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

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Abstract

1. 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 has 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 combination of two, three and six species. Plant density was kept constant across the richness gradient but we additionally grew each species in half-density monoculture to estimate the strength of intraspecific competition for each studied species. We characterized eight functional traits, including root traits, related to nutrient and light acquisition and computed both the functional dissimilarity and the community-weighted mean (CWM) of each trait. We further partitioned above-ground biodiversity effect into complementarity and selection effects.
4. We observed strong positive biodiversity effects on both above-ground 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 *Sanguisorba minor* negatively affected the productivity of plant mixtures, this species suffering 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.

KEYWORDS

biodiversity–ecosystem functioning, complementarity effect, functional distinctiveness, functional trait, niche difference, roots, selection effect, species coexistence

1 | INTRODUCTION

Although numerous plant diversity–ecosystem functioning experiments have reported positive effects of plant species richness on ecosystem productivity (Cardinale et al., 2012; Lefcheck et al., 2015; Tilman et al., 2001), the nature of the mechanisms that cause this pattern remains highly controversial. It is widely accepted that niche complementarity can lead to higher productivity in plant mixtures compared to monocultures (*biodiversity effects*; Huston, 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 to alter their surrounding environment and to subsequently favour the fitness of other species (e.g., abiotic facilitation), or due to plant interactions with other trophic levels (Barry et al., 2019). Positive biodiversity effects can also result from an increased probability of selecting a species with a specific property as the size of the community increases, for example a highly productive species (Loreau & Hector, 2001). The *selection effect* describes whether the species that dominate plant mixtures are the most productive species in monoculture (i.e., positive 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 disproportionate effect on ecosystem functioning irrespective of their biomass in monoculture (Jaillard, Deleporte, Loreau, & Violle, 2018). Such a species-specific effect underpins the well-known concept of keystone species, that is species having 'disproportionately large effects relative to its abundance' (Paine, 1969; see also Violle et al., 2017 for a revisiting concept in the light of functional ecology theory). Recently, Maire et al. (2018) extended this concept by defining ‘key species’ as those species that are 'consistently and significantly associated to a certain level of ecosystem functioning or services' (Maire et al., 2018). Although the search for key species can reveal unsuspected mechanisms for ecosystem functioning (Diaz et al., 2007; Huston, 1997), their role in biodiversity–ecosystem functioning experiments have been largely neglected.

Because ecological niches are theoretically linked to a suite of functional traits (Violle & Jiang, 2009), functional traits appear to be a promising tool for understanding diversity–productivity relationships. On the one hand, differences in functional traits (*functional dissimilarity*) can reflect differences in the use of resources that allow species to partition the local pool of resources and avoid interspecific competition (Violle et al., 2012). For instance, differences in the vertical distribution of roots among species allow the capture of water and 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 trait values (Diaz et al., 2007; Garnier et al., 2004). It has been argued that functional 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, 2017). Disentangling the respective influence of both processes through a trait-based approach thus requires using a set of traits that are directly linked to species’ resource use and competitive ability. For instance below-ground, this requires studying root traits that reflect how species 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, specific nutrient absorption rate; Freschet, Violle, Bourget, Scherer-Lorenzen, & Fort, 2018).

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 et al., 2007). Among others, the fact that every species has a specific density–productivity relationship in monoculture can be an important mechanism for ecosystem functioning. Indeed, in most biodiversity–productivity experiments, species relative density – which directly drives the strength of intraspecific competition (Chesson, 2000) – decreases along the gradient of species richness (i.e., substitutive experimental design; Hector, 1998; Jolliffe, 2000). In parallel, interspecific competition – which by essence is null in monoculture – increases along this 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, Isbell, Purves, Loreau, & Hector, 2016; Turnbull et al., 2013). Despite these evidences, previous experimental biodiversity–ecosystem 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 production in biodiversity–ecosystem functioning experiment, namely species richness, 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 six) and functional diversity. We manipulated three different functional groups (namely 'grasses', 'forbs' and 'legumes') and characterized eight functional traits (three shoot and five root traits) that were directly related to the acquisition of light and nitrogen (Freschet et al., 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 understand how species diversity affects ecosystem functioning, Diaz et al. (2007) suggest to first test for the role of functional diversity and, in a second step, to look for potentially remaining species-specific effects. In parallel, Maire et al. (2018) developed a statistical framework that aims at identifying key species that drive ecosystem functioning (Maire et al., 2018). In this framework, we separately tested the effect of the presence of a candidate species or the effect of a candidate functional trait by adding species presence or functional diversity as 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 quantifying for every species the gain of individual biomass when decreasing plant density in monocultures.

