Title

Context-dependency in biodiversity-multifunctionality relationships is driven by nitrogen availability and plant functional composition

Summary

The ability of an ecosystem to deliver multiple functions at high levels (multifunctionality) typically increases with biodiversity but there is substantial variation in the strength and direction of biodiversity effects, suggesting context-dependency. However, the drivers of this context dependency have not been identified and understood in comparative meta-analyses or experimental studies. To determine how different factors modulate the effect of diversity on multifunctionality, we conducted a large grassland experiment with 216 communities, crossing a manipulation of plant species richness (1-20 species) with manipulations of resource availability (nitrogen enrichment), plant functional composition (gradient in mean specific leaf area [SLA] to manipulate abundances of fast vs. slow species), plant functional diversity (variance in SLA) and enemy abundance (fungal pathogen removal). We measured ten functions, above and belowground, related to productivity, nutrient cycling and energy transfer between trophic levels, and calculated multifunctionality. Plant species richness and functional diversity both increased multifunctionality, but their effects were context dependent. Species richness increased multifunctionality, but only when communities were assembled with fast growing (high SLA) species. This was because slow species were more redundant in their functional effects, whereas fast species tended to promote different functions. Functional diversity also increased multifunctionality but this effect was dampened by nitrogen enrichment, however, unfertilised, functionally diverse communities still delivered more functions than low diversity, fertilised communities. Our study suggests that a shift towards exploitative communities will not only

alter ecosystem functioning but also the strength of biodiversity-functioning relationships, which highlights the potentially complex effects of global change on multifunctionality.

Introduction

The ability of an ecosystem to deliver many functions at high levels simultaneously (multifunctionality) generally increases with diversity [1–6] . Although positive biodiversity-ecosystem multifunctionality relationships are common, studies have found substantial variation in the direction and strength of this relationship [6–8]. Only a few studies have addressed the drivers of context-dependency in biodiversity-multifunctionality relationships and these have been either observational [6,9] or have focussed on one of the multiple potential drivers [10] (but see refs [11,12]). It is therefore not clear how important different environmental or biotic drivers (resource levels, enemy pressure or community composition) are in determining context-dependency in biodiversity-multifunctionality relationships. Experimental approaches are needed to rigorously test this but very few experiments cross diversity gradients with manipulations of resources, enemies or composition.

The main drivers of context dependency are likely to be those that alter the mechanisms by which biodiversity affects function. Two of the main mechanisms behind the positive effects of species diversity on ecosystem functioning are: i) complementary resource use amongst species, and ii) increased enemy attack in species-poor communities [13–15]. If species vary in their resource uptake strategies, then diverse communities should use resources more efficiently [16] while increasing resource levels should remove opportunities for nutrient use complementarity between species and therefore equalise functioning between low and high diversity [17]. We can therefore expect a decrease in the effect of diversity on ecosystem functioning with nitrogen (N) enrichment. However, some experimental studies have shown neutral [18,19] or even positive effects of increased resource levels on the diversity-functioning relationship [20–22]. These results suggest that niche complementarity for nitrogen does not always underlie diversity-functioning relationships. Natural enemy attack is also an important mechanism driving effects of diversity on function: for example, soil pathogens can enhance biodiversity-productivity relationships by reducing biomass production in monocultures [23,24], while

53 aboveground insects and pathogens can dampen diversity-functioning relationships by removing
54 more biomass at high diversity [25]. There is therefore little consensus on how plant enemies, or
55 resource availability, affect diversity-functioning relationships.

56 In addition to the environment, the composition of the species pool (from which local plant
57 communities are drawn) could modify biodiversity-multifunctionality relationships. A key element of
58 composition could be the resource use strategies of the species as those with different resource use
59 strategies might vary in their degree of resource use complementarity. The leaf economics spectrum
60 [26,27] distinguishes slow growing, conservative species from fast growing, acquisitive ones and is
61 indicated by several traits, such as specific leaf area (SLA) and leaf nitrogen content. Slow growing
62 species, with low SLA, are more competitive in the low nutrient environments they tend to dominate
63 [28,29] and might therefore differ more in their competitive abilities for different nutrients, leading to
64 nutrient use complementarity between slow growing species. In contrast, faster growing species, with
65 high SLA, are abundant in high resource environments, where asymmetric light competition is
66 prevalent [30,31]. Nutrient use complementarity between fast growing species might therefore be low.
67 However, fast growing species are also likely to be more sensitive to both resource addition and
68 enemies, due to a growth defence trade-off [32], and enemies might therefore drive stronger diversity-
69 functioning relationships in fast-dominated communities. Such effects of the functional composition
70 of the species pool on diversity-function relationships would lead to different effects of diversity
71 depending on which species are combined and therefore to interactions between changes in
72 composition and diversity. At the community level, functional composition and functional diversity
73 are key drivers of multifunctionality on their own [6,9,33]. A high functional diversity can increase
74 multifunctionality if species with different resource use strategies (fast vs slow) have complementary
75 interactions [34,35]. However, functional diversity can also reduce multifunctionality in harsh conditions
76 where environmental filtering is strong and functionally distinct species are poorly adapted to the
77 local conditions [36]. Community wide changes in functional composition and diversity both have large
78 effects on multifunctionality [9,17] and on individual functions [36–38]. Global changes can simultaneously

affect the diversity, and composition of functional traits linked to resource-use strategy, making it hard to separate effects of functional diversity and composition in observational studies. Experimental approaches are necessary to disentangle the relative important of composition and diversity and to test for interactions between them but have not yet been attempted.

To understand how composition, enemy presence, and resource availability modulate the effect of diversity on multifunctionality, we manipulated plant species richness, N enrichment, fungal pathogen removal (fungicide spraying), plant functional composition (as a gradient of abundance weighted specific leaf area [SLA]) and plant functional diversity in a full-factorial experiment with 216 plots. We therefore manipulated two diversity dimensions, species richness and functional diversity (mean pairwise distance of SLA), to be as orthogonal as possible to each other (see methods). We measured ten functions on each plot, related to biotic interactions and biogeochemical cycling: above and belowground plant biomass, insect herbivore damage (hereafter herbivory) and foliar fungal pathogen infection, plant nitrogen and phosphorus uptake (quantified as ratios between available nitrogen and phosphorus content in the soil and nitrogen and phosphorus content in aboveground plant biomass), two enzymatic activities related to carbon (β-glucosidase) and phosphorus (phosphatase) cycling, soil respiration and soil carbon storage. We used a novel approach to analysing effects on equal weight ecosystem function multifunctionality [39], in which we calculated multifunctionality at several thresholds between 50 and 80%. We then combined all these multifunctionality measures in a single model (for details see methods), which allowed us to estimate the average effect of our treatments on multifunctionality, across thresholds. As any particular threshold is arbitrary, this allowed us to robustly quantify overall effects on multifunctionality. We hypothesised that: (1) species richness and functional diversity will both increase multifunctionality, (2) the diversity effect will depend on the functional traits of the species which are combined (i.e. the functional composition of the species pool), and (3) increased resource levels will reduce and fungal presence will increase the diversity effect on multifunctionality.

