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13 **Biodiversity promotes ecosystem functioning despite environmental**
14 **change**

15

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79

80 **Abstract**

81 Three decades of research have demonstrated that biodiversity can promote the
82 functioning of ecosystems. Yet, it is unclear whether the positive effects of
83 biodiversity on ecosystem functioning will persist under various types of global
84 environmental change drivers. We conducted a meta-analysis of 46 factorial
85 experiments manipulating both species richness and the environment to test how
86 global change drivers (i.e. warming, drought, nutrient addition or CO₂ enrichment)
87 modulated the effect of biodiversity on multiple ecosystem functions across three
88 taxonomic groups (microbes, phytoplankton and plants). We found that biodiversity
89 increased ecosystem functioning in both ambient and manipulated environments, but
90 often not to the same degree. In particular, biodiversity effects on ecosystem
91 functioning were larger in stressful environments induced by global change drivers,
92 indicating that high-diversity communities were more resistant to environmental
93 change. Using a subset of studies, we also found that the positive effects of
94 biodiversity were mainly driven by interspecific complementarity, and that these

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95 effects increased over time in both ambient and manipulated environments. Our
96 findings support biodiversity conservation as a key strategy for sustainable ecosystem
97 management in the face of global environmental change.

98

99 **Introduction**

100 Global environmental changes are reshaping the structure and processes of
101 ecosystems, potentially threatening the functioning and services that ecosystems
102 provide to human society (Zhou *et al.* 2012; Song *et al.* 2019; Jiang *et al.* 2020). In
103 the face of environmental change, biodiversity is a key factor maintaining (Naeem *et al.*
104 *et al.* 2009; Cardinale *et al.* 2012; Hooper *et al.* 2012) and buffering ecosystem
105 functioning (Yachi & Loreau 1999; Hisano *et al.* 2018; Pires *et al.* 2018). However,
106 environmental change also alters species dynamics and interactions, causing rapid
107 changes in biodiversity at various spatial scales (Vellend *et al.* 2013; Dornelas *et al.*
108 2014; Urban 2015; Blowes *et al.* 2019; IPBES 2019). Therefore, changing
109 environments can affect ecosystem functioning both directly, via altering rates of
110 ecosystem processes (Spaak *et al.* 2017), and indirectly, via changing biodiversity
111 (Hautier *et al.* 2015; Giling *et al.* 2019). Furthermore, environmental changes can
112 interact with biodiversity in regulating ecosystem functioning, such that the effects of
113 biodiversity on ecosystem functioning may be enhanced or weakened under altered
114 environmental conditions, even if biodiversity itself does not change (Eisenhauer *et al.*
115 2019; Benkwitt *et al.* 2020). However, the potential interactions between
116 environmental changes and biodiversity are much less understood compared with the
117 direct and indirect effects of environmental change on ecosystems, leaving it unclear
118 whether the positive effects of biodiversity will persist in future environments
119 impacted by global change drivers (De Laender *et al.* 2016).

120 While existing biodiversity experiments have mostly manipulated species
121 richness under ambient environmental conditions, a growing number of experiments
122 examine how environmental change (or global change drivers) may alter the effects of
123 biodiversity on ecosystem functioning across different taxonomic groups, such as
124 terrestrial plants, microbes, or phytoplankton (Hautier *et al.* 2014; Craven *et al.* 2016;
125 García *et al.* 2018; Bestion *et al.* 2020). Using factorial designs in which biodiversity
126 and environmental manipulations were combined, these studies revealed strengthened
127 (Reich *et al.* 2001; Steudel *et al.* 2011; García *et al.* 2018), constant (Thakur *et al.*
128 2015; Eisenhauer *et al.* 2018), or weakened (De Boeck *et al.* 2008) biodiversity

129 effects impacted by various types of global change drivers. Such mixed results may be
130 explained by the context dependency of biodiversity effects, which vary in strength
131 across different types and magnitudes of environmental manipulations, different
132 taxonomic groups, or different aspects of ecosystem functions being measured. For
133 instance, experimental warming in microbial and phytoplankton communities has
134 been found to either dampen or enhance ecosystem productivity (Yvon-Durocher *et al.*
135 2015; García *et al.* 2018; Tabi *et al.* 2019; Bestion *et al.* 2020). Currently, we lack a
136 synthetic understanding of both how different types of environmental change may
137 influence biodiversity effects on ecosystem functioning, and how these interactive
138 effects depend on the experimental context (e.g. taxonomic group, experimental time,
139 etc.) (Eisenhauer *et al.* 2019).

140 One hypothesis about the interactive effects of biodiversity and environmental
141 change is that global change drivers alter the strength and even the type of
142 interspecific interactions (He *et al.* 2013; Hoek *et al.* 2016; Baert *et al.* 2018), which
143 underlie the effects of biodiversity on ecosystem functioning. Two classes of
144 processes have been proposed to explain biodiversity effects, namely
145 complementarity (CE) and selection (SE) effects (Loreau & Hector 2001; Tilman *et al.*
146 2014). CE arises from interspecific niche partitioning or facilitation, and SE arises
147 from a disproportionately high contribution of one or few species to ecosystem
148 functioning. Many studies suggest that the strength and type of species interactions
149 may shift as the environment changes (Maestre *et al.* 2009; He *et al.* 2013; Hoek *et al.*
150 2016; Olsen *et al.* 2016). In particular, the stress-gradient hypothesis predicts that
151 species interactions can switch from higher competition in favorable environments to
152 lower competition or even facilitation in stressful environments (Bertness & Callaway
153 1994; He *et al.* 2013; Hoek *et al.* 2016; but see Metz & Tielbörger 2016). Such a
154 switch may enhance CE and hence overall biodiversity effects in stressful
155 environments. On the other hand, SE may also increase with environmental stress,
156 because more diverse communities may have a higher probability of including stress-
157 tolerant species and such species may be expected to outcompete stress-intolerant
158 ones and dominate in stressful environments (Maestre *et al.* 2009; Baert *et al.* 2018;
159 Bestion *et al.* 2020). Thus, stress intensity induced by environmental changes may
160 provide a useful indicator to predict the influence of environmental changes on the
161 magnitude of biodiversity effects on ecosystem functioning (Baert *et al.* 2018).