2 | MATERIALS AND METHODS

2.1 | Experimental design

The experiment was conducted at the Center for Functional and Evolutionary Ecology, Montpellier, France. We grew six plant species in monoculture (6 combinations), as well as in every combination 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 species combinations and six replicates for the six-species combination. Plant species were common European herbaceous species (see Table 1): two grasses (*Bromus erectus* Huds., *Dactylis glomerata* L.), two forbs (*Plantago lanceolata* L., *Sanguisorba minor* Scop.) and two legumes (*Lotus corniculatus* L., *Trifolium repens* L). We chose this set of species to avoid functional redundancy, these species displaying contrasted functional traits. Seeds were collected from permanent grasslands located in southern France. Plant density was kept constant across the richness gradients (i.e., six individuals per pot with equal species relative abundance) but we additionally grew each species in three replicates of half-density monoculture (i.e., three individuals per pot) to estimate the strength of intraspecific competition for each studied species. Climate conditions in the greenhouse were semi-controlled. Temperature was allowed to fluctuate between 15°C and 19°C at night and between 21°C and 25°C 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 season from 12 hr initially to 14.5 hr at the end of the experiment.

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 = 8.5) with rather low organic matter content (9.7 g/kg), cation-exchange capacity (0.5 g/kg) and total N content (0.5 g/kg). At the start of the experiment, in November 2015, a soil leachate solution was added to ensure the presence of symbiotic N_2-fixing bacteria in the pot. Pots were watered three times a week to provide moisture conditions close to field capacity in the soil profiles; this corresponded to 0.1 L of water at the start of the experiment and 0.6 L at the end in order to account for increasing plant demand. In addition, all pots received three soil enrichments (after 1, 4 and 9 weeks) in phosphorus (P) and potassium (K) in increasing amount over time for a total of 10 g P/m^2 and 24 g K/m. Note that nitrogen was not supplied so that it remained the main limiting resource for plant growth. We randomly placed pots on wheeled carriages and avoided side effects by rearranging carriages every two weeks.

TABLE 1 Species list and average trait values (±*SD*) as grown in monoculture conditions

	Specific leaf area (m^2/kg)	Max photosynthetic capacity (μmol-CO_2 m^{-2} s^{-1})	Plant height (cm)	Specific root length (m/g)	Deep root (<20 cm) fraction	Specific N absorption rate (μg m^{-1} hr^{-1})	Root inter-branch distance (cm)	Root hair length (mm)
Bromus 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
Dactylis glomerata (g)	29.23 ± 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
Plantago 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
Sanguisorba 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
Lotus 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
Trifolium 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

Abbreviations: f, forb; g, grass; l, legume.

2.2 | Biomass measurements

Plants harvest took place 13 weeks after seedling transplantation after all species had shown first signs of flowering. We cut above-ground parts of plants at the base and separated the six plant individuals to measure above-ground 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 oven-dried at 60°C for 48 hr and weighed.

2.3 | Trait measurements

We measured three above-ground traits and five below-ground 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}, $\mu\text{mol}_{\text{CO2}}\ \text{m}^{-2}\ \text{s}^{-1}$) – 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 experiment harvest, we recorded the maximum height (cm) achieved by all plant individuals in all pots. Plant height is a good proxy for light depletion through the canopy (Violle *et al.* 2012). Specific leaf area (SLA, m^2/kg) was assessed at harvest based on two to four leaves (depending on the species) from each plant individual that we immediately scanned for leaf area measurement. Specific leaf area corresponds to the area of light capture per biomass invested in leaves and is related to the fundamental trade-off existing between species acquisition and conservation of resources (Garnier & Laurent, 1994).

Root functional traits were measured from monoculture pots only because of the 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 roots (<0.2 mm) using a digital image analysis system (WinRhizo, version 2009; Regent Instrument). Deep root fraction (DRF), which reflects the relative investment of species to take up nutrient from the deeper soil horizons, was estimated as the ratio of root biomass deeper than 20 cm to total root biomass. Root interbranch distance (RID, cm) is a measure of root cost-efficiency to explore large soil volume (rather than exploit soil volume intensively) and was quantified as the average distance between first-order roots. Specific root length (SRL, m/g) was estimated as the ratio of root length to root dry mass to represent the cost-efficiency of roots to explore and/or exploit soil volume. A second subsample of roots was 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 from the root tips, using IMAGEJ software. Root hair length is a proxy for the soil volume explored around the root. Finally, we used one replicate (pot) from the six species in monoculture to measure specific root nitrogen absorption rate (N_{abs}), which reflects the short-term maximum nitrogen uptake capacity per unit root length. We calculated N_{abs} as the total amount of ^{15}N taken up by plants after injection of different forms of ^{15}N in the soil, per length of fine root and per hour ($\mu\text{g}\ ^{15}\text{N}\ \text{m}^{-1}\ \text{hr}^{-1}$).

2.4 | Biodiversity effects

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

$$\Delta Y_j = N_j . \Delta \overline{\text{RY}} . \bar{M} + N_j . \text{COV}\left(\Delta \text{RY}_{i,j}, M_i\right), \tag{1}$$

we computed the two components of ΔY, the complementarity and selection effects, only for above-ground 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. $\Delta \text{RY}_{i,j}$ is the deviation from the expected relative yield of species i in pot j calculated as:

$$\Delta \text{RY}_{i,j} = \frac{Y_{i,j}}{M_i} - \frac{1}{N_j}, \tag{2}$$

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 ($N_j . \Delta \overline{\text{RY}} . \bar{M}$) 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, $N_j . \text{COV}(\Delta \text{RY}_{i,j}, M_i)$, has been termed the *selection effect*.