Results

Richness-multifunctionality relationships depend on functional composition

Diversity effects on multifunctionality were highly context-dependent in our experiment. The effect of sown species richness on multifunctionality was modified by plant functional composition (community weighted mean SLA). Species richness (SR) decreased multifunctionality slightly in communities with low mean SLA but increased multifunctionality at high mean SLA (Figure 1a and b and Table S1). Species richness therefore had a positive effect on multifunctionality in communities assembled from fast-growing, acquisitive species, but a neutral to negative effect when the species pool contained only slow-growing, conservative species. We also analysed each function individually and found that the SLA x SR interaction was significant for only one function, soil phosphatase activity, and the interaction was negative (Figure 2), meaning that it did not drive the overall SLA x SR effect on multifunctionality. SLA as a main effect had contrasting effects on individual functions, with a positive effect on functions measured aboveground (pathogen presence, herbivory), and a negative effect belowground (belowground biomass, phosphatase activity, soil respiration).

High resource levels dampen effects of functional diversity on multifunctionality

Sown functional diversity, calculated as the mean pairwise distance between species in their SLA, increased multifunctionality in control plots (Figure 1a and c). However, nitrogen enrichment dampened this positive effect of functional diversity by increasing multifunctionality most in the low

127 functional diversity plots. Nitrogen enrichment increased several individual functions (above and
128 belowground biomass, soil β-glucosidase activity, plant P uptake) but the interaction with functional
129 diversity was significant only for soil respiration (Figure 2). Interestingly, N enrichment also interacted
130 with species richness to affect belowground biomass and C storage (Figure 2), but this interaction
131 further depended on SLA and foliar pathogen removal (fungicide treatment) and did not affect
132 multifunctionality.

133 Foliar pathogen removal reduced overall fungal damage to leaves and herbivory, in species rich
134 communities, and increased total soil respiration in high SLA communities and belowground biomass
135 in species rich fertilised communities. Foliar pathogen removal was also involved in some other
136 complex interactions for C storage and phosphatase. These contrasting effects translated into a non-
137 significant effect of pathogen removal on multifunctionality and no interactions between pathogens
138 and diversity (Figure 2).

139

140 Effect of change in species abundances on functional diversity

141

142 The sown functional diversity of the plots increased multifunctionality, see above. However, species
143 have shifted their relative abundances since the start of the experiment and to test the effect of these
144 abundance changes on functional diversity, we calculated MPDw, weighted by realised species
145 abundances. As weighted and unweighted MPD were correlated, because both were 0 in
146 monocultures (see Figure S1), we fitted a second model in which we replaced the unweighted, sown
147 MPD by MPDw. Abundance weighted functional diversity had an opposite effect and decreased
148 multifunctionality (Figure 3). These contradictory effects indicate that the communities with the
149 highest multifunctionality were those which had been sown with functionally distinct species (high
150 unweighted MPD), but in which functional redundancy increased because they became dominated by
151 functionally similar species (lower abundance weighted MPDw). Such high multifunctionality

communities are therefore dominated by functionally similar species but contain functionally distinct rare species.

Effects of individual species on functions

Our results show that combining multiple fast-growing species in a community leads to high multifunctionality, whereas combining slow growing species does not increase multifunctionality. There are two main factors that could cause this: 1) fast species tend to drive different functions, whereas slow species all drive the same function: if slow species are more redundant in their functional effects, then adding slow species to a community (increasing diversity) would not add functions. 2) Slow species tend to trade-off in their functional effects, while fast species have more synergies (positive effects on multiple functions): trade-offs mean that some species increase a given function, while others tend to reduce the same function, and this would mean that increasing diversity would not enhance multifunctionality because adding species to a community would tend to reduce as many functions as it enhanced.

To test these ideas, we calculated the effect of each of our 20 species on each function, by fitting regression models for each function with the presence or abundance of each species as predictors (similar to refs [1,3]). We extracted the significant positive and negative effects of each species and calculated the dissimilarity in functional effects between sets of four species (see methods for more details). This showed that fast species were more dissimilar in the functions they drove (Table S2, Table S3 and Table S4), as an increase in mean SLA between species increased the dissimilarity in the set of functions they affected. The results were similar for presence-based or abundance weighted effects, and for both positive and negative effects, showing that slow species tend to all affect similar functions, while fast species have different effects on different functions.

In order to test whether there are also more trade-offs in functional effects between slow species, we calculated the proportion of functional effects that were trade-offs, for each pair of species (see methods). The effects were non-significant, both when analysed based on species presence or on species abundance (Table S2). It therefore seems that trade-offs in functional effects are not more common for low SLA species and that instead low SLA species are more redundant in their functional effects because they tend to drive similar functions.

