Title

Nitrogen availability and plant functional composition modify biodiversity-multifunctionality relationships

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Abstract

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. A better understanding of the drivers of this context dependency is essential to predict effects of global change on ecosystems. To determine how different factors modulate the effect of diversity on multifunctionality, we established a large grassland experiment with 216 communities, crossing a manipulation of plant species richness (1, 4, 8, 20 species) with manipulations of resources (nitrogen enrichment), plant functional composition (gradient in mean specific leaf area [SLA] to manipulate abundances of exploitative, fast-growing vs. conservative, slow-growing species), plant functional diversity (variance in SLA) and enemy abundance (foliar fungal pathogen removal). We measured ten above- and belowground functions, related to productivity, nutrient cycling and energy transfer between trophic levels, and calculated ecosystem multifunctionality. Plant species richness and functional diversity both increased multifunctionality, but their effects were context dependent. Species richness increased multifunctionality only when communities were assembled with fast growing (high SLA) species. This was because slow species were more redundant in their functional effects, whereas different 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 fast-growing 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 (i.e., multifunctionality) generally increases with diversity (Hector & Bagchi, 2007; Gamfeldt et al., 2008; Isbell et al., 2011; Lefcheck et al., 2015; Meyer et al., 2018; van der Plas, 2019). Although positive biodiversity-ecosystem multifunctionality relationships are common, studies have found substantial variation in the direction and strength of these relationships, which suggests that they depend on the biotic and abiotic environmental context (Balvanera et al., 2006; Soliveres, van der Plas, et al., 2016; van der Plas, 2019). However, only a few studies have attempted to understand this context dependency by determining how different drivers affect the biodiversity-multifunctionality relationship, and these have been either observational (Allan et al., 2015; Jing et al., 2015; van der Plas, 2019) or have focussed on only one of many potential drivers (Giling et al., 2019, but see Alsterberg et al., 2014; Liu et al., 2017). A better understanding of context dependency in biodiversity-multifunctionality relationships is important to predict effects of global change on ecosystems, because global change drivers, like nitrogen (N) enrichment or climate change, reduce biodiversity but also alter other aspects of the environment, and these changes may further alter the effects of biodiversity loss on ecosystem functioning. Experimental approaches are needed to rigorously test for context dependency but very few experiments cross diversity gradients with manipulations of major context drivers such as resources, natural enemies or plant species composition.

The main environmental factors influencing the strength and direction of the diversity-multifunctionality relationship are likely to be those that alter the mechanisms by which biodiversity affects functioning. Two of the main mechanisms behind the positive effects of plant diversity on ecosystem functioning are: i) complementary resource use amongst species (Fornara & Tilman, 2009; Jucker et al., 2015; Oram et al., 2018), and ii) increased enemy attack in species-poor communities , reviewed in Barry et al., 2019). If species vary in their resource uptake strategies, then diverse

communities should use resources more efficiently (Tilman, 1982). Increasing resource levels would therefore remove opportunities for nutrient use complementarity between species and would equalise functioning between low and high diversity communities (Ratcliffe et al., 2017) (see Figure 1, Point 1). However, some experimental studies have shown neutral (Wacker et al., 2009; Hooper et al., 2012) or even positive effects of increased resource levels on the diversity-functioning relationship (Weigelt et al., 2009; Craven et al., 2016; Eisenhauer et al., 2018), suggesting that niche complementarity for soil nutrients does not always underlie diversity-functioning relationships. Nitrogen is one of the major soil nutrients limiting plant growth (Vitousek & Howarth, 1991) and differences in nitrogen use can be a key driver of niche differences between plants (McKane et al., 2002; Harpole & Tilman, 2005) and of positive effects of diversity on functioning (Fornara & Tilman, 2009). In addition, nitrogen enrichment is one of the major drivers of global change (Galloway et al., 2008; Battye et al., 2017) and testing how it modifies diversity effects is therefore of key importance to understand interactions between diversity loss and other aspects of global change. There is increasing evidence that natural enemy attack is also an important mechanism driving effects of diversity on function, and it can either enhance (Maron et al., 2011; Schnitzer et al., 2011), or reduce (Seabloom et al., 2017) the strength of the diversity-functioning relationship (Figure 1, Point 2). Foliar fungal pathogens, have received less attention than insects or vertebrate enemies but they are also key drivers of plant diversity and ecosystem functioning (Allan et al., 2010; Mordecai, 2011). There is little consensus on how plant enemies or resource availability affect diversity-functioning relationships but both could potentially be important drivers of context dependency.

In addition to the environment, the composition of the species pool (from which local plant communities are assembled) could modify biodiversity-multifunctionality relationships. A key element of composition could be the resource use strategies of the species, as those with different strategies might vary in their degree of resource use complementarity. The leaf economics spectrum (Wright et al., 2004; Díaz et al., 2016) distinguishes slow growing, conservative species from fast growing, acquisitive ones and is indicated by several traits, such as specific leaf area (SLA) and leaf nitrogen

content. Slow species, with low SLA, are more competitive in the low nutrient environments they tend to dominate (Tilman & Wedin, 1991; Reich, 2014). They might therefore differ more in their competitive abilities for different nutrients, leading to greater nutrient use complementarity between slow species. In contrast, fast species, with high SLA, are abundant in high resource environments, where asymmetric light competition is prevalent (Hautier et al., 2009; Busch et al., 2019). Nutrient use complementarity between fast species might therefore be low. However, fast species are also likely to be more sensitive to enemies due to a growth defence trade-off (Endara & Coley, 2011), and enemies might therefore drive stronger diversity-functioning relationships in fast-dominated communities. Complementarity effects can lead to positive diversity-ecosystem functioning relationships for individual functions, which could also translate into higher multifunctionality in diverse communities. Such effects of the fast-slow functional composition of the species pool on diversity-function relationships would lead to different effects of diversity, depending on whether communities are dominated by fast or slow species, and therefore to interactions between changes in species composition and diversity (Figure 1, Point 4). Changes in diversity and fast-slow functional composition are typically correlated in observational studies (Allan et al., 2015) and new experimental approaches are therefore necessary to disentangle their interactive effects.

Biodiversity has many dimensions and different aspects of diversity can affect multifunctionality, with functional diversity being a key driver of functioning alongside species richness (Allan et al., 2015; Gross et al., 2017; van der Plas, 2019). A high fast-slow functional diversity could increase multifunctionality if species with different resource use strategies (fast vs slow) have complementary interactions (Cadotte et al., 2011; Handa et al., 2014). However, functional diversity can also reduce multifunctionality in harsh conditions where environmental filtering is strong and functionally distinct species are poorly adapted to the local conditions (Le Bagousse-Pinguet et al., 2019). In general, diversity and mass ratio effects can both occur and functions may in some cases be driven by complementary interactions between many less abundant species (Soliveres, Manning, et al., 2016), while in other cases they may be driven mostly by the dominant species, i.e. "mass ratio effects"

101 (Grime, 1998) (Figure 1, Point 3). Functional diversity measures are strongly affected by rare species
102 if only the presence/absence of species is considered but are mostly driven by differences between
103 dominant species if they are abundance weighted. We therefore predict that non abundance
104 weighted functional diversity should increase functioning when diversity effects and complementarity
105 among rare species are important, e.g. because rare slow species provide novel functions (Mariotte,
106 2014). However, we would expect abundance weighted functional diversity to decrease functioning if
107 mass ratio effects dominate and only the presence of key species is important (Mokany et al., 2008;
108 Ruiz-Benito et al., 2014), e.g. because high productivity is high in communities dominated by fast
109 species (Allan et al., 2015). Comparing effects of abundance vs. non abundance weighted fast-slow
110 functional diversity might therefore shed light on the role of mass ratio vs. diversity effects in
111 determining multifunctionality.