2.5 | 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 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 values measured in monoculture pots only to insure homogeneity between the different traits that were measured in all pots or in monoculture only (Table 1). Since plant height and SLA were quantified at the individual level, we further tested the role of intraspecific trait variability by computing $\text{FDis}_{\text{Height}}$ and FDis_{SLA} based on trait values measured on individuals from all pots. CWM was calculated for each trait by multiplying the mean species trait value measured in monoculture pots by the proportional abundance of each species in each community. Finally, we classified the six species into three functional groups (legumes, herbs and forbs).

2.6 | Data analyses

We investigated the effect of species richness, functional dissimilarity, CWM and species identity on above-ground and root biomass production, above-ground and below-ground biodiversity effects as well as above-ground complementarity and selection effects using linear 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 in a baseline model (M0). Next, we built 'functional group', 'functional dissimilarity', 'CWM' 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 added the presence of each functional group or species (coded as a binary variable) or FDis and CWM of each trait separately as an explanatory variable to M0. The resulting model ($M1_i$), which is the importance of a candidate species i, functional group *i* or functional trait *i* to explain 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 productivity if ΔAIC (AIC_{M0} – AIC_{M1i}) was >4 (Maire et al., 2018). Although a commonly adopted rule of thumb states that a model with ΔAIC < 2 is likely to be the best model (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 the interpretation of the regression coefficients (Schielzeth, 2010). Because in the six-species mixtures each species and functional group were systematically present, we ran the functional group and species identity models without the six-species mixture pots. The sample size was therefore 128 for the functional trait models and 110 for the functional group and species identity models. We further computed the posterior model probabilities to report the probability that each model $M1_i$ is better than M0 using the *bicreg* function of the BMA package (Raftery, Hoeting, Volinsky, Painter, & Yeung, 2018). Posterior model probabilities were highly consistent with the ΔAIC analysis. Consequently, we presented ΔAIC in the main manuscript and posterior model probabilities in Table S1.

In addition, we tested for the influence of intraspecific competition, that is. species-specific density–productivity relationships, on biomass production by computing for each species 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 sown at half-density to the biomass of the 18 individuals grown in monocultures sown at full 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 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 monoculture with half-density and monoculture and mixtures of two, three and six species 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 above-ground biomass. Confidence intervals (α = 0.05) were computed to test whether individual plant biomass in full-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.r-project.org).

3 | RESULTS

3.1 | Effects of species richness on plant above-ground and below-ground biomass production

Among all mixtures, above-ground productivity was the main fraction of plant biomass production (Figure 1a,b), accounting for *c*. 70% of the biomass produced per pot. Above-ground biomass significantly increased with species richness (p < .001, r^2 = .08) while root biomass did not (p = .17, r^2 = .01; Table S2). Most importantly, both mean above-ground and below-ground biodiversity effects (ΔY) were positive at all species richness levels (Figure 1b). However, they did not increase with species richness (p = .09, r^2 = .02; p = .70, r^2 = .01 for above-ground and below-ground net effects, respectively; Table S2).

The additive partitioning of above-ground biodiversity effect (ΔY) revealed that among all mixtures, complementarity effect was the main fraction of ΔY (Figure 1c), accounting for *c*. 83% of above-ground ΔY. Complementarity effect did not increase with species richness (p = .34, r^2 = .01; Table S2) while the selection effect did (p = .02, r^2 = .04; Table S2).

Removing the six-species mixtures from the analyses did not change the effects of species richness on above-ground biomass production, above-ground and below-ground 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).

3.2 | Stronger effects of CWMs compared to functional dissimilarity and functional group diversity

ΔAIC values revealed that the main facet of functional diversity affecting biomass 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 production – except the selection effect (Table 2). Productivity, biodiversity effects and complementarity effect consistently decreased with CWM_{SLA} and CWM_{Amax} (Table 2; Figures S1–S3). In addition, above-ground productivity, root productivity and below-ground net effect increased with CWM_{Height} (Table 2; Figures S1 and S2). Above-ground net effect, below-ground net effect and complementarity effect also increased with CWM_{Nabs} and CWM_{DRF} and decreased with CWM_{RHL} (Table 2; Figures S2 and