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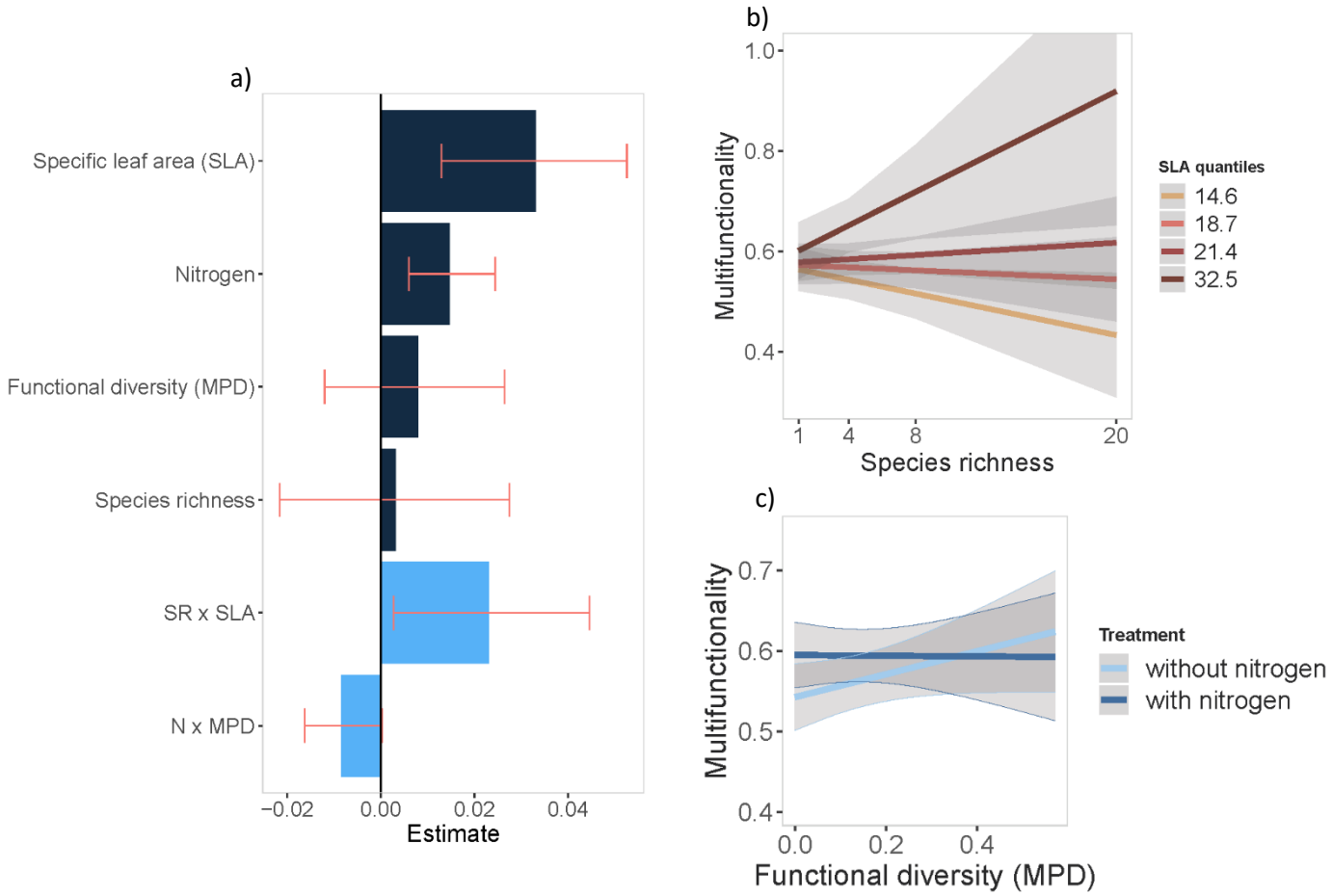

Figure 1: Context-dependent diversity-multifunctionality relationships. Standardised effect (+/- confidence intervals) of each significant variable and their significant interaction on multifunctionality across seven thresholds: a) scaled centred estimates, b) interaction between sown species richness and specific leaf area (SLA, m^2 kg^{-1}), and c) interaction between functional diversity (MPD, mean pairwise distance) and nitrogen enrichment. N = 216 plots. Details of the model output can be found in the Table S1.

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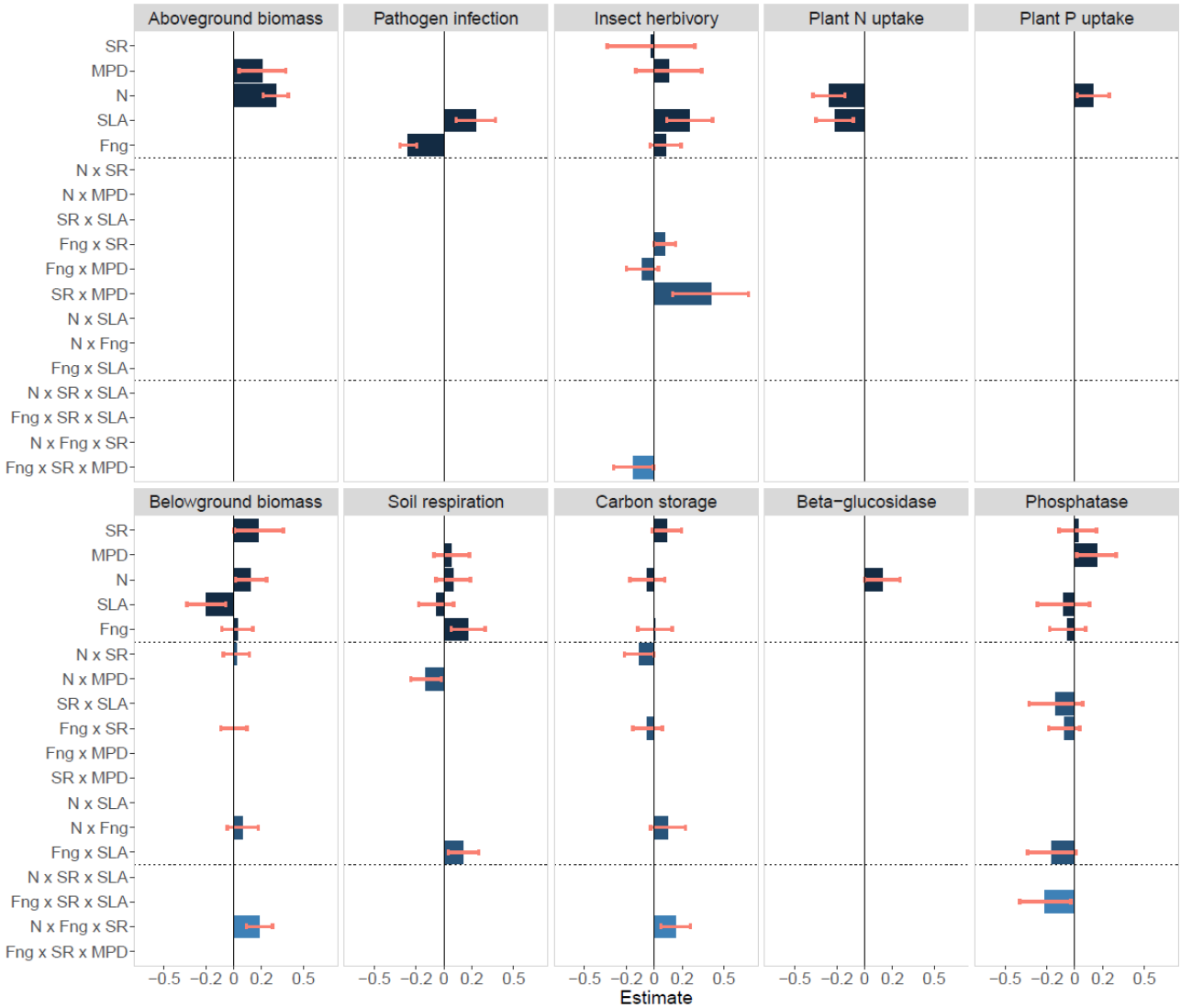

Figure 2: Drivers of individual functions. Mean standardised effect (+/- confidence intervals) of each significant variable and their interaction on functions after model simplification. SR: sown plant species richness, MPD: mean pairwise distance in SLA equally weighted, N: nitrogen enrichment, SLA: abundance weighted community specific leaf area, Fng: fungicide treatment. Each function was measured on 216 plots. See Table S5 and Figure S2 for details.