162 Previous experiments also suggested that biodiversity effects, particularly CE,
163 increased over time (Cardinale *et al.* 2007; Reich *et al.* 2012; Huang *et al.* 2018).
164 Such enhanced biodiversity effects were at least in part due to character displacement
165 during the succession of experimental communities (Zuppinger-Dingley *et al.* 2014;
166 van Moorsel *et al.* 2018). In stressful environments, interspecific facilitation and the
167 compensation of more resistant species may allow high-diversity communities to cope
168 better with stress through time and maintain ecosystem functions at higher levels than
169 less diverse communities (Hisano *et al.* 2018; Wright *et al.* 2021). In such cases, the
170 influence of environmental changes on biodiversity effects may strengthen over time,
171 but the magnitude of these effects is uncertain.

172 In this study, we performed a meta-analysis of 46 factorial experiments in which
173 species richness was manipulated together with at least one of four types of global
174 change drivers (namely warming, drought, nutrient addition or CO₂ enrichment) to
175 systematically assess how environmental change may modify biodiversity effects on
176 ecosystem functioning across three taxonomic groups (namely microbes,
177 phytoplankton, and terrestrial plants [plants for short]). These four global change
178 drivers capture common anthropogenic impacts on ecosystems and are most
179 frequently investigated in the literature (e.g. Hooper *et al.* 2012; Song *et al.* 2019).
180 That said, only warming could be assessed in all three taxonomic groups (i.e.
181 microbes, phytoplankton, and plants, with 4, 3, and 6 studies, respectively), and
182 drought, nutrient and CO₂ enrichment were only assessed in plants (with 14, 11, and 8
183 studies, respectively). Using these data, we asked two questions: (i) does biodiversity
184 promote ecosystem functioning under both ambient and manipulated environmental
185 conditions? (ii) do global change drivers influence the magnitude of biodiversity
186 effects, and do such influences vary through time and depend on the stress intensity
187 induced by environmental changes? Our hypothesis is that biodiversity promotes
188 ecosystem functioning across a range of environmental conditions, but its effect size
189 can be modulated by global change drivers. In stressful environments, mixtures may
190 be less influenced than monocultures if CE increases with stress intensity as predicted
191 by the stress gradient hypothesis (Bertness & Callaway 1994), or if SE increases with
192 stress intensity due to the presence of stress-tolerant species (Baert *et al.* 2018;
193 Bestion *et al.* 2020). In such cases, biodiversity effects increase with stress intensity
194 (H₁ in Fig. 1). Otherwise, biodiversity effects can decrease with stress intensity if
195 mixtures are more sensitive to environmental stress (H₂ in Fig. 1). Finally,

196 biodiversity effects will not change with stress intensity if mixtures and monocultures
197 are similarly sensitive to environmental stress (H_0 in Fig. 1).

198

199 **Methods**

200 ***Data collection***

201 We searched the literature and extracted all factorial experiments that
202 manipulated species richness and at least one of the four focal types of global change
203 drivers, i.e. warming, drought, nutrient addition or CO₂ enrichment (see Appendix B:
204 Table B1 for search terms). We performed the search on February 17th 2020 in the
205 Web of Science and retrieved 2386 papers in total. We then selected studies using the
206 following criteria (See PRISMA diagram, Appendix B: Fig. B1): (i) the experiment
207 includes monocultures and mixtures under both ambient and manipulated
208 environmental conditions; (ii) the study provides measures of at least one ecosystem
209 function under different treatments. In total, 35 experimental studies were selected
210 based on our criteria, and we added 11 experimental studies from cross-referencing
211 that met our criteria (Appendix B: Table B7). This led to a total of 46 experimental
212 studies, including 7,582 experimental units (ranging from a culture dish to a field plot)
213 covering different taxonomic groups and types of global change drivers. Note that the
214 46 experimental studies were treated as independent in our meta-analysis, although
215 some of them came from the same site but involved different types of environmental
216 manipulations (e.g., BioCON experiment with nutrient addition or CO₂ enrichment;
217 Reich *et al.* 2001). This simplification was justified by a likelihood ratio test which
218 reported no significant difference between models including and excluding the non-
219 independence between studies (see Appendix A).

220 We categorized our dataset by taxonomic groups (microbes, phytoplankton, and
221 plants), types of global change drivers (warming, drought, nutrient addition, and CO₂
222 enrichment) and two categories of ecosystem functions (biomass production and
223 biogeochemical process) (Appendix B: Table B2; Chapin *et al.* 2011). In our study,
224 microbes referred to non-photosynthetic microorganisms, such as bacteria, fungi and
225 protozoans. Because only the warming treatment was found for microbes and
226 phytoplankton, we have in total six combinations of taxonomic groups and global
227 change drivers, i.e. warming in all three taxonomic groups, as well as drought,
228 nutrient and CO₂ enrichment in plants. The 46 studies included 3, 4, and 39
229 experimental studies on microbes, phytoplankton, and plants, respectively (Appendix

230 B: Table B7). For studies on plants, 10 studies were from pots in the greenhouse, and
231 29 studies were from field experiments. Experimental duration ranged from 6 to 40
232 days in microbial studies, from 7 to 19 days in phytoplankton studies, and from 1 to
233 15 years in plant studies. The highest species richness varied among studies on
234 microbes (6 ~ 24), phytoplankton (12 ~ 64), and plants (2 ~ 60). For each type of
235 global change drivers, we recorded the level(s) of experimental manipulation, e.g. the
236 degree of temperature increase, the proportion of water reduction, the type and
237 amount of nutrient added (e.g. N and NPK enrichment), and the amount of CO₂
238 enrichment. For warming treatments in microbes and phytoplankton, which usually
239 contained several temperature levels in addition to the ambient or long term-culture
240 temperature (as the control, e.g. 15°C in Pennekamp *et al.* 2018 and 20°C in García *et al.*
241 2018), we only used temperature levels above this control as warming treatments
242 and excluded data with cooling treatments.

