we tested for the effect of species

743 richness without the six-species plant mixtures.

		Abov	Above ground			Post productivity									Complementarity			Salaatian offaat		
		prod	ductiv	vity	коот р	coot productivity			Aboveground $\Delta 1$			Belowground A1			effect			selection effect		
		Estimate	r ²	AIC	Estimate	r ²	AIC	Estimate	r ²	AIC	Estimate	r ²	AIC	Estimate	r²	AIC	Estimate	r ²	AIC	
Baseline	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	
(M0)	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). Δ AIC 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 Belowground				Above	Aboveground ΔY			Belowground ΔY			Complementarity effect				Selection effect		
	Estimate	r ²	ΔAIC	Estimate	r ²	ΔAIC	Estimate	r ²	ΔΑΙΟ	Estimate	r²	ΔΑΙΟ	Estimate	r²	ΔΑΙΟ	Estimate	r²	ΔΑΙΟ
Multitraits	s 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
B. erectus	0.25
D. glomerata	0.77
P. lanceolata	0.27
S. minor	0.28
L. corniculatus	0.45
T. repens	0.25
S. minor L. corniculatus T. repens	0.28 0.45 0.25



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







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