112 To better understand which contexts modify effects of diversity on multifunctionality, we measured
113 multifunctionality in 216 plots of a grassland biodiversity-ecosystem functioning experiment. In this
114 experiment, we tested the context-dependency of biodiversity-multifunctionality relationships to the
115 addition of resources (N), enemy attack (fungal pathogens), and composition of species pool
116 (functional composition). We factorially manipulated plant species richness, N enrichment, fungal
117 pathogen removal (fungicide spraying), and plant fast-slow functional composition (by creating a
118 gradient of abundance weighted specific leaf area [SLA]) and fast-slow functional diversity (the mean
119 pairwise distance in SLA). We refer to these hereafter as functional composition and functional
120 diversity. We therefore manipulated a specific element of functional composition and diversity in
121 terms of the mean and variance in resource economics traits and did not explicitly manipulate
122 composition and diversity in other trait axes. Our aim was to focus on the resource-economics axis
123 because it has been identified as one of the key axes of plant functional variation (Wright et al., 2004;
124 Díaz et al., 2016) and it represents a key set of traits predicting responses to N enrichment and effects
125 on many ecosystem functions.

126 We measured ten functions on each plot, related to biotic interactions and biogeochemical cycling.
127 We selected focussed on measures or proxies of process rates and consider high rates and low losses
128 to indicate high functioning (Manning et al., 2018). We measured: above and belowground plant
129 biomass, insect herbivore damage (hereafter herbivory) and foliar fungal pathogen infection, plant
130 nitrogen and phosphorus uptake (quantified as ratios between available nitrogen and phosphorus
131 content in the soil and nitrogen and phosphorus content in aboveground plant biomass), two
132 enzymatic activities related to carbon (β-glucosidase) and phosphorus (phosphatase) cycling, soil
133 respiration and soil carbon (C) storage, for more details see methods. We used a novel approach to
134 analysing treatment effects on equal weight ecosystem function multifunctionality (Manning et al.,
135 2018), in which we calculated multifunctionality at several thresholds between 50 and 80% of
136 maximum function. We then combined all these multifunctionality measures in a single model (for
137 details see methods), which allowed us to estimate the average effect of our treatments on
138 multifunctionality, across thresholds. As any particular threshold is arbitrary, this allowed us to
139 robustly quantify overall effects on multifunctionality. We hypothesised that: 1) species richness and
140 fast-slow functional diversity will both increase multifunctionality, 2) the strength of the diversity
141 effect will depend on the functional traits of the species which are combined (i.e. the functional
142 composition of the species pool), and 3) increased resource levels and removal of fungal pathogens
143 will decrease the effect of diversity on multifunctionality.

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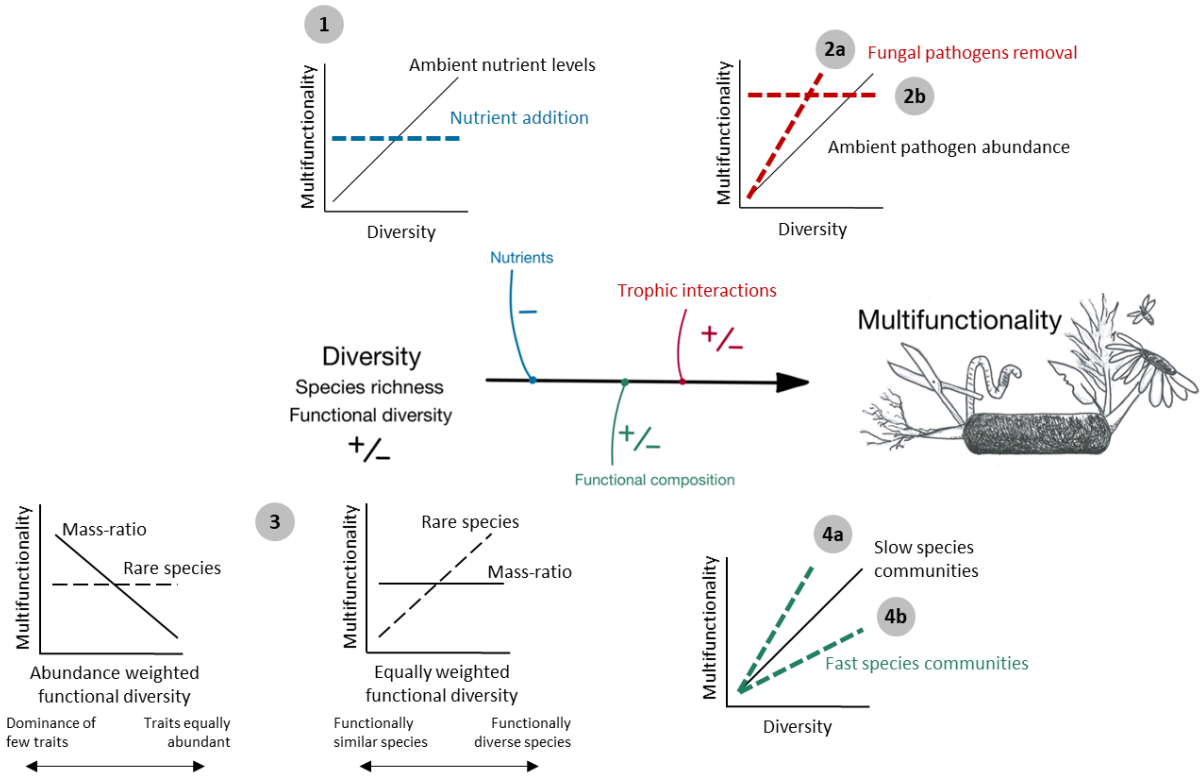

Figure 1: Concept of context dependency in plant communities.

1 Nutrient addition can reduce the potential for complementarity in diverse communities, and therefore dampen the diversity-multifunctionality relationship (Rattcliffe et al., 2017).

2a Pathogens can remove more biomass in diverse communities. Removing them would increase the diversity-productivity relationship (Seabloom et al., 2017).

2b Specialist pathogens preferentially attack low-diversity communities (Maron et al., 2011; Schnitzer et al., 2011). Removing them would dampen the diversity-productivity relationship due to higher functioning at low levels of diversity.

3 Functional diversity can be calculated in different ways. Weighting functional diversity by the species abundance assumes that a species contributes to functioning proportionately to its abundance, while equally weighted functional diversity assumes that the presence or absence of a species determines its effect on functioning.
Mass-ratio effects, solid lines: if dominant species are key in supporting functioning, multifunctionality will decrease when abundance weighted functional diversity increases, and will not respond to equally weighted functional diversity.
Importance of rare species, dashed lines: if rare species are increasing functioning, then multifunctionality will increase with equally weighted functional diversity, and will not respond to abundance weighted functional diversity.
We show here the two extreme scenarios, but there are intermediate options between the importance of only mass-ratio or only rare species.

4a Fast species are more sensitive to resources and pathogen presence due to the growth-defence trade-off (Endara & Coley, 2011) and respond more strongly to environmental conditions: higher diversity-multifunctionality relationship can be more context-dependent in fast than in slow communities.

4b Slow species are more complementary in their resource uptake because they are adapted to low nutrient environments (Tilman & Wedin, 1991; Reich, 2014): lower diversity-multifunctionality relationship in fast communities than in slow.

We also included in the analyses possible interactions, not represented here, between the different factors (nutrient and pathogens for instance) and with more than two factors.

Results

Richness-multifunctionality relationships depend on functional composition

Diversity effects on multifunctionality were highly context-dependent in our experiment, as we found three interactions between effects of richness and other factors. The strongest of these was the interaction between SLA and richness (estimate of the interaction: 0.025 +/- 0.009 SE), which meant that the effect of sown species richness on multifunctionality was modified by fast-slow functional composition. These results were consistent when using multiple trait measures of functional composition instead of just SLA (Table S1). Species richness decreased multifunctionality slightly in communities with low mean SLA but increased multifunctionality in high mean SLA communities (Figure 2a and b and Table S2). 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. At the same time, SLA generally increased multifunctionality (and the main effect of SLA was the single strongest driver of multifunctionality) but the interaction with richness meant that SLA increased multifunctionality more strongly in diverse communities. Subsequent analyses revealed that these results were not driven by any particular function (Table S3 and Figure S1) and remained consistent regardless of the number of functions included in our multifunctionality metric (Figure S2 and Figure S3), or the use of the realised [as opposed to the sown] species richness (Table S4). 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, Figure 3). This shows that fast and slow species drive different functions. We further explored whether the different functional effects of fast vs. slow species may explain why diversity has different effects on multifunctionality in slow vs. fast communities (see below).