243 Regarding the two categories of ecosystem functions, biomass production
244 captured the total biomass produced during a given period (e.g. grassland biomass
245 production within a year), which has been the most commonly used metric of
246 ecosystem functioning; biogeochemical processes captured soil characteristics (e.g.
247 the concentration of key elements or organic materials in the soil), soil microbial
248 functions (e.g. microbial biomass, microbial growth and abundance) and nutrient
249 cycling (e.g. ectoenzyme activity and organic phosphorus). We considered soil
250 microbial growth and abundance as functions, because soil microbial community
251 composition and activity play key roles in mediating biogeochemical cycling
252 (Cavicchioli *et al.* 2019) and have been used to indicate belowground secondary
253 productivity (Eisenhauer *et al.* 2018).

254

255 ***Biodiversity effects under ambient and manipulated environments***

256 We first quantified the net biodiversity effect (NBE) on ecosystem functioning
257 by calculating the bias-corrected estimation of the log response ratio (Koricheva *et al.*
258 2013; Lajeunesse 2015):

$$259 \quad NBE = \ln\left(\frac{\bar{X}_{mix}}{\bar{X}_{mono}}\right) + \frac{1}{2}\left(\frac{SD_{mix}^2}{n_{mix}\bar{X}_{mix}^2} - \frac{SD_{mono}^2}{n_{mono}\bar{X}_{mono}^2}\right) \quad (1)$$

260 where \bar{X}_{mix} , SD_{mix} , and n_{mix} represent the average, standard deviation, and sample
261 size (i.e. number of replicates) of ecosystem function, respectively, in mixtures at a
262 given biodiversity level. \bar{X}_{mono} , SD_{mono} , and n_{mono} represent similar metrics in

263 monocultures. A positive value of NBE indicates a higher ecosystem functioning in
 264 mixtures compared with that in monocultures, and vice versa. We calculated NBE
 265 under both ambient (NBE_A) and manipulated (NBE_M) environments, for each type
 266 and level of global change drivers, each taxonomic group, each ecosystem function,
 267 each level of species richness in mixtures, and each time point (if the experiment
 268 contained multiple observations). Overall, we obtained 1997 NBE values, including
 269 508, 74 and 146 pairs of NBE_A and NBE_M for the warming treatment in microbes,
 270 phytoplankton, and plants, respectively, and 170 for drought, 201 for nutrient addition
 271 and 136 for CO_2 enrichment in plants (see Appendix B: Table B1).

272 To quantify the influence of environmental manipulations (i.e. global change
 273 drivers) on biodiversity effects, we calculated the difference in biodiversity effects
 274 between ambient and manipulated environments (Lajeunesse 2011, 2015):

$$275 \quad \Delta NBE = NBE_M - NBE_A \quad (2)$$

276 where the subscripts A and M indicate ambient and manipulated environments,
 277 respectively. A positive value of ΔNBE indicates a higher biodiversity effect under
 278 the manipulated environment, and vice versa. The relative change in biodiversity
 279 effects induced by environmental manipulations can be derived by rescaling ΔNBE

$$280 \quad (\text{Hooper } et al. 2012): e^{\Delta NBE} - 1 = \frac{e^{NBE_M}}{e^{NBE_A}} - 1.$$

281 To understand the mechanisms underlying biodiversity effects, we used the
 282 additive partition by Loreau & Hector (2001) to derive the complementarity (CE) and
 283 selection effect (SE) on biomass production, based on the 12 studies with available
 284 raw data of monocultures (Appendix B: Table B7). We first calculated CE and SE for
 285 each mixture and then obtained the mean and standard deviation for each species
 286 richness level, each level of environmental manipulation and each experimental time
 287 point. For comparison among studies, we standardized CE and SE by the average
 288 value of ecosystem function in monocultures (Loreau & Hector 2001; Craven *et al.*
 289 2016). In doing so, we excluded monocultures with too low biomass (i.e. less than 2.5
 290 $g\ m^{-2}$ in grassland and 0.005 $mg\ ml^{-1}$ in microbes) following Reich *et al.* (2012), and
 291 omitted 100 (out of 1974) CE or SE values accordingly. Specifically, CE and SE were
 292 calculated as:

$$293 \quad CE = T_{sqrt} \left(\frac{N \cdot \overline{\Delta RY} \cdot \bar{X}_{mono}}{\bar{X}_{mono}} \right) \quad (3)$$

$$294 \quad SE = T_{sqrt} \left(\frac{N \cdot cov(\overline{\Delta RY}, \bar{X}_{mono})}{\bar{X}_{mono}} \right) \quad (4)$$

295 where N and ΔRY are the number of species in the mixture and difference between
 296 species' observed relative yield in the mixture and expected relative yield,
 297 respectively (Loreau & Hector 2001). $T_{sqrt}(x) = sign(x) * \sqrt{|x|}$ represented a
 298 square-rooted transformation while keeping the original sign, which has commonly
 299 been used in previous studies to reduce the influence of skewed distributions of CE
 300 and SE (e.g. Isbell *et al.* 2009). By definition, we can derive the link between different
 301 metrics: $e^{NBE} = \frac{N \cdot \overline{\Delta RY} \cdot \overline{X}_{mono}}{\overline{X}_{mono}} + \frac{N \cdot cov(\overline{\Delta RY}, \overline{X}_{mono})}{\overline{X}_{mono}} + 1$. We calculated CE and SE in both
 302 ambient (CE_A and SE_A) and manipulated environment (CE_M and SE_M). We then
 303 calculated the difference in CE or SE between the manipulated and ambient
 304 environments:

$$305 \qquad \qquad \qquad \Delta CE = CE_M - CE_A \qquad (5)$$

$$306 \qquad \qquad \qquad \Delta SE = SE_M - SE_A \qquad (6)$$

307 In addition to NBE, we also quantified biodiversity effects using the regression
 308 slope (BE_{Slope}) between ecosystem functioning and species richness (Baert *et al.*
 309 2018). We calculated the log-log regression slope between species richness and
 310 ecosystem functioning in both ambient (BE_{Slope_A}) and manipulated (BE_{Slope_M})
 311 environments, for each type and level of environmental manipulations, each
 312 taxonomic group, each ecosystem function, and each time point. We then derived
 313 their difference ($\Delta BE_{Slope} = BE_{Slope_M} - BE_{Slope_A}$) to characterize the response of
 314 biodiversity effects to global change drivers.