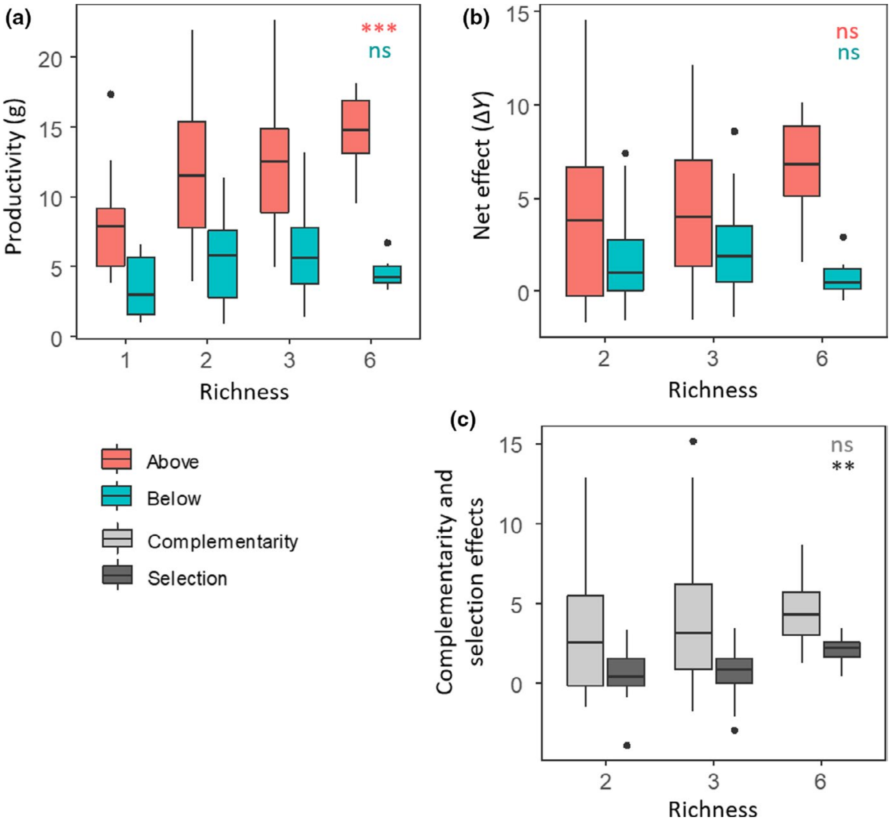

FIGURE 1 Effect of species richness on mean (a) above-ground and root productivity and (b) above-ground and below-ground biodiversity effects and (c) above-ground complementarity and selection effects. Differences across the richness gradients are tested using linear models. $^{***}p < .001$; $^{**}p < .01$; $^{*}<0.05$; ns: non-significant. Barplots represent the 1st, 2nd and 3rd quartiles

S3). By contrast, plant functional group identity poorly affected plant productivity and biodiversity effects beyond the overall effect of species richness (Table 2). The only exception was the presence of leguminous species that exerted a negative effect on root productivity in plant mixtures ($p < .001$). The ΔAIC analysis also revealed that functional dissimilarity slightly affected plant productivity and biodiversity effects (Table 2). After controlling for species richness effect, root productivity significantly increased with $\mathrm{FDis}_{\mathrm{Height}}$, $\mathrm{FDis}_{\mathrm{SRL}}$ and $\mathrm{FDis}_{\mathrm{Nabs}}$ (Table 2; Figure S4). Finally, above-ground net effect, below-ground net effect and complementarity effect significantly decreased with $\mathrm{FDi}_{\mathrm{RID}}$ (Table 2; Figures S5 and S6).

3.3 | Key species associated to changes in productivity

The presence of *P. lanceolata* in the mixture was the principal driver of change in productivity (for above-ground and root productivity: ΔAIC = 20.307, $r^2 = .225$ and ΔAIC = 69.211, $r^2 = .471$, respectively), net effects (for above-ground and below-ground net effects: ΔAIC = 26.224, $r^2 = .229$ and ΔAIC = 45.967, $r^2 = .366$, respectively) and complementarity effect (ΔAIC = 26.578, $r^2 = .230$; Table 2). All these components of biomass production were significantly higher when *P. lanceolata* was in the plant mixtures (Figure 2). The presence of *S. minor* and *T. repens* in plant mixtures also markedly affected biomass production. Above-ground and root productivity, net effects and complementarity effects were lower in presence of *S. minor* while the selection effect was higher. Above-ground productivity was higher in the presence of *T. repens* while root productivity and selection effects were lower (Figure 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).

3.4 | Species-specific effect and intraspecific competition

Species' logarithmic response ratio calculated based on above-ground biomass production was positive for all species (Figure 3), meaning that biomass production was in average higher in half-density plots for all species. However, we found significant differences between species (ANOVA, $F = 41.3$, $p < .001$), mean logarithmic response ratio being the highest for *P. lanceolata* (1.36 ± 0.45) and the lowest for *S. minor* (0.41 ± 0.69; Figure 3). In other words, the biomass of *P. lanceolata* individual plants was four times lower in the full-density monoculture than in the half-density monoculture. In addition, we found that the biomass of individual plants of *P. lanceolata* in the three and six-species mixtures did not significantly differ from their biomass in the half-density monoculture (Figure 4). Similarly, the biomass of individual plants of *T. repens* in the six-species mixture was equivalent to their biomass in the half-density monoculture, whereas it was otherwise lower (Figure 4). By contrast, the biomass of individual 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 monoculture and half-density monoculture (Figure 4).