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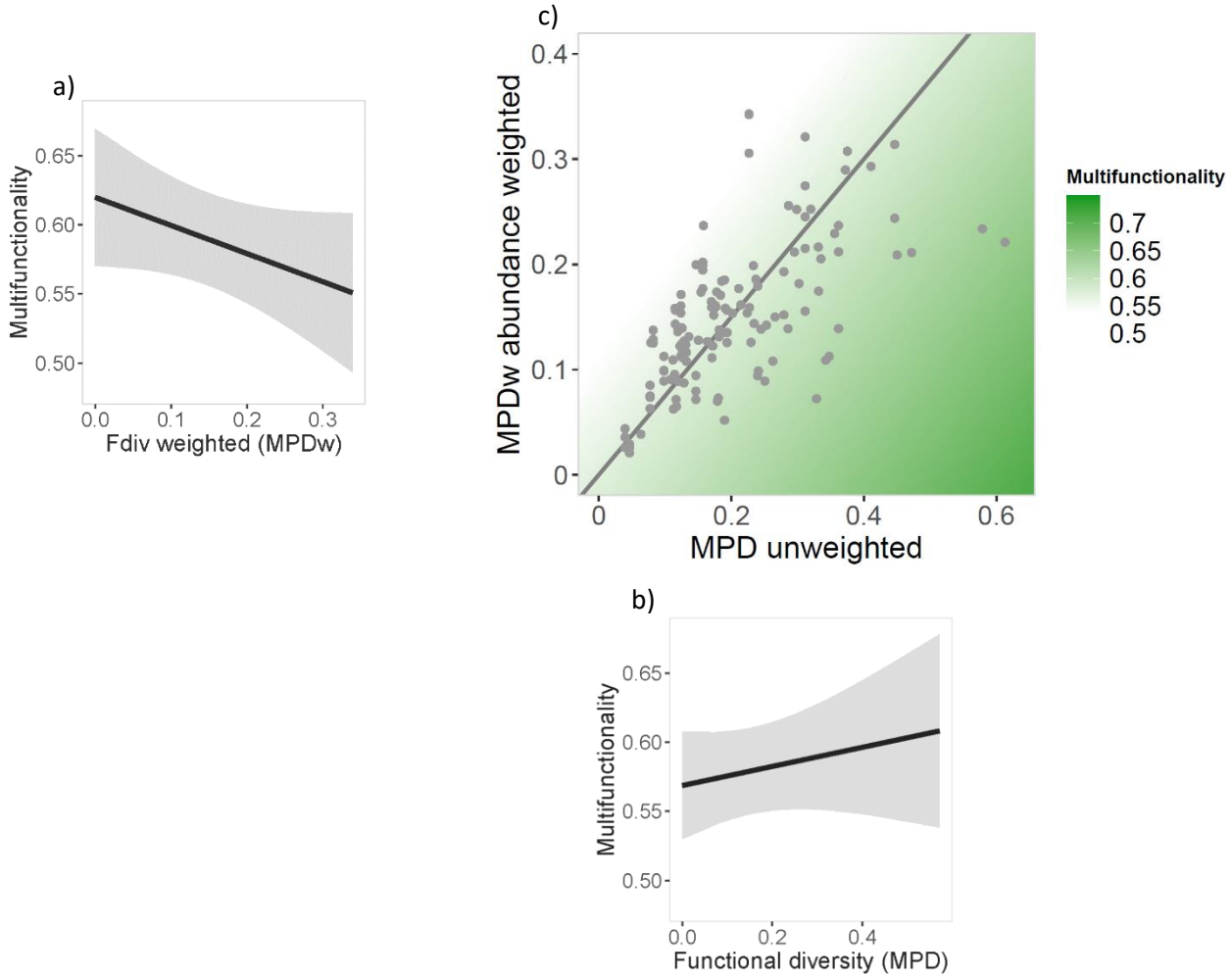

Figure 3: Effect of sown vs. realised functional diversity on multifunctionality. Effect on multifunctionality of a) unweighted, sown, functional diversity (MPD) and b) abundance weighted, realised, functional diversity (MPDw). Effect (+/- confidence intervals) from individual models. c) MPDw plotted against MPD. The green lines represent the model predicted multifunctionality values at a 0.65 threshold. The high multifunctionality plots are those with both a relatively high MPD and a relatively low MPDw (bottom right corner). Monocultures were included but are not shown in c) as they are all coded as 0 MPD and MPDw. See Table S6 for details on the model output.

190 # Discussion

191

192 Our results show that there is substantial context dependency in biodiversity-multifunctionality
193 relationships. This context-dependency is mostly explained by the functional composition of the
194 species pool, and also to some extent by resource availability. Previous diversity experiments have
195 generally isolated diversity effects from compositional variation, and when experimental [40,41] or
196 observational (e.g. [9]) studies have considered compositional and diversity effects, they have compared
197 their relative importance but have never tested whether they might interact. In general, biodiversity
198 experiments have focused on diversity as a driver of functioning (e.g. ref [42]), while many observational
199 studies have considered mean trait values and mass ratio effects (e.g. refs [43,44]). By experimentally
200 crossing functional composition and diversity treatments, we were able to show that composition and
201 diversity are not always independent drivers of multifunctionality, and that they can enhance each
202 other's effects. Our results also support recent observational evidence [36,41] that multiple biodiversity
203 dimensions (including species richness, functional diversity and functional redundancy) need to be
204 considered together. Taken together our findings emphasise that a better understanding of
205 multifunctionality requires approaches that can disentangle the influence of multiple, interacting
206 drivers.