315 Both NBE and BE_{Slope} have been widely used for quantifying biodiversity effects
 316 in experimental studies and meta-analyses (e.g. Balvanera *et al.* 2006; Hooper *et al.*
 317 2012; Hautier *et al.* 2015; Duffy *et al.* 2017; Baert *et al.* 2018). NBE is more
 318 appropriate if ecosystem functioning saturates rapidly, e.g. from monocultures to two-
 319 species mixtures. In comparison, BE_{Slope} is more appropriate if ecosystem functioning
 320 exhibits a (quasi-) linear increase with species richness on log-log scales (Appendix
 321 A). As the realistic scenarios should occur along the continuum between a rapid
 322 saturating curve and a (quasi-) linear trend (Cardinale *et al.* 2012), our usage of both
 323 NBE and BE_{Slope} facilitates a comprehensive picture of biodiversity effects (see
 324 Appendix A for more detailed discussion). For brevity, we presented the results of
 325 NBE (and its additive partitions into CE and SE) in the main text and those of BE_{Slope}
 326 in the Appendix B.

327

328 ***Environmental stress intensity and biodiversity effects***

329 For a given taxonomic group and type of global change drivers, experimental
330 communities might respond to environmental manipulations differently across studies.
331 Following Steudel *et al.* (2012), we defined stress intensity as the response of
332 monoculture functions to environmental manipulations within each study:

333
$$\text{Stress intensity} = 1 - \left(\frac{\bar{X}_{mono_M}}{\bar{X}_{mono_A}} \right) \quad (7)$$

334 where \bar{X}_{mono_M} and \bar{X}_{mono_A} were average functioning of monocultures in manipulated
335 and ambient environments, respectively. A positive (negative) value of stress intensity
336 indicated that global change drivers decreased (increased) monoculture functions and
337 thus provided a stressful (favorable) condition. We calculated stress intensity for each
338 ecosystem function, level of environmental manipulation, and experimental time in
339 each study. We then derived average stress intensity through time over the
340 experimental duration, and we also tested the robustness of our results using the value
341 of stress intensity at the end of the experiment (Steudel *et al.* 2012).

342 We note that in our definition of stress intensity, the responses of mixtures were
343 not taken into account because they involved both the direct effects of global change
344 drivers and the potential buffering effects of biodiversity (Hisano *et al.* 2018), which
345 would have confounded our analysis on the relationship between stress intensity and
346 ΔNBE . However, in the appendix, we also quantified the responses of mixtures to
347 global change drivers, in order to examine the overall effects of environmental
348 changes.

349

350 ***Statistical analyses***

351 To derive pooled effect sizes for biodiversity effects (NBE, ΔNBE , BE_{slope} , and
352 $\Delta\text{BE}_{\text{slope}}$) and their 95% confidence intervals (CIs), we used three-level, hierarchical
353 mixed-effects models to account for the non-independence between biodiversity
354 effect sizes (Nakagawa & Santos 2012; see Appendix A for details). In these models,
355 samples were weighted by the inverse of their variance (see Appendix A for
356 derivation). Fixed-effects terms are type of global change drivers (α), ambient or
357 manipulated environmental conditions (τ), taxonomic group (β) and category of
358 ecosystem functions (γ). Random-effects terms are study (θ) and the combination of
359 species richness (η), level of environmental manipulation (λ), specific ecosystem

360 function (ψ) and experimental time (φ) nested within study (i.e. as a sub-study ID).

361 The models thus read:

$$362 \quad NBE \sim (\alpha\tau\beta\gamma)_{ijkl} + (\theta/\eta\lambda\psi\varphi)_{mnrst} + \epsilon_{ijklmnrst} \quad (8)$$

$$363 \quad \Delta NBE \sim (\alpha\beta\gamma)_{ijk} + (\theta/\eta\lambda\psi\varphi)_{mnrst} + \epsilon_{ijkmnrst} \quad (9)$$

$$364 \quad BE_{Slope} \sim (\alpha\tau\beta\gamma)_{ijkl} + (\theta/\lambda\psi\varphi)_{mnrst} + \epsilon_{ijklmnrst} \quad (10)$$

$$365 \quad \Delta BE_{Slope} \sim (\alpha\beta\gamma)_{ijk} + (\theta/\lambda\psi\varphi)_{mnrst} + \epsilon_{ijkmnrst} \quad (11)$$

366 Similarly, we estimated the average and 95% CIs of CE and SE and the differences
367 between ambient and manipulated environment (i.e. ΔCE and ΔSE) using the
368 following models:

$$369 \quad CE \text{ or } SE \sim (\alpha\beta\tau)_{ijk} + (\theta/\eta\lambda\varphi)_{mnrs} + \epsilon_{ijkmnrs} \quad (12)$$

$$370 \quad \Delta CE \text{ or } \Delta SE \sim (\alpha\beta)_{ij} + (\theta/\eta\lambda\varphi)_{mnrs} + \epsilon_{ijmnrs} \quad (13)$$

371 We used the function “`rma.mv()`” of the *metafor* package in R to estimate these effect
372 sizes (Viechtbauer 2010).