TABLE 2 Effects of functional group, functional dissimilarity, community-weighted mean of trait (CWM) and species identity on biomass production (productivity), biodiversity effects (net effect), complementarity effect and selection effect

		Above ground productivity			Below-ground productivity			Above-ground net effect			Below-ground 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
Functional group	Legume	1.82*	2.07	.10	**−2.27*****	**17.27**	**.19**	0.24	−1.92	.01	−0.30	−1.58	.00	0.87	−0.88	.00	−0.63*	3.42	.03
	Herbs	−1.43	0.51	.09	1.25*	3.48	.09	−1.42	0.85	.02	−0.52	−0.73	.01	−0.99	−0.55	.00	−0.43	0.46	.01
	Forbs	−0.53	−1.67	.07	1.21*	3.03	.09	0.85	−0.99	.00	0.94*	2.24	.04	0.73	−1.23	.01	0.13	−1.79	.02
Functional dissimilarity	Height	0.37	−1.27	.08	**0.87*****	**9.57**	**.09**	−0.21	−1.66	.01	0.27	−0.07	.00	−0.30	−1.29	.00	0.09	−1.49	.04
	SLA	0.47	−0.80	.08	0.46	1.22	.02	0.33	−1.20	.02	0.44*	3.12	.03	0.30	−1.29	.00	0.03	−1.94	.04
	Amax	0.20	−1.80	.07	0.48	1.35	.03	−0.44	−0.53	.02	0.10	−1.76	.02	−0.38	−0.84	.00	−0.06	−1.73	.04
	SRL	0.20	−1.77	.07	**0.71****	**6.18**	**.06**	−0.43	−0.62	.02	0.18	−1.21	.00	−0.31	−1.22	.00	−0.12	−1.04	.04
	Nabs	0.60	−0.17	.08	−0.090	−1.89	.00	0.06	−1.98	.01	−0.10	−1.74	.02	0.15	−1.82	.01	−0.10	−1.37	.04
	RHL	0.06	−2.52	.07	0.350*	3.68	.04	−0.57	0.40	.03	0.03	−1.97	.02	−0.43	−0.55	.00	−0.14	−0.67	.05
	DRF	0.54	−0.52	.08	**0.79****	**7.04**	**.07**	−0.26	−1.50	.01	0.14	−1.54	.01	−0.07	−1.96	.01	−0.19	0.51	.06
	RID	−0.918*	2.23	.10	−0.214	−1.38	.00	**−1.29*****	**11.17**	**.12**	**−0.60****	**7.49**	**.07**	**−1.17*****	**9.43**	**.09**	−0.12	−0.99	.04
CWM	Height	**1.20****	**7.47**	**.14**	**1.46*****	**42.16**	**.29**	0.63	1.06	.04	**0.67*****	**10.35**	**.90**	0.61	1.08	.02	0.02	−1.98	.03
	SLA	**−1.39*****	**10.74**	**.16**	**−1.82*****	**73.88**	**.45**	**−1.72*****	**23.53**	**.21**	**−1.21*****	**43.58**	**.33**	**−1.62*****	**21.73**	**.19**	−0.11	−1.19	.04
	Amax	**−1.02***	**4.78**	**.12**	**−1.94*****	**90.60**	**.52**	**−1.01****	**6.13**	**.08**	**−1.09*****	**33.99**	**.27**	**−1.01****	**6.64**	**.07**	−0.01	−1.99	.03
	SRL	0.47	−0.60	.08	**0.79*****	**9.40**	**.09**	−1.19	−1.73	.01	0.19	−1.11	.00	−0.13	−1.87	.00	−0.06	−1.75	.04
	Nabs	0.31	−1.39	.07	**1.28*****	**29.91**	**.22**	**1.17****	**8.80**	**.10**	**1.06*****	**31.22**	**.25**	**1.19*****	**10.11**	**.10**	−0.03	−1.95	.04
	RHL	−0.88*	3.04	.11	−0.26	−0.76	.01	**−1.20*****	**9.53**	**.11**	**−0.57****	**6.72**	**.06**	**−1.05****	**7.38**	**.07**	−0.15	−0.49	.05
	DRF	0.92*	3.52	.11	0.03	−1.99	.01	**1.18****	**9.12**	**.10**	**0.50***	**4.48**	**.04**	**1.03****	**7.02**	**.07**	0.14	−0.51	.05
	RID	−0.41	0.92	.08	0.42	1.17	.02	−0.66	1.45	.04	−0.26	−0.31	.00	−0.47	−0.17	.01	−0.19	0.76	.06
Species identity	*Bromus erectus*	**−2.31****	**5.64**	**.13**	−0.186	−1.86	.05	−1.07	−0.02	.01	**−1.10****	**5.26**	**.06**	−1.11	0.26	.01	0.04	−1.97	.02
	Dactylis glomerata	0.46	−1.71	.07	**1.53****	**7.44**	**.12**	−0.59	−1.41	.01	0.27	−1.57	.00	−0.21	−1.92	.01	−0.38	0.33	.00
	Plantago lanceolata	**3.89*****	**20.31**	**.23**	**3.76*****	**69.21**	**.47**	**3.79*****	**26.22**	**.23**	**2.57*****	**45.97**	**.37**	**3.71*****	**26.58**	**.23**	0.08	−1.89	.17
	Sanguisorba minor	**−3.74*****	**19.03**	**.22**	**−1.78*****	**11.04**	**.15**	**−1.95***	**4.77**	**.05**	**−1.05***	**4.61**	**.06**	**−2.60*****	**11.00**	**.11**	**0.64****	**4.94**	**.05**
	Lotus corniculatus	−2.031*	3.77	.11	**−1.58****	**7.98**	**.12**	−1.19	0.41	.01	−0.35	−1.28	.00	−1.49*	2.02	.03	0.30	−0.55	.00
	Trifolium repens	**3.31*****	**19.93**	**.22**	**−1.66*****	**9.27**	**.13**	0.98	−0.34	.00	−0.35	−1.31	.00	1.67*	3.16	.00	**−0.69****	**5.99**	**.06**