207

208 ## Functional composition modulates richness effects on ecosystem functioning

209

210 Species richness increased multifunctionality, but only when plant communities were assembled with
211 fast growing species. Some studies have considered how the functional *diversity* of the species pool
212 impacts species richness-functioning relationships [17,45] but our results show that the functional
213 *composition* of the species pool may be a stronger driver. Our analysis of individual species effects on

214 functions showed that slow species were more redundant in their functional effects, this was because
215 some slow species drove multiple functions (*Achillea millefolium, Centaurea jacea, Festuca rubra* and
216 *Salvia pratensis*), while fast species affected just one function each. Therefore, combining multiple
217 fast species together increased multifunctionality because each species increased a different function.
218 However, slow species were also more variable in their functional effects with several having only
219 negative effects on functions, meaning that monocultures of slow species did not have high
220 multifunctionality, on average. This suggests that amongst slow species there might be a
221 "multifunctional selection effect" with high multifunctionality driven by the presence of particular
222 species that promote several functions, while amongst fast species there is "multifunctional
223 complementarity" with different species driving different functions. This idea is further supported by
224 the fact that a similar diversity x composition interaction was not present for individual functions.
225 Instead, species richness increased belowground biomass and carbon storage regardless of
226 community SLA, and increased phosphatase activity the most in plots dominated by slow growing
227 species. Diversity therefore did increase several individual functions within slow species communities,
228 presumably because the slow species were complementary in their effects on these functions.
229 However, this did not translate into higher multifunctionality when slow species were combined, as
230 the slow species were not complementary in their effects on multifunctionality. While species richness
231 and composition have usually been seen as alternative or opposing drivers of functioning (i.e. mass
232 ratio vs. diversity effects [46–49]), we show here that they are dependent and modify each other's effects.

233

234 Resource level modulates functional diversity effects on ecosystem functioning

235

236 In addition to sown species richness, sown functional diversity was an important driver of
237 multifunctionality but its positive effect was dampened by N enrichment. N enrichment increased
238 functioning in low diversity communities, but not in high diversity ones. However, high diversity,

239 unfertilised communities still delivered higher multifunctionality than low diversity, fertilised
240 communities (0.624 and 0.588 respectively), suggesting low input, high diversity grasslands could
241 deliver high functioning relative to intensive systems. Previous studies have found mixed effects of
242 increased resource supply on diversity-functioning relationships. One study in the Jena Experiment
243 showed that the strength of the diversity-productivity relationship increased under nutrient
244 enrichment [20]. However, the Jena Experiment added multiple nutrients, which increased total
245 resource levels, whereas we added nitrogen alone which may have led to an unbalanced nutrient
246 stoichiometry and therefore a reduction in complementarity [50]. Results from a meta-analysis showed
247 that the effect of diversity on productivity was independent of nutrient levels, although
248 complementarity was reduced in fertilised communities due to higher productivity in monocultures [21].
249 Consistent with this, our study also found that the effect of diversity on aboveground productivity was
250 independent of fertilisation (Figure 2), and that the interaction between N and either species richness
251 or functional diversity was inconsistent across individual functions. However, we do find a clear,
252 negative, effect of N enrichment on the diversity-multifunctionality relationship. This result is partially
253 supported by a study on soil multifunctionality [22], who showed that the positive diversity effect on
254 multifunctionality was weaker under N enrichment, but only at higher thresholds. Therefore, adding
255 N to functionally diverse communities would not further increase multifunctionality.

256 Foliar fungal pathogen removal had no significant effect on multifunctionality or on diversity-
257 multifunctionality relationships, although it did modulate the diversity effect on individual functions.
258 Previous studies have shown that specialist soil pathogens can drive diversity-productivity
259 relationships by reducing biomass particularly at low diversity [23,24]. In our experiment, foliar pathogen
260 impact was not reduced in (untreated) high diversity communities, perhaps due to a shift towards
261 generalist pathogens [51] or because increased spillovers of pathogens (between species) counteracted
262 resource concentration effects in diverse mixtures [52]. The absence of an effect of foliar fungal removal
263 on biodiversity-multifunctionality relationships suggests that resources are more important context

264 drivers than foliar enemies, but changes in other enemy groups or in foliar fungal species composition
265 still need to be investigated further.

266

267 Contrasting effects of weighted and unweighted functional diversity

268

269 Multifunctionality was maximised at high levels of sown functional diversity but was reduced by high
270 levels of abundance weighted functional diversity. These contrasting effects of functional diversity
271 depending on whether it was weighted by abundance or not, mean that multifunctionality was highest
272 when communities became dominated by functionally similar species but retained some distinct rare
273 species (relatively low abundance weighted functional diversity combined with high sown functional
274 diversity). The increase in multifunctionality with non-abundance weighted functional diversity
275 emphasises the importance of species identity effects in affecting multifunctionality [53,54]. These
276 findings are also in accordance with a body of literature on the importance of locally rare species for
277 the provision of multiple ecosystem functions [55–57]. The negative effects of abundance weighted
278 functional diversity mean that multifunctionality was maximised when the dominants in a community
279 were functionally similar, which suggests that, alongside the effects of rare species, mass ratio effects
280 were also important for increasing multifunctionality. Evenness has been shown to reduce
281 multifunctionality in species-rich biocrust systems [58], and a recent study showed that
282 multifunctionality in dryland ecosystems was maximised when communities were dominated by
283 functionally similar species that were well adapted to the environmental conditions [36]. In our
284 experiment, a high functional evenness (functionally different dominants) could reduce the levels of
285 certain functions if more even communities contained a higher proportion of low functioning species,
286 for instance a higher proportion of low SLA species would reduce functions related to fast
287 biogeochemical cycling (herbivory, pathogen infection, see Figure 2). On the other hand, the presence
288 of low SLA species led to an increase in belowground biomass (Figure 2) and soil respiration (on plots

without fungicide), perhaps indicating increased microbial activity in slow growing communities [59]. The addition of a few rare slow growing species could therefore have increased levels of certain soil functions and could have boosted multifunctionality in fast dominated communities. In our experiment, the highly functioning communities contained a large proportion of species linked to acquisitive strategies, as well as a few functionally distinct species supplying a complementary set of functions, further highlighting the complex interplay between diversity and mass ratio effects in driving multifunctionality.

Conclusions

Our results shed light on the context dependence of diversity effects on multifunctionality. The most important driver of context dependency was the functional composition of the species pool, a novel context driver not considered in previous biodiversity-functioning experiments. Our findings show that shifts in functional composition due to global change will not just alter ecosystem functioning themselves but will also alter the strength of diversity-functioning relationships. This could result in complex interactions between global change drivers, for instance, if some drivers alter functional composition and others change diversity. For the functions considered here, the optimal community for multifunctionality contained several different fast growing species at high abundance and some functionally distinct slow growing species at low abundance. However, the optimal community is likely to differ for other sets of functions and considering which functions should be maximised will be important to define optimal functional composition and diversity. Overall, these findings underline the need to consider multiple diversity dimensions and interactions between them and abiotic conditions to optimise multifunctionality in the context of multiple simultaneous global changes.