373 Between-study heterogeneity of effect sizes was evaluated using the extended I^2
374 and Cochran’s Q statistic (Nakagawa *et al.* 2012; see Appendix A for details). The
375 extended I^2 quantified the fraction of variation in effect size attributed to between-
376 study variance in multi-level models, and the Cochran’s Q statistic evaluated the
377 significance of between-study variance (Appendix A). Our analyses found high
378 between-study heterogeneity of effect sizes ($I^2 > 60\%$ and $p < 0.01$ for NBE, ΔNBE ,
379 BE_{Slope} and ΔBE_{Slope} ; see Appendix B: Table B3). We thus conducted multi-level
380 meta-analyses for both NBE and BE_{Slope} to explore how between-study heterogeneity
381 may be explained by potential moderators. Our analyses showed significant
382 differences in NBE and BE_{Slope} across different combinations of taxonomic groups,
383 type of global change drivers and category of ecosystem functions (Appendix B:
384 Table B4 & B5). Therefore, we did not estimate overall effect sizes across all 46
385 studies. We also tested the effects of other potential moderators (type of nutrient
386 addition, vegetation type, and experimental unit), which were found to have non-
387 significant effects on NBE or BE_{Slope} and thus omitted in the main text (see Appendix
388 A).

389 Using five long-term studies in our dataset (one on microbes and four on
390 grasslands; see Appendix B: Table B7), we tested whether the effects of global
391 change drivers on NBE and BE_{Slope} for biomass production varied through time. For
392 each study, we used mixed-effects models with experiment duration as a fixed effect,

393 and the combination of species richness level and level of environmental
394 manipulation as the random effect. Similarly, we further tested the relationship
395 between $\Delta\text{NBE}/\Delta\text{BE}_{\text{Slope}}$ and experimental duration. We fitted each model using
396 linear, quadratic, and logarithmic forms of environment duration and calculated the
397 Akaike information criterion (AIC) to determine the best model. We used the function
398 “lmer()” of the *nlme* package in R to fit these models.

399 We also used mixed-effects models to test the relationships between ΔNBE ,
400 $\Delta\text{BE}_{\text{Slope}}$, ΔCE or ΔSE and stress intensity (SI):

$$401 \quad \Delta\text{NBE}, \Delta\text{BE}_{\text{Slope}}, \Delta\text{CE or } \Delta\text{SE} \sim SI + (\alpha\beta\gamma/\theta/\eta\lambda\psi)_{ijkmnr s} + \epsilon_{ijkmnr s} \quad (14)$$

402 where *SI* was the fixed effect, and other variables ($\alpha, \beta, \gamma, \theta, \eta, \lambda, \psi$) were random effects.
403 We also tested the two-way interactions of stress intensity with taxonomic group, type
404 of global change drivers, and category of ecosystem function (Appendix B: Table B6).
405 Again we used the function “lmer()” to fit this model.

406 Publication bias was analyzed using the function “funnel()” from the *metafor*
407 package in R (Viechtbauer 2010) and Egger’s test was conducted to test the
408 asymmetry of the funnel plot of our model (with only random effect) in NBE, ΔNBE ,
409 CE, ΔCE , SE, and ΔSE , as well as BE_{Slope} and $\Delta\text{BE}_{\text{Slope}}$ (Nakagawa *et al.* 2017). We
410 found overall low publication biases in our dataset; a significant bias occurred only
411 for ΔSE (Egger’s $p = 0.0110$, Appendix B: Fig. B2). But our further sensitivity
412 analysis showed that the publication bias in ΔSE did not influence the robustness of
413 our results (see Appendix A).

414

415 **Results**

416 Biodiversity had generally positive effects (NBE and BE_{Slope}) on biomass
417 production in both ambient and manipulated environments, regardless of the type of
418 global change drivers and taxonomic group ($p < 0.05$; Fig. 2 & Appendix B: Fig. B3).
419 Biodiversity also tended to enhance biogeochemical processes, but these effects were
420 weaker and non-significant for certain combinations of global change drivers and
421 taxonomic groups ($p > 0.05$; Fig. 2 & Appendix B: Fig. B3). NBEs under ambient and
422 manipulated environmental conditions were positively correlated in each of the six
423 combinations of global change drivers and taxonomic groups ($r = 0.42 \sim 0.82$;
424 Appendix B: Fig. B4).

425 Although warming did not change the sign of NBEs, it modulated their
426 magnitude (as measured by Δ NBE) in microbes and phytoplankton (Fig. 2; $Q_M =$
427 24.76, $p < 0.0001$, Appendix B: Table B4). In microbial communities, warming
428 decreased NBEs on biomass production on average by 20% ($e^{-0.222}$, number of effect
429 sizes (N) = 506, number of studies (n) = 3, $p = 0.0726$). In phytoplankton
430 communities, however, warming increased NBEs on biomass production on average
431 by 61% ($e^{0.360}$, N = 64, n = 3, $p = 0.002$; Fig. 2), and this increase was stronger as the
432 degree of warming increased (Appendix B: Fig. B5). For biodiversity effects
433 measured by BE_{Slope} , warming also increased BE_{Slope} on biomass production in
434 phytoplankton ($\Delta BE_{Slope} = 0.109$, N = 12, n = 3, $p = 0.019$; Appendix B: Fig. B3), but
435 it had a non-significant effect in microbes ($p > 0.05$; Appendix B: Fig. B3).

436 In plants, global change drivers had overall non-significant effects on NBE,
437 regardless of the type of global change drivers and ecosystem functions measured ($p >$
438 0.05; Fig. 2). Global change drivers also did not influence BE_{Slope} for biogeochemical
439 processes, but BE_{Slope} for biomass production responded significantly to global
440 change drivers, except for CO_2 enrichment. Specifically, BE_{Slope} was decreased by
441 warming ($\Delta BE_{Slope} = -0.103$, N = 28, n = 4, $p = 0.034$; Appendix B: Fig. B3) and
442 nutrient addition ($\Delta BE_{Slope} = -0.085$, N = 49, n = 7, $p = 0.011$; Appendix B: Fig. B3),
443 whereas it was increased by drought ($\Delta BE_{Slope} = 0.099$, N = 21, n = 10, $p = 0.026$;
444 Appendix B: Fig. B3).