Note: 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 and grey shades). For the functional group and species identity models, estimates represent the effect of the presence of each functional group and species in the mixture, respectively, while for the functional dissimilarity and CWM models, estimates represent the slope of the effect of increasing functional dissimilarity (CWM) in the mixture.
*p-value < .05; **p-value < .01; ***p-value < .001.

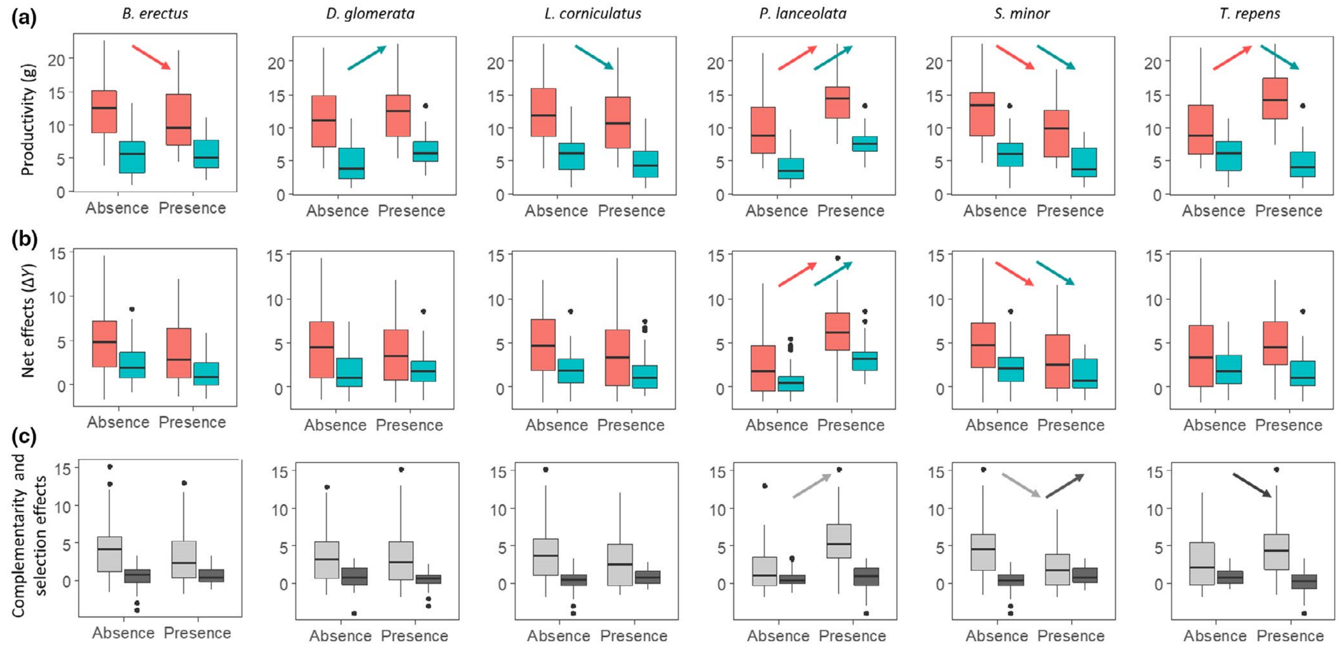

FIGURE 2 Species-specific effect on above-ground (red) and below-ground (blue) productivity (a), net effects (b) and complementarity (light grey) and selection (dark grey) effects on above-ground productivity (c). Arrows represent significant effect of the presence of a species and its direction (*p* < .05). Barplots represent the 1st, 2nd and 3rd quartiles