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Authors contribution

N.A.P., S.L.C. and E.A. designed and set up the PaNDiv Experiment; N.A.P., S.L.C., T.M., TZ.N., H.V. collected the data; N.A.P., T.M., N.H., V.H.K. and T.K. processed and analysed the NIRS samples; N.A.P. analysed the data and wrote the first manuscript with substantial input from E.A., S.S. and S.L.C. All authors contributed to revisions of the manuscript.

Material and methods

The PaNDiv Experiment

We set up a field experiment in October 2015 in Münchenbuchsee (Switzerland, 47°03'N, 7°46'E, 564 m a.s.l.) with factorial manipulations of plant species richness, plant functional composition, N enrichment and foliar fungal pathogens [60]. The site had been unfertilised for at least 10 years before the start of the experiment. The soil is characterized as 0.7 to 1m deep brown earth (Cambisol), according to the Geoportal of the Canton Bern (http://www.geo.apps.be.ch). We measured total soil N and carbon (C) concentrations and pH in the top 20 cm of soil at the start of the experiment and found concentrations of 2.3-4.2% C, 0.26-0.43% N and a pH of 7.4. The grassland was an Arrhenaterion, with some characteristic plant species of Mesobromion and Polygono-Trisetion communities (classification based on Delarze 2015 [61]). The area was cleared from vegetation and ploughed before the establishment of experimental plots.

The whole experiment consisted of 216 plots of 2 x 2m separated from one another by a 1m path and arranged in four blocks. We sowed the different communities with enough seeds to obtain a density of 1000 seedlings per m^2, equally divided between the species and corrected for species germination rates. The species pool consisted of 20 herbs and grasses typical of mesic, Central European grasslands (see list of species Table **S7**). We divided the species into two pools corresponding to different resource economic strategies [26], using literature values of leaf N content and specific leaf area (SLA) to classify the species. We created a pool of 10 species with high SLA and leaf N, which have a fast-growing, acquisitive resource use strategy, with short leaf lifespans and high photosynthetic rates, and a pool of 10 species with a more slow-growing, conservative strategy, long leaf lifespans and low photosynthetic rates. For simplicity we refer to these species as "fast" and "slow" throughout. We

excluded legumes from the species pool as they are expected to decline with N enrichment and including them in the slow growing pool only would add an additional difference between the pools. We therefore might have underestimated the diversity effects by excluding legumes from the species pool.

All 20 monocultures were established, together with 60 four species, 60 eight species and 16 twenty species plots. Plots with four and eight species could contain either only fast or only slow species, or a mix of the two strategies. This allowed us to create a large gradient in functional composition (mean SLA) and functional diversity (variance in SLA), independent of species richness. Species compositions for each plot were randomly selected from the respective species pool, with the constraint that all plots (except monocultures) had to contain both grasses and herbs. Each particular species composition received the four combinations of N enrichment and fungicide application. Fertilised plots received N in the form of urea twice a year in April and late June, for an annual addition of 100 kg N $ha^{-1}y^{-1}$, which corresponds to intermediately intensive grassland management[62]. Urea addition had no significant effect on soil pH measured in autumn 2017 (data not shown). In order to manipulate multitrophic interactions we removed foliar fungal pathogens using fungicide. The plots were sprayed with two fungicides to try to achieve broad suppression of the fungal community ("Score Profi", 24.8 % Difenoconazol 250 $g.L^{-1}$ and "Ortiva", 32.8% Chlorothalonil 400 $g.L^{-1}$ 6.56% Azoxystrobin 80 $g.L^{-1}$) four times during the growing season (beginning of April and June, late July and September) and the same amount of water was applied to the untreated plots. The fungicides were very effective in suppressing rusts and mildews but less effective in reducing infection by leaf spots, and had very few non target effects[51]. The experiment was weeded three times a year to maintain the diversity levels. All plots were mown twice a year, in mid-June and mid-August, which corresponds to intermediate to extensive grassland management.

Further details about the site characteristics and experimental setup of the PaNDiv Experiment can be found under ref [60].

Measurements on the plant community

Plant traits

We measured specific leaf area (SLA = surface/dry weight, $m^2\ kg^{-1}$) in August 2017 and in June and August 2018, one leaf from each of five individuals in all monocultures. We rehydrated the leaves and measured leaf surface, and dry weight according to the protocol of Garnier et al. [63]. The SLA per species is the average of the trait values across the five samples and across the three sampling dates. We used only SLA to calculate functional diversity and composition as our experimental design involved manipulating the mean and variation in SLA within communities (species were defined as fast and slow based on SLA).

Functional composition (CWM SLA)

We visually estimated the cover of each plant species (target species and all weeds together) before mowing. We calculated the community weighted mean (CWM) SLA per plot using the relative cover estimates: CWM = $\sum p_i * x_i$; with p_i the relative abundance of the species i and x_i the trait value of i in each monoculture of the same treatment (i.e. nitrogen and fungicide added or not).

Functional diversity (MPD and MPDw)

As a measure of functional diversity, we calculated a community mean pairwise distance, as the mean distance in SLA between the species sown in the plot [64]. The SLA values used were the control monoculture traits, and all monocultures had an MPD value of 0 by definition.

To assess how changes in species relative abundances affected the realised MPD of the experimental communities, we calculated an abundance weighted index, MPDw. The two indices were highly correlated (see Figure S1), partly due to coding the monocultures as 0. We therefore analysed the effect of MPD and MPDw in two separate models (Table S6). Model output calculated with equally-

weighted species MPD excluding the species that were not recorded at least once between 2017 and 2018 did not differ from the main model output (see Table S8).

Ecosystem functions

The functions described in this study were measured between June 2017 and autumn 2018. We excluded June 2016 aboveground measurements as the experiment had just started to establish and the weed and bare ground cover were still large [60]. For each function measured more than once, we used the mean value per plot over the whole period (see Table S5 and Figure S3).