445 Based on the 12 studies with monocultures where raw data were available, we
446 found that complementarity effects (CE) were generally positive ($p < 0.05$) and
447 selection effects (SE) were generally not different from 0 in both ambient and
448 manipulated environments, regardless of the type of global change drivers or
449 taxonomic group (Fig. 3). Warming decreased CE for microbial biomass production
450 by 24.3% (N = 470, n = 2, $p < 0.0001$) and increased CE for phytoplankton
451 production by 82.6% (N = 10, n = 1, $p = 0.008$) (Fig. 3a). But warming did not alter
452 SE in either microbes or phytoplankton communities (Fig. 3b). In plant communities,
453 global change drivers had no significant effects on either CE or SE on biomass
454 production ($p > 0.05$; Fig. 3).

455 Using the five long-term studies in our dataset, we found that biodiversity effects
456 (i.e. NBE and BE_{Slope}) generally increased with experimental duration in both ambient
457 and manipulated environments (Fig. 4; Appendix B: Fig. B6). The difference in
458 biodiversity effects between ambient and manipulated environments, measured by

459 either ΔNBE or $\Delta\text{BE}_{\text{Slope}}$, decreased with experimental duration in microbial
460 experiments ($p < 0.05$; Appendix B: Fig. B7 & B8). Yet, such differences did not vary
461 with experimental duration in the four grassland studies ($p > 0.1$; Fig. 4; Appendix B:
462 Fig. B7 & B8).

463 Warming in phytoplankton communities and drought in plant communities on
464 average decreased monoculture functions (positive value of stress intensity), and
465 nutrient addition in plant communities on average increased monoculture functions
466 (negative value of stress intensity) ($p < 0.05$; Fig. 5a). However, the effects of drought
467 and nutrient addition on ecosystem functions became non-significant in more diverse
468 plant communities ($p > 0.10$; Appendix B: Fig. B9). We found that both ΔNBE and
469 $\Delta\text{BE}_{\text{Slope}}$ increased as stress intensity increased ($p < 0.001$ for both; Fig. 5b,c),
470 indicating stronger biodiversity effects in more stressful environments. These results
471 were robust whether we used biodiversity effects (i.e. ΔNBE and $\Delta\text{BE}_{\text{Slope}}$) averaged
472 across time or at the end of the experiment (Appendix B: Fig. B10). Moreover, the
473 positive relationship between stress intensity and ΔNBE or $\Delta\text{BE}_{\text{Slope}}$ also held in
474 models that incorporated the effects of taxonomic groups, type of global change
475 drivers, category of ecosystem function, and their interaction with stress intensity
476 (Appendix B: Table B6).

477

478 **Discussion**

479 The past decades have seen major progress in understanding the responses of
480 ecosystems to environmental and biodiversity changes. Recent meta-analyses have
481 documented the individual effects of global environmental change (Yuan *et al.* 2017;
482 Song *et al.* 2019) or biodiversity (Balvanera *et al.* 2006; Cardinale *et al.* 2012; Hooper
483 *et al.* 2012) on ecosystem functioning. Our synthesis of 46 factorial experiments
484 advances current understanding by demonstrating the interactive effects between
485 biodiversity and environmental changes on ecosystem functions. We found that
486 biodiversity consistently enhanced ecosystem functioning in both ambient and
487 manipulated environments, but global change drivers could modulate the strength of
488 biodiversity effects. Specifically, the effects of biodiversity on ecosystem functioning
489 were stronger in stressful environments than in more favorable environments.
490 Therefore, biodiversity contributes to buffering ecosystem functions across a range of
491 stressful conditions associated with current and future global change scenarios.

492

493 ***Biodiversity effects in ambient and manipulated environments***

494 Biodiversity generally promoted ecosystem functioning in both ambient and
495 changing environments (Fig. 2; Appendix B: Fig. B3), although its positive effects on
496 biogeochemical processes were relatively weak and often non-significant, possibly
497 due to small sample sizes. Based on a subset of our dataset (12 studies where the
498 necessary data were available), we found that these positive biodiversity effects were
499 mainly due to complementarity effects (Fig. 3), which was consistent with earlier
500 findings from plant diversity experiments under ambient environmental conditions
501 (Loreau & Hector 2001; Tilman *et al.* 2014; Huang *et al.* 2018) as well as under
502 altered conditions (Craven *et al.* 2016).

503 While global change drivers did not change the directions of biodiversity effects
504 (both NBE and BE_{slope}), they mediated the magnitude of biodiversity effects (Fig. 2,
505 Appendix B: Fig. B3). Warming increased biodiversity effects on biomass production
506 in phytoplankton, but decreased it in microbes. The contrasting responses of
507 biodiversity effects to warming in microbes versus phytoplankton may be explained
508 by differential effects of warming on interspecific interactions. In microbial
509 communities, warming has been shown to enhance interspecific competition between
510 culturable microbial species, even leading to competitive exclusion (Jiang & Morin
511 2004). Such intensified competition by warming should lead to a reduction in CE in
512 microbes (Fig. 3; Parain *et al.* 2019). In phytoplankton communities, however,
513 warming might promote interspecific facilitation, for instance by stimulating certain
514 groups or species such as N_2 -fixing cyanobacteria (Brauer *et al.* 2015; Striebel *et al.*
515 2016), which would lead to an increased CE (Fig. 3).

516 In plant communities, warming and nutrient addition decreased, and drought
517 increased biodiversity effects quantified by the regression slope (BE_{slope}) between
518 species richness and biomass production (Appendix B: Fig. B3). These global change
519 drivers also similarly influenced NBEs (as well as CE), but the effects were weak and
520 often non-significant (Figs. 2 & 3). These apparently inconsistent results for ΔNBE
521 and ΔBE_{slope} may be due to the fact that BE_{slope} usually have smaller variances
522 compared with NBE, which makes it easier to detect statistically significant effects
523 for ΔBE_{slope} (see Appendix A). Furthermore, the responses of NBE and BE_{slope} to
524 global change drivers are reconciled from the perspective of stress intensity (see
525 below).