High resource levels dampen effects of functional diversity on multifunctionality

Sown fast-slow functional diversity, calculated as the mean pairwise distance between species in their SLA, increased multifunctionality in unfertilised plots (Figure 2a and c). However, nitrogen enrichment dampened this positive effect because it increased multifunctionality in plots with low functional diversity (estimate of the interaction: -0.010 +/-0.004 SE). Nitrogen enrichment increased soil respiration, in particular, in plots with low functional diversity (Figure 3). N enrichment also increased several individual functions related to plant productivity and soil microbial activity overall (above and belowground biomass, soil β-glucosidase activity, plant P uptake, see Figure 3). Interestingly, N enrichment also interacted with species richness to affect belowground biomass and C storage (Figure 3), but this interaction further depended foliar pathogen removal (fungicide treatment).

Foliar pathogen removal also dampened effects of fast-slow functional diversity on multifunctionality, as functional diversity only increased multifunctionality where foliar pathogens were not reduced by fungicide application (estimate of the interaction: -0.008 +/-0.004 SE, Figure 2a and d). However, this interaction should be treated with caution as it seems to be driven mainly by the response of fungal pathogen damage (see Table S5), which was reduced by fungicide, as expected. Fungicide also increased total soil respiration in high SLA communities and belowground biomass in species-rich, fertilised communities and was also involved in some other complex interactions for C storage and phosphatase.

Effect of change in species abundances on functional diversity

Although all species started at equal abundance in our experiment, species shifted their relative abundances over time. To test the effect of these abundance changes on functional diversity, we calculated abundance weighted mean pairwise distance (MPDw), weighted by realised species abundances. While sown functional diversity increased multifunctionality, the abundance-weighted functional diversity showed the opposite pattern (Figure 4). These contrasting effects indicate that the communities with the highest multifunctionality were those which had been sown with functionally distinct species (i.e. with high unweighted MPD), but in which functional diversity decreased because they became dominated by species with similar functional trait values (they ended up with lower abundance weighted MPDw). Such high multifunctionality communities are dominated by functionally similar species but contain functionally distinct rare species.

Effects of individual species on functions

The positive effects of both SLA and functional diversity on multifunctionality show that combining multiple fast-growing species in a community leads to high multifunctionality, whereas combining slow species does not increase multifunctionality. There are two main factors that could cause this. First, if slow species were more redundant in their functional effects (they all drive similar functions), then adding more slow species to a community (increasing diversity of slow species) would not increase multifunctionality. Second, slow species could have trade-offs in their functional effects (i.e. they increase some functions and reduce others), while fast species have more synergies (positive effects on multiple functions). This would mean that increasing diversity of slow species would not enhance multifunctionality in the temperate grassland we studied, because adding a slow species to a slow community would tend to reduce as many functions as it enhanced.

To test these ideas, we calculated the effect of our 20 species on each function, by fitting regression models for each function with the abundance of each species as predictors (following the approach

218 used in Hector & Bagchi, 2007; Isbell et al., 2011). We extracted the significant positive and negative
219 effects of each species on each function. To explore how combining sets of slow or fast species would
220 affect multifunctionality, we calculated the dissimilarity in functional effects between sets of four
221 species (see methods for more details). This showed that fast species were more dissimilar in the
222 functions they drove (Table S6, Table S7 and Table S8), as an increase in mean SLA between species
223 increased the dissimilarity in the set of functions they affected. The results were similar regardless of
224 the use of presence-based or abundance weighted effects, the number of species considered when
225 calculating dissimilarity, and for both positive and negative effects (see methods and Tables S5 to S7),
226 showing that all slow species tend to affect similar functions, while fast species affect different
227 functions. For instance, slow species like *Achillea millefolium, Centaurea jacea, Festuca rubra* and
228 *Salvia pratensis* all drove biomass production and insect herbivory, while fast species tended to drive
229 different functions, e.g. *Crepis biennis* increased N uptake, while *Holcus lanatus* increased pathogen
230 infection.

231 In order to test whether there are also more trade-offs in functional effects between slow species, we
232 calculated, for each pair of species, the proportion of functional effects that were trade-offs (see
233 methods). The effects were non-significant, both when analysed based on species presence or on
234 species abundance (Table S6). It therefore seems that trade-offs in functional effects are not more
235 common for slow species and that instead slow species are more redundant in their functional effects
236 because they tend to drive similar functions.

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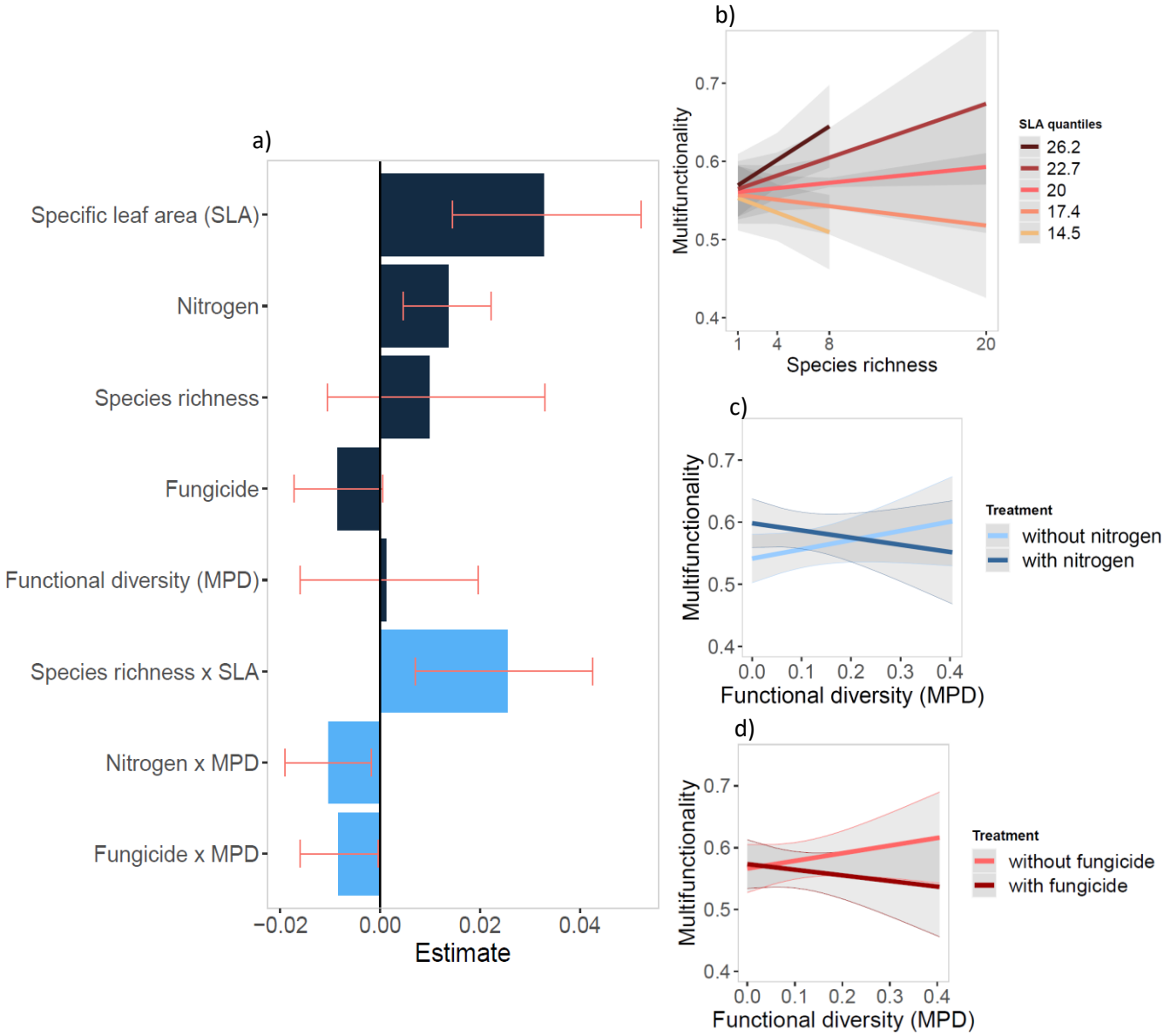

Figure 2: Context-dependent diversity-multifunctionality relationships. a) Standardised effect (+/- confidence intervals) of each scaled centred variable on multifunctionality, across seven thresholds. Only significant effects are shown to facilitate interpretation. All main effects are shown regardless of significance, as they are all part of at least one significant interaction. b) Interaction between sown species richness and community weighted mean specific leaf area (SLA, m^2 kg^{-1}), represented as quantiles of SLA (see raw data in Figure S4). c) Interaction between functional diversity (MPD, mean pairwise distance) and nitrogen enrichment. d) Interaction between functional diversity and fungicide application. N = 216 plots. Details of the model output can be found in Table S2. Species richness is here sown richness.