Aboveground biomass

We collected aboveground biomass twice per year, before the mowing. The samples were taken by clipping plant material to 5cm above ground level, in two quadrats of 20x50 cm located in the centre of each plot. We weighed the biomass after 2 days of drying at 65°C. The plot target biomass production (i.e. of the sown species without weeds) was calculated by multiplying the percentage cover of weeds by the total biomass and subtracting this estimated weed biomass from the total weight. To control if the estimation was accurate, we sorted the biomass per species in June 2017 for all plots of one block. The sorted target biomass (without the weeds) was highly correlated with the estimated target biomass (R^2 = 0.994, data not shown). The mean weed percentage was around five percent and therefore removing the weeds made little difference to the total biomass [60].

Herbivory

Herbivory was assessed in May and August 2018. Five individuals of each target species were randomly selected from each plot and five leaves per individual were assessed for damage. Leaves were selected from the middle tier of each individual, and juvenile and senescent leaves were excluded. Damage was characterised by the type of herbivory; chewing, sucking, leaf mining and rasping damage based

424 on the methods of Loranger et al. [65]. In this study, we calculated the community weighted mean total
425 damage using the sum of damage types per leaf, per species, weighted by the cover of the particular
426 species.

427 Pathogens

428 Fungal infection was measured per species per plot once in October 2017 and twice in 2018, in July
429 and October. Ten randomly chosen individuals in the central square meter of the plots were visually
430 screened for signs of infection and the percentage of infected individuals was recorded. If there were
431 less than 10 individuals in the central square meter, individuals in the rest of the plot were screened.
432 If there were fewer individuals, the percentage of infected individuals was calculated based on all
433 individuals present. The species level infection and the percentage cover data were used to calculate
434 a community weighted mean of fungal infection per plot and season.

435 Plant N and P uptake

436 We included two ecosystem functions representing the potential N and P flux within a community.
437 The goal was to compare the resource use efficiency independently of biomass output or nutrient
438 stock. We calculated plant N and P uptake using total biomass and soil available N and P content. The
439 biomass collected in June and August 2018 was homogenised per plot and we ground a minimum of
440 5g per plot with a cyclone mill to obtain a fine powder. We then used near infrared reflectance
441 spectroscopy (NIRS) analyses to estimate biomass N and P content using calibrations by Kleinebecker
442 et al. [66]. Soil samples were collected five times in 2018 using two homogenised cores per plot. Soil NO_3^-
443 , NH_4^+ and PO_4^{3-} were extracted with $CaCl_2$ and analysed using a Continuous Flow Optical-Absorption
444 Spectrometer (CF-OAP; model Skalar Scan+; Skalar Analytical, Breda, The Netherlands). The plant N
445 and P uptake are the mean plant N and P content divided by the mean available N (NO_3^- and NH_4^+) and
446 available P (PO_4^{3-}), respectively.

447 Enzymatic activity

448 The activity of two enzymes related to carbon and phosphorus cycling, β-glucosidase and
449 phosphatase, was measured in autumn 2017 and in April, May, July and August 2018. These functions
450 give an estimate of soil microbial activity, and β-glucosidase has been shown to be a good soil health
451 indicator [67]. We took two soil samples per plot of 1.5 cm diameter to 20 cm depth. The fresh samples
452 were homogenised and sieved through 2mm meshes. In each sample, we measured the β-glucosidase
453 and phosphatase enzymatic activities, following the protocol of Tabatabai [68]. For the analyses
454 presented here, we calculated the mean value of each enzymatic activity for all the periods sampled.

455 Belowground biomass

456 Root biomass was measured once in autumn 2017. We took two cores per plot to 20 cm depth (440
457 cm^3 of soil). We homogenised the two samples and used a subset of 40g fresh soil in which we sorted
458 out the roots. The samples were washed in 200 µm sieves and the roots sorted out with tweezers. We
459 dried the roots at 65°C for 48 hours. We estimated soil bulk density by weighing 40g of soil from the
460 same plot before and after drying for 24 hours at 105°C. Bulk density did not differ between the
461 treatments (data not shown). The final belowground biomass per plot is the weight of roots per g of
462 dry soil.

463 Respiration

464 We measured overall soil respiration five times during 2018. We placed one PVC ring per plot at least
465 a week before taking the measurements. The vegetation was clipped before starting the measures
466 without disturbing the soil. We took two measures per plot and repeated the measures in case of large
467 difference between the respiration rates. We took the measurements using a soil CO_2 flux chamber
468 (6400-09) attached to a LI-6400XT (Li-Cor Inc.). Soil respiration varies during the day and between
469 days. To minimise this variation, we took the measurements starting at 10am and finishing the latest
470 at 2pm, as this time span is expected to provide rates representative of the mean daily respiration
471 [69,70]. We measured one block per day (54 plots), avoided humid days and kept the measurement days

472 as close to each other as possible (max 6 days for one sampling session). The final soil respiration
473 measure is the mean measure per plot.

474 Carbon storage

475 We measured soil carbon concentration on soil samples of 440 cm^3, taken to 25 cm depth in autumn
476 2017. We took two samples per plot, homogenised them and removed stones and living material
477 (roots, fauna). We weighed the samples before and after drying at 65°C for 48 hours. To calculate
478 carbon storage, we compared the 2017 samples to soil samples taken in autumn 2015 before the start
479 of the experiment. In 2015, we took 5 soil samples per plot from a subset of 89 plots distributed across
480 the field. As the field had just been ploughed and homogenised there was relatively little variation
481 between adjacent plots and we estimate soil C concentrations for all plots using kriging (package geoR,
482 estimating sill and range of the data variogram using the variofit function). Analyses of soil total C were
483 conducted in a CNS Analyser at the Institute of Geography of the University of Bern. The carbon
484 storage per plot is the difference between the percentage carbon in autumn 2017 and in autumn 2015.

485

486 Analyses

487

488 Multifunctionality

489 We calculated multifunctionality from our 10 ecosystem functions using a multiple threshold
490 approach [71]. We therefore calculated "ecosystem function multifunctionality" [39] using a set of distinct
491 functions, representing key above and belowground carbon and nutrient fluxes. We first standardised
492 each function to a common scale (see Table S5 and Figure S4) and then calculated multifunctionality
493 using thresholds from 0.5 to 0.8 with an interval of 0.05 [36]. We excluded very large (>0.8) or very small
494 (<0.5) thresholds as multifunctionality values tend to have small ranges at the extremes (i.e. most
495 plots either have 0 multifunctionality or maximum multifunctionality). The thresholds were defined

496 relative to the mean of the five highest values of each function, in order to reduce the influence of
497 outliers [72]. Multifunctionality was the proportion of functions reaching this threshold per plot,
498 calculated using the multidiv function (available at https://github.com/eric-allan/multidiversity).