526 Several recent studies showed that biodiversity effects increased with time
527 (Reich *et al.* 2012; Guerrero-Ramírez *et al.* 2017; Huang *et al.* 2018). In line with this
528 finding, our analysis based on five long-term studies (one on microbes and four on
529 plants) showed that biodiversity effects generally increased with time under both
530 ambient and altered environmental conditions (Fig. 4, Appendix B: Fig. B6).
531 Moreover, we found a negative interaction between warming and experimental
532 duration on biodiversity effects in the microbial experiment (Appendix B: Fig. B7 &
533 B8), suggesting that the negative effect of warming on biodiversity effects increased
534 over time. In the four plant experiments, interactions between global change drivers
535 and time were all non-significant, possibly explained by their longer generation times
536 and less intense manipulations of global change drivers compared with microbes. In
537 particular, the longest plant experiment in our data lasted 15 years, which may not be
538 sufficient for the plants to acclimate to environmental changes and for novel
539 interspecific interactions to manifest or evolve (Jessup *et al.* 2004; but see Zuppinger-
540 Dingley *et al.* 2014).

541

542 ***Biodiversity buffers environmental stress***

543 By quantifying the responses of monocultures in each study, we found that the
544 stress induced by the altered environment differed markedly among studies, even for
545 the same global change driver and taxonomic group (Fig. 5). In other words, the same
546 environmental manipulation can be perceived as either more or less stressful by
547 different experimental communities (e.g. different plant species pools used in
548 different experiments). Interestingly, we found that stress intensity was positively
549 related to both ΔNBE and $\Delta\text{BE}_{\text{Slope}}$. Thus, stress intensity provides a useful indicator
550 to predict how global change drivers alter biodiversity effects. The positive
551 relationship between ΔNBE or $\Delta\text{BE}_{\text{Slope}}$ and stress intensity could be due to higher
552 resistance to environmental stress of diverse mixtures compared with monocultures
553 (H1 in Fig. 1; Appendix B: Fig. B9). When global change drivers induced high stress
554 intensity (e.g. warming in phytoplankton communities or drought in plant
555 communities), diverse mixtures exhibited higher resistance to environmental stress
556 and better maintained their functions (in line with Isbell *et al.* 2015), resulting in an
557 enhanced biodiversity effect. Conversely, when global change drivers reduced
558 environmental stress compared with ambient conditions (e.g. nutrient addition on
559 plants), diverse mixtures benefitted less than monocultures, resulting in a weakened

560 biodiversity effect. Overall, communities with higher species diversity were less
561 influenced by environmental changes, because biodiversity could buffer the negative
562 or positive effects of global change drivers on ecosystem functioning (Fig. 5,
563 Appendix B: Fig. B9). This can occur directly through niche complementarity, via
564 buffering of microenvironmental stress (Wright *et al.* 2014), or both. Such buffering
565 effects can increase not only ecosystem resistance to directional changes in the
566 environment, but also the temporal and spatial stability of ecosystems in fluctuating
567 environments (Yachi & Loreau 1999; Wang *et al.* 2019).

568 Our results are consistent with recent findings that biodiversity can increase the
569 resistance and resilience of ecosystems (Mori *et al.* 2013; Isbell *et al.* 2015; Hisano *et*
570 *al.* 2018; but see Baert *et al.* 2016; De Boeck *et al.* 2018; Pennekamp *et al.* 2018). The
571 results are also in line with the stress gradient hypothesis (Bertness & Callaway 1994),
572 which predicts increased biodiversity effects (particularly CE) with increasing stress
573 intensity due to reduced interspecific competition or enhanced facilitation (He *et al.*
574 2013; Wright *et al.* 2017). That said, our analyses based on a small sample size
575 showed that neither CE nor SE exhibited a significant relationship with stress
576 intensity, although both showed positive trends (Appendix B: Fig. B11).

577 Recent studies hypothesized that biodiversity effects could first increase but then
578 decrease with stress intensity, because high stress intensity may restrict population
579 growth to such a level that ecosystem functions are extremely low regardless of the
580 level of biodiversity (Baert *et al.* 2018). Our results did not support this hypothesis.
581 This could be due to the fact that our data included few experiments with extreme
582 environmental conditions, hence most values of stress intensity in our data fell into a
583 relatively narrow interval (e.g. the 5% and 95% quantiles of stress intensity were [-
584 0.54, 0.60], see Fig. 5). Alternatively, it may be intrinsically difficult to detect the
585 threshold level of environmental conditions based on empirical data, even if such a
586 threshold exists (Hillebrand *et al.* 2020). Disentangling these possibilities will require
587 future experiments that cover more extreme values of stress intensity (De Boeck *et al.*
588 2018).

589

590 ***Future directions***

591 Several future directions emerge from our study. On the experimental side, more
592 efforts are needed to better understand the interactions between biodiversity and the
593 environment. First, most studies in our datasets (34 out of 46) are from grasslands; so,

594 research efforts should be extended to other ecosystems (e.g. forests) and taxonomic
595 groups (e.g. microbes and phytoplankton). In particular, we did not find any study that
596 tested the interaction between biodiversity and eutrophication in microbes or
597 phytoplankton. Recent studies showed that nutrient addition in microbial communities
598 could shift species interactions from facilitation to competition (Hoek *et al.* 2016;
599 Piccardi *et al.* 2019), whereas nutrient addition in phytoplankton communities shifted
600 competition from nutrients to light and thus altered species interactions (Burson *et al.*
601 2018). Thus, biodiversity effects might be altered by eutrophication in microbes and
602 phytoplankton. Second, all studies in our dataset manipulated species richness as the
603 main facet of biodiversity. However, recent studies highlighted effects of other facets
604 of biodiversity (e.g. functional or phylogenetic diversity) on ecosystem functioning
605 (Steudel *et al.* 2016; Craven *et al.* 2018; Huang *et al.* 2018). Whether environmental
606 change alters the effects of different facets of biodiversity in different ways remains
607 unclear and should be explored further. Third, very few experiments (one in our
608 dataset) tested the interaction between biodiversity and multiple environmental
609 change drivers (Reich *et al.* 2001). Although a recent meta-analysis suggested that
610 different global change drivers might have weak interactive effects (Song *et al.* 2019),
611 there are case studies showing significant interactions (Rillig *et al.* 2019; Reich *et al.*
612 2020), and whether they exhibit higher-order interactions with biodiversity remains
613 unknown. Future experiments should address the interactions between different global
614 change drivers, including additional ones to those considered here (e.g. climatic
615 variability). On the other hand, new theory is required for clarifying the ecological
616 mechanisms underlying interactions between biodiversity and the environment.
617 Classic theories on biodiversity–ecosystem functioning were built upon competition
618 models that assumed constant environmental conditions (Tilman *et al.* 1997; Loreau
619 1998). A constant environment can be readily achieved in experimental settings but
620 rarely in natural ecosystems. New theoretical studies should allow for different
621 environmental conditions under which biodiversity–ecosystem functioning
622 relationships are predicted, to explore possible mechanisms by which the physical and
623 biological environments might modify biodiversity effects (e.g. De Laender 2018).