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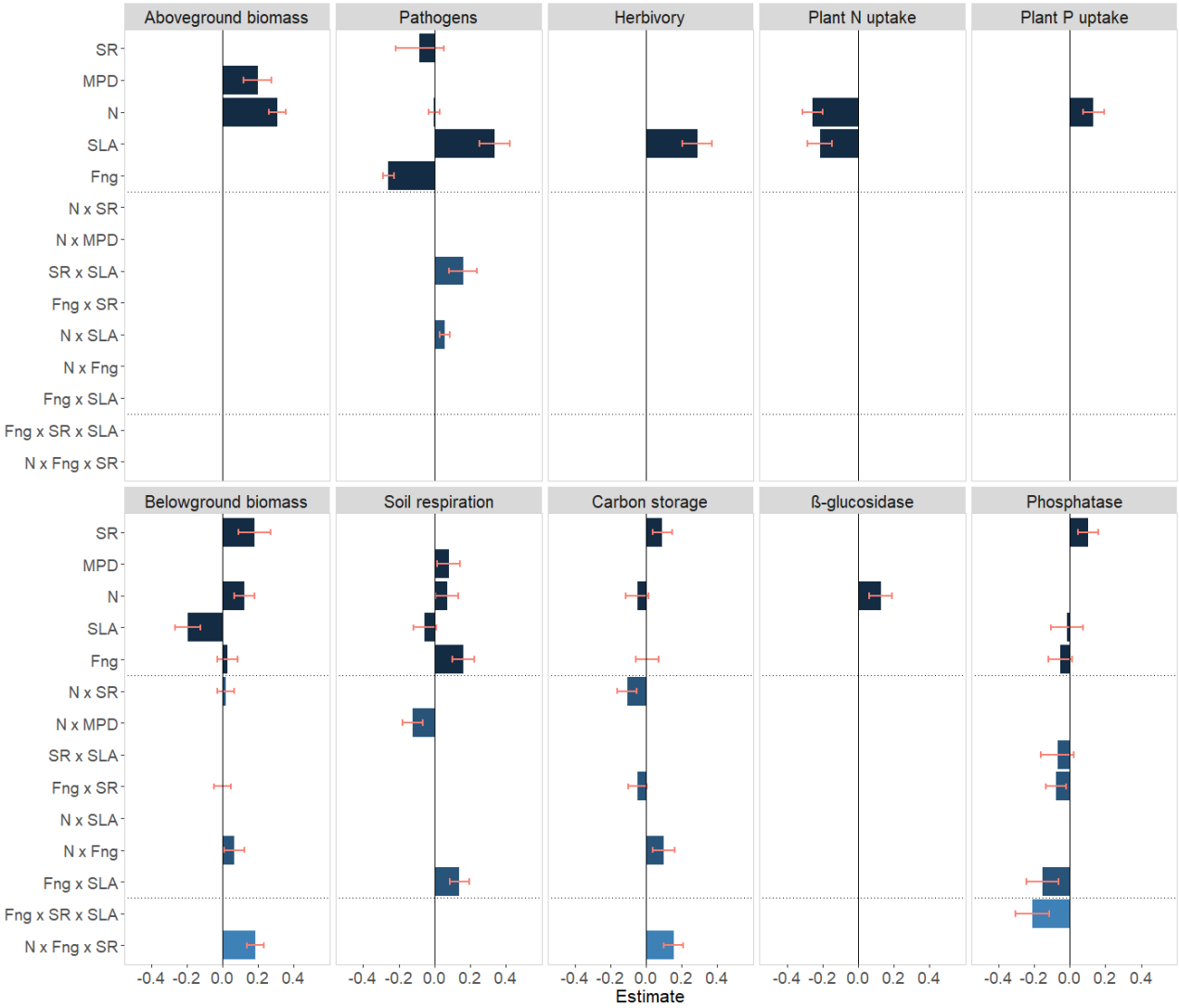

Figure 3: Drivers of individual functions. Mean standardised effect (+/- confidence intervals) of each scaled and centred variable on individual functions after model simplification. Only significant effects are shown but main effects and interactions which are part of higher order interactions are displayed regardless of significance, see Figure S1 for the full model. 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 S9 and Figure S1 for details.

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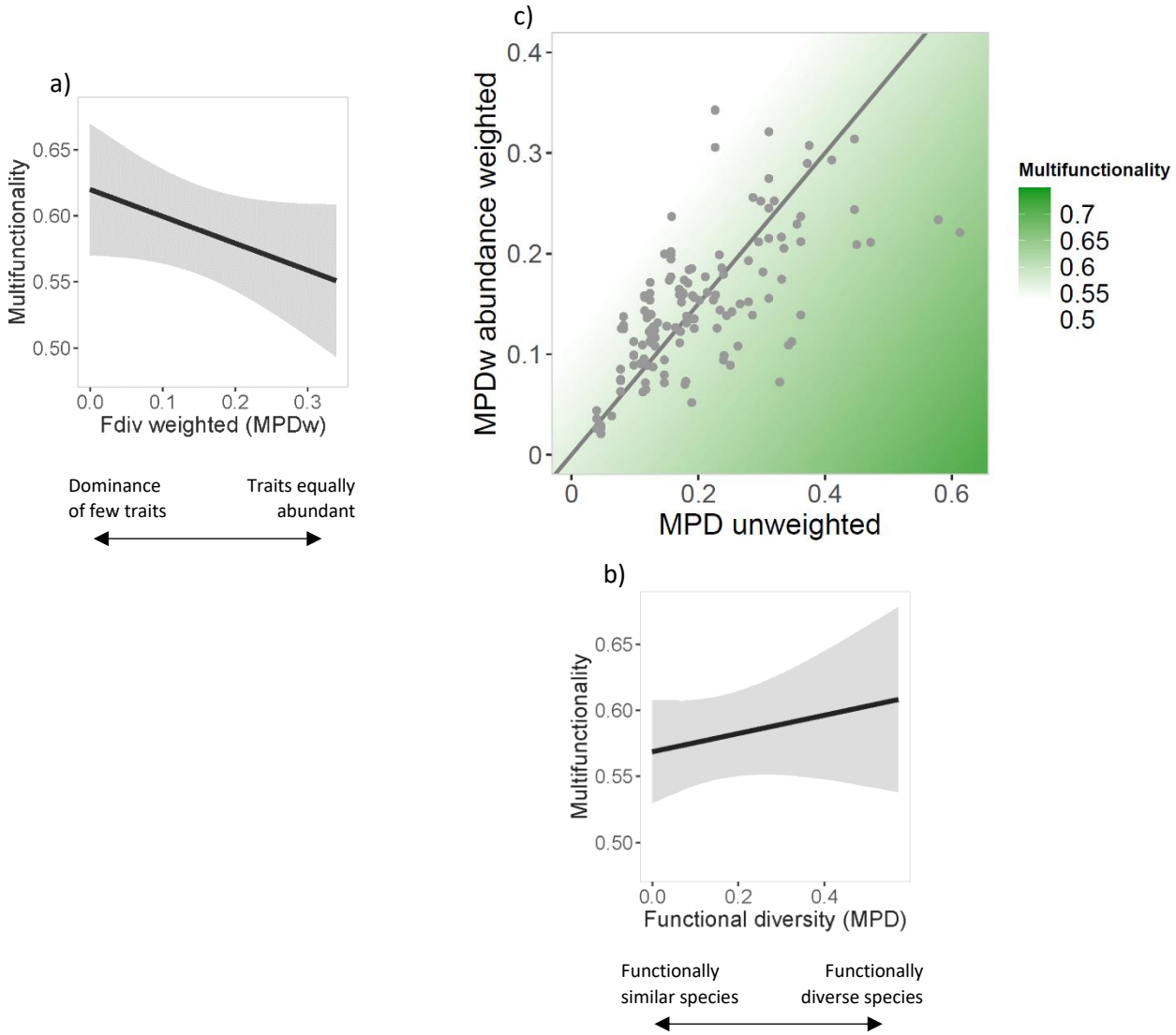

Figure 4: Effect of sown vs. realised functional diversity on multifunctionality. Effect (+/- confidence intervals) on multifunctionality of a) abundance weighted, realised, functional diversity (MPDw) and b) non-abundance weighted, sown, functional diversity (MPD). c) MPDw plotted against MPD. The green area represents the model-predicted multifunctionality from a 65% threshold (midpoint between 50% and 80% thresholds), but the effect is similar at other thresholds, as there is no interaction between threshold and MPD. The high multifunctionality plots are those with both a relatively high MPD and a relatively low MPDw (bottom right corner). Left of the grey line: functional diversity increases from sown communities. Right of the grey line: functional diversity decreases from sown communities. Monocultures were included in the individual models but are not shown in c) as they are all coded as 0 MPD and MPDw. See Table S10 for details on the model output.