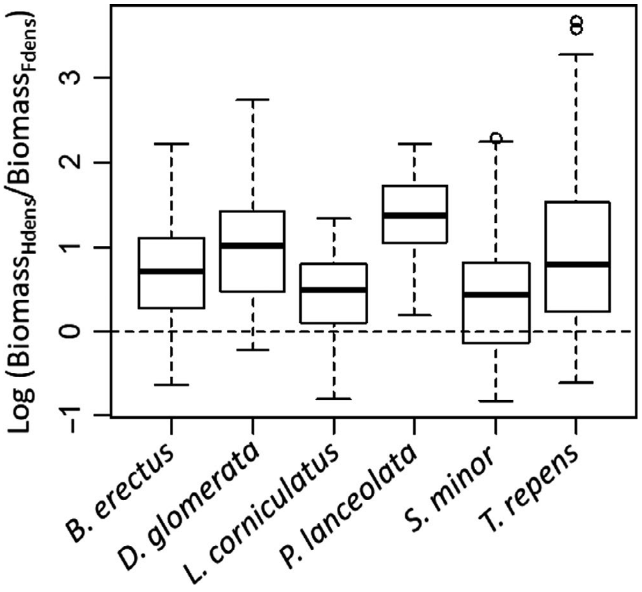

FIGURE 3 Variation of the intraspecific competition log-response ratio between species. We computed log-response ratio between individual plant above-ground biomass in monoculture sown at half-density (Biomass$_{\mathrm{Hdens}}$) and individual plant above-ground biomass in monoculture sown at full-density (Biomass$_{\mathrm{Fdens}}$). Positive log-response ratio corresponded to higher above-ground biomass for the individual of the monoculture sown at half-density. Barplots represent the 1st, 2nd and 3rd quartiles

4 | 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 observed biodiversity effects.

The significantly higher above-ground and root biomass production observed here in plant mixtures compared to monoculture is a common pattern in biodiversity–ecosystem functioning studies (Cardinale et al., 2012; Lefcheck et al., 2015; Tilman et al., 2001). We also reported a strong dominance of the complementarity effect over the selection effect, which 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 the probability of selecting a highly productive species that over-produce in mixture increases with the size of the community (Huston, 1997). However, species richness per se did not affect above-ground and below-ground biodiversity effects or complementarity effect (Figure 1). This reveals the limited value of species number per se to predict biodiversity–ecosystem functioning relationships and emphasizes the importance of considering other biodiversity facets.

Since niche complementarity theoretically relies on functional trait differences (Violle & Jiang, 2009), we expected that biodiversity and complementarity effects would increase with functional dissimilarity (Cadotte, 2017). Surprisingly, we found weak effects of functional dissimilarity, except for a decrease of the biodiversity and complementarity effects with the 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 combinations of traits may better describe species differentiation along the multiple