499 We first analysed multifunctionality at each threshold separately, using linear mixed effects models,
500 testing the effects of N enrichment, fungicide, species richness, SLA (as a continuous measure of
501 functional composition), MPD, and their interaction on multifunctionality. We included *block* and
502 *species composition* (random assemblages within diversity and functional composition levels) as
503 random terms. Replacing the effect of sown by realised species richness gave similar results (Table
504 S8). Our data met the model assumptions of homogeneity of variance and normal distribution of
505 residuals. All explanatory variables were scaled and centred to a mean of 0 and standard deviation of
506 1, so that their effect sizes are comparable. We included block and combination (specific set of species
507 per richness and functional composition level) as random terms. We did not test for SLA x MPD
508 interactions, as the two factors are not fully orthogonal in the experimental design (MPD is inevitably
509 maximal at intermediate SLA, see Figure S1).

510 The effects of different factors can vary according to the threshold used to calculate multifunctionality.
511 Previous approaches have tested how diversity effects vary depending on the threshold [71] but
512 visualising how multiple factors vary with multifunctionality thresholds is more challenging. We
513 therefore used a new approach to test which treatment effects were consistent across thresholds and
514 which depended on the threshold level. To do this, we constructed models with all multifunctionality
515 measures (calculated using different thresholds) combined. This meant that each plot had seven
516 measures of multifunctionality (at the 50, 55, 60, 65, 70, 75 and 80% thresholds). We analysed all the
517 multifunctionality values with linear mixed effects models with the same structure as the individual
518 thresholds model, but including threshold as a fixed continuous term which could interact with the
519 treatment variables, and including plot as a random effect to correct for the fact that we had several
520 measures of multifunctionality per plot. We also included random slopes for the effect of threshold

521 on multifunctionality in each plot, which corrects for additional autocorrelation between
522 multifunctionality values measured in the same plot. This is a similar approach to that used in Soliveres
523 et al. [8] but extended to multifunctionality calculated at different thresholds. Using this method, we
524 could estimate which effects were significant across all thresholds, and which ones changed
525 continuously as the threshold was increased. We then estimated the overall effect of each treatment
526 and interaction across the thresholds and calculated a confidence interval around the effect.
527 Confidence intervals were calculated using a script from Ben Bolker (available at
528 https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html#predictions-andor-confidence-or-
529 prediction-intervals-on-predictions).

530 In addition, all functions were analysed separately using linear mixed effect models.

531 Monocultures all get an arbitrary MPD of 0 causing some correlation between MPD and species
532 richness (Figure S1). To ensure that the effect of diversity is not driven only by the difference between
533 monocultures and polycultures, we did an additional analysis in which we added a binary variable for
534 the monoculture/not monoculture contrast. Results using this approach were qualitatively similar to
535 those presented in the main text (Table S9).

536 All analyses were conducted in R using the package lme4 [73,74]. We simplified full models by dropping
537 terms that did not significantly improve the overall model fit using likelihood-ratios.

538

539 Effects of individual species on functions

540 To test the effect of each species on each function we fitted two separate models for each function,
541 one with the presence and one with the abundance (relative cover) of each of the 20 species. We used
542 the following model structure:

543 *Function ~ Nitrogen * Fungicide + Species1 + … + Species20 + (1|Block)*

544 We extracted the effect of each species presence and abundance on each function, non-significant
545 effects were set to 0 (Table S3 and Table S4.). We then calculated how similar different sets of species
546 were in the functions they affected. We calculated the similarity in functional effects for all possible
547 combinations of four species. We chose four species as this corresponds to one of our diversity
548 treatments and allows us to explore differences in the functions provided by sets of species differing
549 in their mean functional traits. We calculated the similarity in both positive and negative functional
550 effects for all combinations of four species, and for effects of species presence and abundance. We
551 used the CqN similarity index [75], as this allows a calculation of dissimilarity (beta diversity) among any
552 number of communities. We used a q value of 2, which means larger functional effects were weighted
553 as more important. This corresponds to the multicommunity extension of the Morisita-Horn index.

554 We then calculated the mean and variance in SLA between all sets of four species and regressed them
555 against the dissimilarity in functional effects between the four species (CqN). We are principally
556 interested in the effect of mean SLA, to determine if sets of species with higher mean SLA are more
557 different in the functions they provide, however we included the variance in SLA between the species
558 to account for the fact that a set of four species with intermediate mean SLA could either be composed
559 of low and high SLA (slow and fast) species or a set of species all with intermediate SLA. To test if the
560 effects were significant, we randomly shuffled the SLA values between the species and recalculated
561 the relationships between mean and variance in SLA and functional dissimilarity 1000 times. We
562 tested whether the observed slopes between mean SLA and variance in SLA and functional
563 dissimilarity (CqN) lay outside the 2.5 and 97.5% quantiles of the random slopes. These analyses were
564 repeated for the positive and negative effects and effects of species presence and abundance. Output
565 in Table S2.

566 In a second step, we tested for trade-offs between the functions supplied by different species and
567 whether this was related to their SLA. We only considered significant effects in this analysis. For each
568 pair of species, we summed the number of functional effects that were opposing (e.g. one species has

a positive effect on a given function while the other species has a negative effect). We related the number of trade-offs to the mean and difference in SLA for the species pair, to test if pairs of low SLA (slow) species tend to have more opposing effects. We again randomly shuffled the SLA values between the species, recalculated the relationships 1000 times and tested whether the observed slopes lay outside the 2.5 and 97.5% quantiles of the random slopes. Output in Table S2.

Number of functions

In addition to the threshold chosen, multifunctionality values depend on the number and identity of functions included, which makes generalisation across studies challenging [5,10,76]. In order to test the sensitivity of our results to the number and identity of functions, we calculated multifunctionality with all possible combinations of between two and ten functions (1013 combinations) for four thresholds from 0.5 to 0.8 (4052 multifunctionality measures). We extracted the effects of our factors and interactions from a linear mixed effect model for each multifunctionality measure. In order to correct for the uncertainty of each estimate, we weighted each estimate by the inverse of the standard error. We then calculated an overall mean and confidence interval for multifunctionality per threshold depending on the number of functions included. The number of functions included did not significantly change the mean effect of our variables on multifunctionality, except for the interaction between SLA and SR at the 50% threshold, which strengthened as more functions were considered. The variation around the mean got larger with a decreasing number of functions, going from positive to negative depending on the functions included (Figure S5 and Figure S6). This variation was driven more by variation in the identity rather than in the number of functions included (Figure S6).

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