Discussion

Functional trait composition modulates richness effects on ecosystem functioning

Our results show that there is substantial context dependency in biodiversity-multifunctionality relationships. The most important driver of this context-dependency in our study was the functional composition of the species pool, in terms of whether communities were composed of fast-growing acquisitive species or slow-growing conservative species. When experimental (Hector et al., 2011; Craven et al., 2018) or observational (e.g. Allan et al., 2015) studies have considered compositional and diversity effects together, they have compared their relative importance but not potential interactions between them. By experimentally crossing manipulations of fast-slow functional composition and of species richness, we were able to show that community SLA and species richness had an interactive effect on multifunctionality, which means that composition and diversity are not always independent drivers of multifunctionality. Some studies have considered how the functional *diversity* of the species pool impacts species richness-functioning relationships (Ratcliffe et al., 2017; Wagg et al., 2017) but our results show that the functional *composition* of the species pool may be a stronger driver. Two different analyses provided evidence that multifunctionality was affected by both mass ratio, or selection, effects and diversity, or complementarity, effects and that these interacted. The analysis of individual species effects on functions showed that certain slow species drove many functions and at the same time abundance weighted functional diversity reduced multifunctionality, indicating mass ratio effects because multifunctionality was highest when the dominants were functionally similar. In contrast, fast species drove different functions, suggesting complementarity between them, and non-abundance weighted functional diversity increased multifunctionality, indicating that functionally distinct rare species also provided different functions. Our results therefore highlight that while species richness and composition have usually been seen as alternative

265 or opposing drivers of functioning (i.e. mass-ratio vs. diversity effects, Tilman, 1997; Grime, 1998;
266 Mokany et al., 2008; Ruiz-Benito et al., 2014), they can modify each other's effects (Craven et al., 2018;
267 Le Bagousse-Pinguet et al., 2019).

268 Our analysis of individual species effects on functions showed that slow species were more redundant
269 in their functional effects, because some slow species (especially *Achillea millefolium, Centaurea*
270 *jacea, Festuca rubra* and *Salvia pratensis*) drove multiple functions, while fast species tended to affect
271 a different function each. Therefore, combining multiple fast species increased multifunctionality
272 because each species increased a different function, while combining multiple slow species did not
273 add more functions, as they were more redundant in the functions they provided. We also found that
274 fast and slow species were complementary with each other and provided different functions, also see
275 below. At the same time, some slow species had only negative effects on functioning, meaning that
276 on average monocultures of slow species had low multifunctionality. This suggests that amongst slow
277 species there might be a "multifunctional selection effect" with high multifunctionality driven by the
278 abundance of those species that promote several functions, while amongst fast species there is
279 "multifunctional complementarity" with different species driving different functions. This idea is
280 further supported by the fact that diversity x composition interactions were not significant for most
281 individual functions, as opposed to what we found for multifunctionality. Instead, species richness
282 increased belowground biomass and carbon storage regardless of community SLA, and phosphatase
283 activity peaked in plots dominated by slow species, regardless of their richness. Diversity therefore
284 did increase several individual functions within slow species communities, presumably because the
285 slow species were complementary in their effects on these individual functions (Cappelli et al., 2022),
286 but this complementarity was not realised when combining multiple functions.

287 Here, we focussed on the fast-slow resource use axis as a key element of functional composition
288 (which was well represented by the usage of SLA as a unique trait; Table S1). However, other functional
289 traits or axes, such as size (Díaz et al., 2016), dispersal and root strategies (Bergmann et al., 2020) also

290 determine overall functional composition. Future work manipulating these elements of functional
291 composition in combination with diversity would be very valuable.

292

293 ## Resource levels modulate functional diversity effects on ecosystem functioning

294

295 In addition to sown species richness, sown functional diversity was an important driver of
296 multifunctionality but its positive effect was dampened by N enrichment. This results is at odds with
297 reports of stronger (Weigelt et al., 2009) or consistent (Craven et al., 2016) diversity-productivity
298 relationship in response to increased resource supply. There are three main reasons why our results
299 may differ from these previous findings. Firstly, most other studies added multiple nutrients, which
300 increased total resource levels, whereas we added nitrogen only which may have led to an unbalanced
301 nutrient stoichiometry and therefore a reduction in complementarity (Cardinale et al., 2009).
302 Secondly, N addition may have a larger effect on the diversity-*multifunctionality* relationship than on
303 the diversity-*productivity* relationships examined in previous studies. Consistent with this, our study
304 also found that the effect of diversity on aboveground productivity was independent of fertilisation
305 (Figure 3), and that the interaction between N and either species richness or functional diversity was
306 inconsistent across individual functions. Further, a study on soil multifunctionality (Eisenhauer et al.,
307 2018), also showed that the positive diversity effect on multifunctionality was weaker under N
308 enrichment. Finally, we only found that N modified the effect of functional diversity, not of species
309 richness, and it may be that N addition is more likely to reduce effects of fast-slow functional diversity
310 than of species richness because the fast slow continuum is more closely linked to resource use.
311 Overall, our results show that N addition only increases functioning in low diversity communities while
312 adding N to functionally diverse communities would not further increase multifunctionality. However,
313 high diversity, unfertilised communities still delivered higher multifunctionality than low diversity,

314 fertilised communities (0.624 and 0.588 respectively), suggesting low input, high diversity grasslands
315 could deliver high overall multi-functioning relative to intensive systems.

316 Foliar fungal pathogen removal also reduced diversity-multifunctionality relationships and modified
317 the diversity effect on individual functions. Previous studies have shown that specialist soil pathogens
318 can drive diversity-productivity relationships by reducing biomass particularly at low diversity levels
319 (Maron et al., 2011; Schnitzer et al., 2011). In our experiment, reducing foliar fungal pathogen
320 abundance reduced multifunctionality in functionally diverse communities, suggesting that fungal
321 endophytes present in diverse plant communities may boost certain functions. Fungicide application
322 might alter the composition of pathogen communities by removing specialists (Cappelli et al., 2020),
323 but it might also reduce the abundance of mutualists (fungal endophytes, Karlsson et al., 2014; Ayesha
324 et al., 2021), particularly in diverse plant communities. A high diversity of bacterial leaf endophytes
325 has been shown to drive effects of tree diversity on ecosystem functioning (Laforest-Lapointe et al.,
326 2017), and fungal endophyte diversity might therefore also be important. However, the interaction
327 between fungicide and diversity was sensitive to the inclusion of pathogen damage in the
328 multifunctionality measure, even though functional diversity and fungicide application did not interact
329 to affect pathogen damage itself, meaning the effect of pathogen removal on the diversity-
330 multifunctionality relationship should be treated with caution. Nevertheless, our results indicate that
331 fungal endophyte communities may deserve more attention as potential drivers of diversity-
332 multifunctionality relationships.