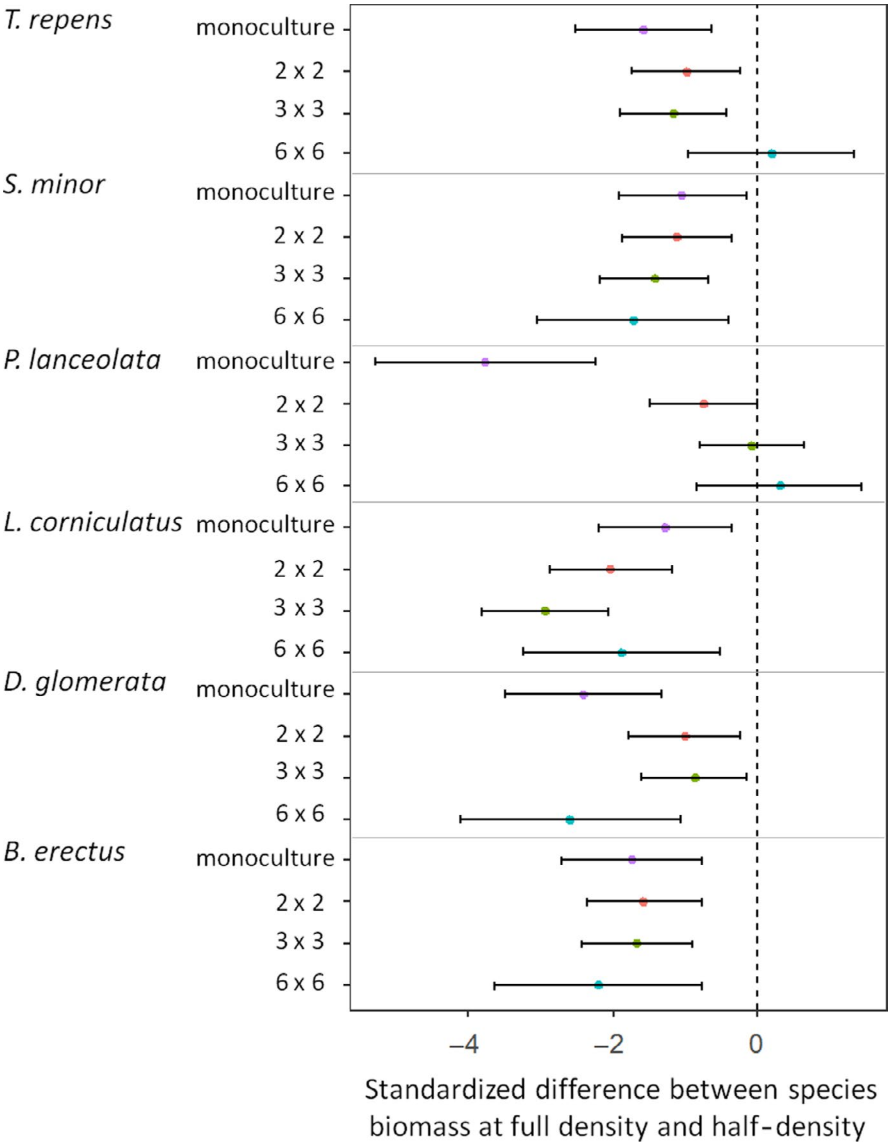

FIGURE 4 Standardized difference between individual plant biomass of species grown in monoculture with half-density (three individuals) and monoculture and mixtures of two, three and six species grown at full density (six individuals). Whiskers are confidence intervals (α = 0.05): if confidence interval 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 monoculture at half-density. A negative value means that individual plant biomass in full-density pot is lower than in half-density pot, suggesting the influence of negative density-dependence mechanisms

ecological dimensions of species niche (Kraft et al., 2015), using a multi-dimensional functional dispersion index did not improve the observed relationship between functional dissimilarity and biodiversity effects (see Table S3). Another reason may be that we computed functional dissimilarity in plant mixtures based on mean species trait values in monoculture. Doing so, we did not account for intraspecific trait variations, which can vary in conditions of competition and affect resource uptake (e.g., below-ground, Mommer, van Ruijven, Jansen, van de Steeg, & de Kroon, 2012; Schenk, 2006). However, above-ground, accounting for intraspecific trait variations in plant height and specific leaf area, both traits being measured at the individual level, did not change the results (see Table S3). Overall, given our targeted choice of traits capturing multiple facets of light and nutrient acquisition above- and below-ground (Freschet et al., 2018), the weak relationship between functional dissimilarity and the complementarity effect confirms that the complementarity effect does not only reflect resources partitioning but a larger set of biotic interactions in species mixtures (Carroll, Cardinale, & Nisbet, 2011; Barry et al., 2019; Loreau & Hector, 2001; Niklaus, Baruffol, He, Ma, & Schmid, 2017).

By contrast, we reported strong influence of five out of eight community-weighed trait means on the complementarity effect – and by extent on biodiversity effects. Species ability to take up nitrogen resources was a main driver of biomass productivity, as suggested by the positive relationships between the community-weighted mean of both nitrogen absorption rate and deep root fraction and biodiversity effects. Furthermore, biodiversity and complementary effects increased with decreasing the community-weighted mean of specific leaf area and maximum photosynthetic rate, implying that biomass production was maximum when plant 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, it may reflect the fact that low nutrient availability in this experiment has favoured plants with the more conservative resource strategies (Carmona, Bello, Azcarate, Mason, & Peco, 2019; Wright et al., 2004). More globally, the importance of functional trait values gives evidence that in this experiment, 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 and the selection effect while this is a main expectation under the mass-ratio hypothesis (Cadotte, 2017). This shows that the effect of the dominant species on ecosystem functioning differs from the selection effect sensu Loreau and Hector (2001) and calls for a more mechanistic approach to understand the relationships between biodiversity and ecosystem functioning.

We found a disproportionate contribution of one species, *P. lanceolata*, on the production of biomass and biodiversity effects in plant mixtures. Among the six species of this experiment, *P. lanceolata* displayed the lowest biomass in monoculture but the highest biomass in the 6 × 6-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 most productive species in monoculture produce even more biomass in mixture (Loreau & 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 intraspecific competition, which was relieved in half-density monocultures and even more in species mixtures (Figure 3). Consequently, the much lower level of interspecific competition as compared to intraspecific competition for this particular species, appeared as the most critical 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 (Adler et al., 2018), we expect that such a mechanism may be widespread in biodiversity – 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 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 competition on species production was inversely related to the effect of interspecific competition (Figure 4), suggesting that a priori knowledge of species-specific density dependence production may be particularly useful to explain (and potentially predict) biomass gains in mixtures. An increasing number of biodiversity-productivity studies already accounts for the effect of negative density dependence mechanisms such as density dependence plant disease (Mommer et al., 2018; Schnitzer et al., 2011). 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 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 species. However, computing species functional distinctiveness (sensu Violle et al., 2017) based on the traits used in this study (Table S4) revealed that *P. lanceolata* is not particularly different from the other species. This suggests that other aspects of plant eco-physiology (e.g., three-dimensional architecture, Schenk, 2006) may drive the response of *P. lanceolata* to intraspecific and interspecific competition.

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

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 intraspecific competition plays in shaping biodiversity-ecosystem functioning relationships, although the traits underlying species intraspecific competitive ability remain unknown. The fact that intraspecific competition also plays a dominant role for species coexistence (Adler et al., 2018) claims for a more integrative approach in community and ecosystem ecology to better understand biodiversity-ecosystem functioning relationships (Turnbull et al., 2016, 2013). Accounting for nonlinear species-specific density-productivity relationships will be critical to predict the effect of species diversity on ecosystem functioning (Baert, Jaspers, Janssen, De Laender, & Aerts, 2017).

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AUTHORS' 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.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.1jwstqjqh (Mahaut, Fort, Violle, & Freschet, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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