333

334 Both dominant and rare species increase multifunctionality

335

336 Multifunctionality was maximised at high levels of sown functional diversity but was reduced by high
337 levels of abundance weighted functional diversity. These contrasting effects of non-abundance and
338 abundance weighted functional diversity mean that multifunctionality was highest when communities

339 became dominated by one or a few functionally similar species, but still retained some distinct rare
340 species (relatively low abundance weighted functional diversity, combined with high sown functional
341 diversity; Fig. 4). The negative effects of abundance weighted functional diversity mean that
342 multifunctionality was maximised when the dominants in a community were functionally similar,
343 which suggests that mass-ratio effects were important for increasing multifunctionality, this is
344 analogous to a multifunctional selection effect where species with certain traits are key for providing
345 multifunctionality. Studies in biocrust systems (Maestre et al., 2012) and global drylands (Le Bagousse-
346 Pinguet et al., 2019) have also shown that multifunctionality was maximised when communities were
347 dominated by functionally similar species, which were well adapted to the environmental conditions.
348 In our experiment, communities dominated by high SLA species could enhance multifunctionality
349 (CWM SLA had the strongest effects on multifunctionality in our study) by enhancing functions related
350 to fast biogeochemical cycling (herbivory, pathogen infection, see Figure 3). At the same time some
351 individual slow species were also able to provide many functions. On the other hand, the increase in
352 multifunctionality with non-abundance weighted functional diversity emphasises the importance of
353 diversity and functionally unique species in driving multifunctionality (McLaren & Turkington, 2010;
354 Vogel et al., 2019). Our analysis of individual species effects on multifunctionality indicated that fast
355 species tended to be more complementary in the functions they drove, but this result indicates that
356 fast and slow species are also complementary and provide different functions from each other. These
357 findings are also in accordance with a body of literature on the importance of locally rare species for
358 the provision of multiple ecosystem functions (Lyons et al., 2005; Mouillot et al., 2013; Soliveres,
359 Manning, et al., 2016). In our experiment the presence of low SLA species led to an increase in
360 belowground biomass (Figure 3) and soil respiration (on plots without fungicide), perhaps indicating
361 increased microbial activity in slow growing communities (Delgado-Baquerizo et al., 2018). The
362 addition of a few rare slow species could therefore have increased the levels of certain soil functions
363 and could have boosted multifunctionality in otherwise fast dominated communities (Le Bagousse-
364 Pinguet et al., 2021).

Conclusions

Our results shed light on the context dependence of diversity effects on multifunctionality. The most important driver of context dependency in our study was the functional trait composition of the species pool (whether communities were assembled with fast or slow species). Our findings show that shifts in fast-slow functional composition due to global change will not just alter ecosystem functions 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 fast-slow functional composition and others change diversity. In addition, they suggest that managing functional composition can buffer the impacts of other global change drivers on ecosystem functioning and biodiversity-functioning relationships. For the functions considered here, the optimal community for multifunctionality contained several different fast species at high abundance and some functionally distinct slow species at low abundance. However, the optimal community is likely to differ for other sets of functions or environmental conditions, and considering which functions should be maximised will be important to define optimal functional composition and diversity for a given scenario. 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 change factors.

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 (Pichon et al., 2020). The site had been unfertilised for at least 10 years before the start of the experiment. The soil is characterized as 0.7 to 1 m deep brown earth (Cambisol), according to the Geoportal of the Canton Bern (http://www.geo.apps.be.ch). We measured total soil N and 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 original grassland was dominated by *Dactylis glomerata, Lolium multiflorum, Crepis biennis, Plantago lanceolata* and *Trifolium sp*. The area was cleared from vegetation and ploughed before the establishment of experimental plots.

The whole experiment consisted of 216 plots of 2 m × 2 m separated from one another by a 1 m 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 S11). We divided the species into two pools corresponding to different resource economic strategies (Wright et al., 2004), 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 15 four species, 15 eight species and 4 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 (54 in total) received the four combinations of N enrichment and fungicide application, for a total of 216 plots. 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 (Blüthgen et al., 2012). Urea addition had no significant effect on soil pH measured in autumn 2017 (Table S12). 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). The same amount of water was applied to the untreated plots at the same time. 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 (Cappelli et al., 2020). The experiment was weeded three times a year to maintain the diversity levels. Realised species richness values were very close to sown values (Pearson’s correlation = 0.997). All plots were mown twice a year, in mid-June and mid-August, which corresponds to intermediate, to extensive, grassland management in the region.

434 Further details about the site characteristics and experimental setup of the PaNDiv Experiment can be
435 found under Pichon et al. (2020).

436

437 Measurements on the plant community

438

439 Plant traits

440 We measured specific leaf area (SLA = surface/dry weight, $m^2\ kg^{-1}$) in August 2017 and in June and
441 August 2018, by taking one leaf from each of five individuals in all 80 monoculture plots. We sampled
442 treatment-specific monocultures to include effects of nitrogen addition and pathogen removal on trait
443 expression. We rehydrated the leaves and measured leaf surface, and dry weight according to the
444 protocol of Garnier et al. (2001). The SLA per species is the average of the trait values across the five
445 samples and across the three sampling dates and therefore averages across seasonal variation. We
446 used only SLA to calculate functional diversity and composition as our experimental design involved
447 manipulating the mean and variation in SLA within communities (species were defined as fast and
448 slow based on SLA). However, we also tested how well SLA represented the overall resource
449 economics spectrum by using a combined strategy index based on SLA, LDMC and nitrogen
450 concentration in plant aboveground biomass, see Table S1.

451 Functional composition (CWM SLA)

452 We visually estimated the cover of each plant species (target species and all weeds together) before
453 mowing. We calculated the community weighted mean (CWM) SLA per plot using the relative cover
454 estimates averaged across 2017 and 2018: CWM = $\sum p_i * x_i$; with p_i the relative abundance of the
455 species i and x_i the trait value of i in each monoculture of the same treatment (i.e. nitrogen and
456 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 (de Bello et al., 2016). This represents the initial (sown) functional diversity of the plots when species were at equal abundance. The SLA values used were the monoculture traits of the same treatment, 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, using cover values from 2017 and 2018 as abundance measures. The two indices were highly correlated (see Figure S5), partly due to coding the monocultures as 0. To avoid issues of multicollinearity, which could bias regression coefficients, we therefore analysed the effect of MPD and MPDw in two separate models (Table S10). Model output calculated with non-abundance weighted MPD, but excluding the species that were not recorded at least once between 2017 and 2018 did not differ from the main model output (see Table S4).

Ecosystem functions

Selection of functions

We measured ten functions related to resource and energy transfer both above and belowground: above and belowground biomass production, foliar fungal pathogen infection, insect herbivore damage, N and P uptake, soil respiration, C storage, and beta-glucosidase and phosphatase activity. Half the functions were characteristic of aboveground processes (aboveground biomass, pathogens, herbivores, N and P uptake), and half of belowground processes (belowground biomass, soil respiration, C storage, beta-glucosidase, phosphatase). The functions were related to primary

481 production (above and belowground biomass), to secondary production (pathogens, herbivores), and
482 to microbial activity (soil respiration, beta-glucosidase, phosphatase). The functions included
483 measures of nutrient cycling (N and P uptake, phosphatase) and C cycling (soil respiration, C storage,
484 beta-glucosidase). In addition, we aimed to measure fluxes not stocks, as we were interested in the
485 transfer rate within the ecosystem (Barnes et al., 2018) and we consider high rates of transfer and low
486 loss rates to indicate high functioning. We therefore calculated N and P uptake instead of soil available
487 N and P stocks. Two functions could be considered as stocks, i.e. belowground biomass and C storage,
488 but they can also be seen as fluxes over several years, as they measure the difference in C stock and
489 in belowground biomass between the end and the start of the experiment. Pathogen and herbivore
490 damage are measures of energy transfer to higher trophic levels and high levels of these therefore
491 indicate high functioning because they mean that energy is transferred more rapidly between trophic
492 levels and that secondary production is higher (Meyer et al., 2015; Barnes et al., 2018; Manning et al.,
493 2018; Wang et al., 2019; Barnes et al., 2020; Buzhdygan et al., 2020). Soil respiration can be considered
494 either as an indicator of high functioning (increased soil activity) or as an indicator of low functioning
495 (C loss from the system). Due to the positive correlation between respiration and plant biomass (Figure
496 S8), we chose to consider soil respiration as indicating high functioning. However, the results were not
497 altered when we reversed respiration values to consider high respiration to be low functioning, see
498 Table S14. Our results are therefore robust to the uncertainty in how to consider soil respiration.

499 We also insured that all functions were not strongly correlated with each other and that no one
500 function strongly correlated with multifunctionality (Fig. S6). The functions described in this study
501 were all measured between June 2017 and autumn 2018. For each function measured more than
502 once, we used the mean value per plot over the whole period (see Table S9).

503

504 Aboveground biomass

505 We collected aboveground biomass twice per year, before the mowing. The samples were taken by
506 clipping plant material to 5cm above ground level, in two quadrats of 20 cm × 50 cm located in the
507 centre of each plot. We weighed the biomass after 2 days of drying at 65°C. The plot target biomass
508 production (i.e. of the sown species without weeds) was calculated by multiplying the percentage
509 cover of weeds by the total biomass and subtracting this estimated weed biomass from the total
510 weight. To determine if the estimation was accurate, we sorted the biomass per species in June 2017
511 for all plots of one block. The sorted target biomass (without the weeds) was highly correlated with
512 the estimated target biomass (R^2 = 0.994, Figure S7). The mean weed percentage was around five
513 percent and therefore removing the weeds made little difference to the total biomass (Pichon et al.,
514 2020).

515 Herbivory

516 Herbivory was assessed in May and August 2018. Five individuals of each target species were randomly
517 selected from each plot and five leaves per individual were assessed for damage. Leaves were selected
518 from the middle tier of each individual, and juvenile and senescent leaves were excluded. Damage
519 was characterised by the type of herbivory; chewing, sucking, leaf mining and rasping damage based
520 on the methods of Loranger et al. (2014). In this study, we calculated the community weighted mean
521 total damage using the sum of damage types per leaf, per species, weighted by the cover of the
522 particular species.

523 Pathogens

524 Fungal infection was measured per species per plot once in October 2017 and twice in 2018, in July
525 and October. Ten randomly chosen individuals in the central square meter of the plots were visually
526 screened for signs of infection and the percentage of infected individuals was recorded. If there were
527 less than 10 individuals in the central square meter, individuals in the rest of the plot were screened.
528 If there were fewer individuals, the percentage of infected individuals was calculated based on all

individuals present. The species level infection and the percentage cover data were used to calculate a community weighted mean of fungal infection per plot and season.

Plant N and P uptake

We calculated plant N and P uptake using total biomass and soil available N and P content. The biomass collected in June and August 2018 was homogenised per plot and we ground a minimum of 5g per plot with a cyclone mill to obtain a fine powder. We then used near infrared reflectance spectroscopy (NIRS) analyses to estimate biomass N and P content using calibrations by Kleinebecker et al. (2011). Soil samples were collected five times in 2018 using two homogenised cores per plot. Soil NO_3^-, NH_4^+ and PO_4^{3-} were extracted with $CaCl_2$ and analysed using a Continuous Flow Optical-Absorption Spectrometer (CF-OAP; model Skalar Scan+; Skalar Analytical, Breda, The Netherlands). The plant N and P uptake are the mean plant N and P content divided by the mean available N (NO_3^- plus NH_4^+) and available P (PO_4^{3-}), respectively.

Enzymatic activity

The activity of two enzymes related to carbon and phosphorus cycling, β-glucosidase and phosphatase, was measured in autumn 2017 and in April, May, July and August 2018. These functions give an estimate of soil microbial activity, and β-glucosidase has been shown to be a good soil health indicator (Turner et al., 2002). We took two soil samples per plot of 1.5 cm diameter to 20 cm depth. The fresh samples were homogenised and sieved through 2mm meshes. In each sample, we measured the β-glucosidase and phosphatase enzymatic activities, following the protocol of Tabatabai (1983). For the analyses presented here, we calculated the mean value of each enzymatic activity for all the periods sampled.

Belowground biomass

Root biomass was measured once in autumn 2017. We took two cores per plot to 20 cm depth (440 cm^3 of soil). We homogenised the two samples and used a subset of 40 g fresh soil in which we sorted out the roots. The samples were washed in 200 µm sieves and the roots sorted out with tweezers. We

554 dried the roots at 65°C for 48 hours. We estimated soil bulk density by weighing 40g of soil from the
555 same plot before and after drying for 24 hours at 105°C. Bulk density did not differ between the
556 treatments (Table S13). The final belowground biomass per plot is the weight of roots per g of dry soil.

557 Respiration

558 We measured overall soil respiration five times during 2018. We placed one PVC ring per plot at least
559 a week before taking the measurements. The vegetation was clipped before starting the measures
560 without disturbing the soil. We took two measures per plot and repeated the measures in case of large
561 difference between the respiration rates. We took the measurements using a soil CO_2 flux chamber
562 (6400-09) attached to a LI-6400XT (Li-Cor Inc.). Soil respiration varies during the day and between
563 days. To minimise this variation, we took the measurements starting at 10 am and finishing the latest
564 at 2 pm, as this time span is expected to provide rates representative of the mean daily respiration
565 (Mielnick & Dugas, 2000; Castillo-Monroy et al., 2011). We measured one block per day (54 plots),
566 avoided humid days and kept the measurement days as close to each other as possible (max 6 days
567 for one sampling session). The final soil respiration measure is the mean measure per plot.

568 Carbon storage

569 We measured soil carbon concentration on soil samples of 440 cm^3, taken to 25 cm depth in autumn
570 2017. We took two samples per plot, homogenised them and removed stones and living material
571 (roots, fauna). We weighed the samples before and after drying at 65°C for 48 hours. To calculate C
572 storage, we compared the 2017 samples to soil samples taken in autumn 2015 before the start of the
573 experiment. In 2015, we took 5 soil samples per plot from a subset of 89 plots distributed across the
574 field. As the field had just been ploughed and homogenised there was relatively little variation
575 between adjacent plots and we estimate soil C concentrations for all plots using kriging (package geoR,
576 estimating sill and range of the data variogram using the variofit function). Analyses of soil total C were
577 conducted in a CNS Analyser at the Institute of Geography of the University of Bern. The C storage per
578 plot is the difference between the percentage carbon in autumn 2017 and in autumn 2015.

Analyses

Multifunctionality

The functions we measured are all related to fast cycling and low resource losses, and thus we considered all to be positive when calculating our "ecosystem function multifunctionality" metrics (Manning et al., 2018). We used a multiple threshold approach because, unlike the averaging approach, it does not assume substitutability of functions and can distinguish cases where functions are at intermediate values from cases where some functions are high and other low (see Byrnes et al., 2014; Manning et al., 2018). We transformed each function in order to fit more closely to a normal distribution, which means functions contribute more equally to multifunctionality (see Table S9 and Figure S6) and standardised the data around the mean to have all functions on a common scale (using the formula x-mean/sd). We then calculated multifunctionality using thresholds from 0.5 to 0.8 with an interval of 0.05 (Le Bagousse-Pinguet et al., 2019). We excluded very large (>0.8) or very small (<0.5) thresholds as multifunctionality values tend to have small ranges at the extremes (i.e. most plots either have 0 multifunctionality or maximum multifunctionality). The thresholds were defined relative to the mean of the five highest values of each function, in order to reduce the influence of outliers (Zavaleta et al., 2010). Multifunctionality was the proportion of functions reaching this threshold per plot, calculated using the multidiv function (available at https://github.com/eric-allan/multidiversity).

We then tested the effects of our experimental treatments on multifunctionality: N enrichment, fungicide, species richness, SLA (as a continuous measure of functional composition), MPD, and their interaction. We used sown species richness as our main measure, following recommendations and common practice in analysing biodiversity experiment data (Schmid et al., 2002) (however, using realised richness resulted in very similar results, see Table S4). However, we used realised CWM SLA

604 because functional composition should be important if mass ratio effects (Grime, 1998) dominate and
605 weighting trait values by abundance better reflects the theoretical expectation. We explored both
606 realised and abundance weighted effects of functional diversity (MPD in SLA), see above. We did not
607 test for SLA x MPD interactions, as the two factors are not fully orthogonal in the experimental design
608 (MPD is inevitably maximal at intermediate SLA, see Figure S5). We allowed all possible interactions
609 between the other experimental treatments.

610 The effects of these different factors can vary according to the threshold used to calculate
611 multifunctionality. Previous approaches have tested how diversity effects vary depending on the
612 threshold (Byrnes et al., 2014) but visualising how multiple factors vary with multifunctionality
613 thresholds is more challenging. We therefore used a new approach to test which treatment effects
614 were consistent across thresholds and which depended on the threshold level. To do this, we first
615 calculated multifunctionality per plot at seven different thresholds: 50, 55, 60, 65, 70, 75 and 80%
616 thresholds. We then analysed all the multifunctionality values using linear mixed effects models,
617 fitting all the treatment variables described above as fixed effects. We included *plot number*, *block*
618 and *species combination* (random assemblages within diversity and functional composition levels) as
619 random terms. We also included threshold as a fixed continuous term which could interact with the
620 treatment variables, and random slopes for the effect of threshold on multifunctionality in each plot,
621 which corrects for additional autocorrelation between multifunctionality values measured in the same
622 plot. Our data met the model assumptions of homogeneity of variance and normal distribution of
623 residuals. All explanatory variables were scaled and centred to a mean of 0 and standard deviation of
624 1, so that their effect sizes are comparable. Fitting all multifunctionality measures in the same model
625 is a similar approach to that used in Soliveres, van der Plas, et al. (2016) but extended to
626 multifunctionality calculated at different thresholds. Using this method, we could estimate which
627 effects were significant across all thresholds, and which ones changed continuously as the threshold
628 was increased. We then estimated the overall effect of each treatment and interaction across the
629 thresholds and calculated a confidence interval around the effect. Confidence intervals were

630 calculated using a script from Ben Bolker (available at https://bbolker.github.io/mixedmodels-
631 misc/glmmFAQ.html#predictions-andor-confidence-or-prediction-intervals-on-predictions).
632 Since any multifunctionality metric depends on the number and identity of functions, which makes
633 generalisation across studies challenging (Bradford et al., 2014; Meyer et al., 2018; Giling et al., 2019;
634 Jing et al., 2020), all functions were also analysed separately using linear mixed effect models with the
635 same fixed and random terms.

636 Monocultures all get an arbitrary MPD of 0 causing some correlation between MPD and species
637 richness (Figure S5). To ensure that the effect of diversity was not driven only by the difference
638 between monocultures and polycultures, we did an additional analysis in which we added a binary
639 variable for the monoculture/not monoculture contrast. Results using this approach were qualitatively
640 similar to those presented in the main text (Table S15). Replacing the effect of sown by realised species
641 richness gave similar results (Table S4).

642 All analyses were conducted in R using the package lme4 (Bates et al., 2015; R. Core Team, 2019). We
643 simplified full models by dropping terms that did not significantly improve the overall model fit using
644 likelihood-ratios. All models had conditional R-squared higher than 0.87.

645

646 Effects of individual species on functions

647 To better understand the interaction between species richness and SLA, we conducted an additional
648 analysis testing if individual species from the same functional group (slow or fast) were similar in the
649 set of functions they increased or decreased, and if there were trade-offs between the functions
650 supplied by different species of the same group. In short, we followed a six-step approach: i) extract
651 the functional effect of each species using linear models (Hector & Bagchi, 2007; Isbell et al., 2011), ii)
652 calculate the similarity in these functional effects in all possible 4-species assemblages, iii) repeat step
653 ii for both positive and negative functional effects, iv) analyse if that similarity in functional effects
654 changes depending on the mean (and variation in) SLA of the 4-species assemblages. If low-SLA

assemblages show higher similarity, this means that slow-growing species are more functionally redundant than fast-growing species. Finally, two more steps were performed to analyse the likelihood that species with similar functional (slow-growing) trait values showed stronger functional trade-offs: steps v) take all pairwise species combinations and quantify the number of times that one of the species in the pair have a functional effect of opposite sign than the other species in the pair (e.g., one has a positive effect on biomass production and the other a negative effect on the same function), and vi) relate the number of functional trade-offs (as quantified in step v) to the mean and difference in SLA between the two species in the pair. If the number of trade-offs was higher in pairs of species with low SLA, then we can conclude than slow-growing species are more likely to have opposite functional effects than may cancel each other out.

First step: we tested the effect of each species on each function, following approaches in Hector & Bagchi (2007) and Isbell et al. (2011). To do so, we first extracted the effect of species on each function. We fitted two separate models, one with the presence and one with the abundance (relative cover) of each of the 20 species, using the following model structure:

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

Non-significant effects were set to 0 (Table S7 and Table S8).

We then calculated (step ii) how similar different sets of species were in the functions they affected in order to test how many functions different communities of fast vs. slow species would be expected to provide. We calculated the similarity in functional effects for all possible combinations of four species. We chose four species as this allows us to test the effect of different species combinations, varying in mean and variance of their functional traits, and because it corresponds to one of our diversity treatments. However, we also tested combinations of 3 and 6 species, which did not change the results (Table S6). We calculated the similarity in both positive and negative functional effects for all combinations of four species (step iii), and for effects of species presence and abundance. We used the CqN similarity index (Jost et al., 2011), which is a common measure of beta diversity and allows a

680 calculation of dissimilarity among any number of communities. We weighted the effects to give more
681 importance to larger functional effects by using a q value of 2. This corresponds to the multicommunity
682 extension of the Morisita-Horn index.

683 We then calculated the mean and variance in SLA between all sets of four species and regressed them
684 against the dissimilarity in functional effects between the four species (CqN; step iv). We were
685 principally interested in the effect of mean SLA, to determine if sets of species with higher mean SLA
686 are more different in the functions they provide. However, we included the variance in SLA between
687 the species to account for the fact that a set of four species with intermediate mean SLA could either
688 be composed of low and high SLA (slow and fast) species or a set of species all with intermediate SLA.
689 To test if the effects were significant, we randomly shuffled the SLA values between the species and
690 recalculated the relationships between mean and variance in SLA and functional dissimilarity 1000
691 times. We then tested whether the observed slopes between mean SLA and variance in SLA and
692 functional dissimilarity (CqN) lay outside the 2.5 and 97.5% quantiles of the random slopes. These
693 analyses were repeated for the positive and negative effects and effects of species presence and
694 abundance, see Table S6.

695 Then, we tested for trade-offs between the functions supplied by different species and whether this
696 was related to their SLA (steps v and vi). For each pair of species, we summed the number of significant
697 functional effects that were opposing (e.g. one species has a positive effect on a given function while
698 the other species has a negative effect). We related the number of trade-offs to the mean and
699 difference in SLA for the species pair, to test if pairs of low SLA (slow) species tend to have more
700 opposing effects. We again randomly shuffled the SLA values between the species, recalculated the
701 relationships 1000 times and tested whether the observed slopes lay outside the 2.5 and 97.5%
702 quantiles of the random slopes, see Table S6.

703

704 Number and identity of functions

705 In addition to the threshold chosen, multifunctionality values depend on the number and identity of
706 functions included, which makes generalisation across studies challenging (Bradford et al., 2014;
707 Meyer et al., 2018; Giling et al., 2019; Jing et al., 2020). To test the sensitivity of our results to the
708 number and identity of functions, we calculated multifunctionality for all possible combinations of
709 functions between two and ten functions (1013 combinations), and for four thresholds from 0.5 to 0.8
710 (4052 multifunctionality measures). We extracted the effects of our treatments and their interactions
711 from a linear mixed effect model fitted to each multifunctionality measure. In order to correct for the
712 uncertainty in each estimate, we weighted each estimate by the inverse of its standard error. We then
713 calculated an overall mean and confidence interval for multifunctionality per threshold depending on
714 the number of functions included. The number of functions included did not significantly change the
715 mean effect of our variables on multifunctionality, except for the interaction between SLA and species
716 richness at the 50% threshold, which strengthened as more functions were considered. The variation
717 around the mean got larger with a decreasing number of functions, going from positive to negative
718 depending on the functions included (Figure S2 and Figure S3). This variation was driven more by
719 variation in the identity rather than in the number of functions included (Figure S2).

Acknowledgements

We would like to thank Pete Manning and Jasper van Ruijven for very helpful comments on earlier drafts of the manuscript. We would also like to thank Mervi Laitinen and Marlise Zimmermann, the technicians working with us on the PaNDiv Experiment, as well as the large team of helpers on the field and in the lab. This study was supported by funding of the Swiss National Science Foundation (31003A_160212). SS was supported by the Spanish Government under a Ramón y Cajal contract (RYC-2016- 20604).

Competing interests

The authors declare that they have no competing interests.

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.

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