624 Lastly, experimental and theoretical findings need to be reconciled with the
625 increasing number of observational studies along natural gradients of biodiversity and
626 environmental conditions, for both terrestrial (Fei *et al.* 2018; Guo *et al.* 2019) and
627 marine (Benkwitt *et al.* 2020) ecosystems. Recent observational studies revealed

628 either enhanced (Fei *et al.* 2018; Hisano & Chen 2020), similar (Liang *et al.* 2016) or
629 weakened (Mori 2018) effects of tree diversity on ecosystem productivity in warmer
630 regions. In comparison, our meta-analysis revealed an overall weak, negative effect of
631 warming on plant biodiversity effects. Moreover, several continental-scale studies
632 showed that plant diversity increased ecosystem productivity or biomass in dry
633 regions, but such effects were weakened or even reversed in moist regions (Ratcliffe
634 *et al.* 2017; Fei *et al.* 2018; Guo *et al.* 2019). These results are consistent with the
635 overall positive effects of drought on plant biodiversity effects in our analyses (Fig. 2
636 & Appendix B: B3). Syntheses across different approaches (e.g. experimental,
637 theoretical, and observational) will help clarify which patterns and mechanisms are
638 general and which are context dependent.

639

640 **Conclusions**

641 By synthesizing experiments across various taxonomic groups and types of
642 global change drivers, our study demonstrates persistent positive effects of
643 biodiversity on ecosystem functions across taxa despite environmental change. The
644 positive effects of biodiversity increased over time under both ambient and
645 manipulated environmental conditions and were stronger when environmental change
646 increased stress intensity. Independent of the level of environmental stress,
647 biodiversity helps to maintain ecosystem functioning at relatively stable levels,
648 whereas stability is lowered in species-poor communities or monocultures. Moreover,
649 our synthesis contributes to exposing knowledge gaps and informing future research
650 to advance our understanding of the interaction between biodiversity and environment.
651 Recent studies showed that the magnitude of biodiversity effects on ecosystem
652 functioning was comparable to that of effects of environmental changes in both
653 experimental and natural communities (Hooper *et al.* 2012; Tilman *et al.* 2012; Duffy
654 *et al.* 2017). Taken together, biodiversity provides an important biological buffer to
655 maintain ecosystem functioning in the face of environmental changes.

656

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669

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671 assembled the data, with help from all coauthors; P.H. did the statistical analyses,
672 with inputs from B.S, F.D.L, S.W.; P.H. and S.W. wrote the first draft of the
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675

676 **References**

677 Baert, J.M., De Laender, F., Sabbe, K. & Janssen, C.R. (2016). Biodiversity increases
678 functional and compositional resistance, but decreases resilience in
679 phytoplankton communities. *Ecology*, 97, 3433–3440.

680 Baert, J.M., Eisenhauer, N., Janssen, C.R. & De Laender, F. (2018). Biodiversity
681 effects on ecosystem functioning respond unimodally to environmental stress.
682 *Ecol. Lett.*, 21, 1191–1199.

683 Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D.,
684 *et al.* (2006). Quantifying the evidence for biodiversity effects on ecosystem
685 functioning and services. *Ecol. Lett.*, 9, 1146–1156.

686 Benkwitt, C.E., Wilson, S.K. & Graham, N.A.J. (2020). Biodiversity increases
687 ecosystem functions despite multiple stressors on coral reefs. *Nat. Ecol. Evol.*, 4,
688 919–926.

689 Bertness, M.D. & Callaway, R. (1994). Positive interactions in communities. *Trends*
690 *Ecol. Evol.*, 9, 191–193.

-
- 691 Bestion, E., Barton, S., García, F.C., Warfield, R. & Yvon-Durocher, G. (2020).
692 Abrupt declines in marine phytoplankton production driven by warming and
693 biodiversity loss in a microcosm experiment. *Ecol. Lett.*, 23, 457–466.
- 694 Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., *et al.*
695 (2019). The geography of biodiversity change in marine and terrestrial
696 assemblages. *Science*, 366, 339–345.
- 697 Brauer, V.S., Stomp, M., Bouvier, T., Fouilland, E., Leboulanger, C., Confurius-Guns,
698 V., *et al.* (2015). Competition and facilitation between the marine nitrogen-fixing
699 cyanobacterium *Cyanothece* and its associated bacterial community. *Front.*
700 *Microbiol.*, 5, Article 795.
- 701 Burson, A., Stomp, M., Greenwell, E., Grosse, J. & Huisman, J. (2018). Competition
702 for nutrients and light: testing advances in resource competition with a natural
703 phytoplankton community. *Ecology*, 99, 1108–1118.
- 704 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.*
705 (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.
- 706 Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S.,
707 *et al.* (2007). Impacts of plant diversity on biomass production increase through
708 time because of species complementarity. *Proc. Natl. Acad. Sci.*, 104, 18123–
709 18128.
- 710 Cavicchioli, R., Ripple, W.J., Timmis, K.N., Azam, F., Bakken, L.R., Baylis, M., *et al.*
711 (2019). Scientists’ warning to humanity: microorganisms and climate change.
712 *Nat. Rev. Microbiol.*, 17, 569–586.
- 713 Chapin, F.S., Matson, P.A. & Vitousek, P.M. (2011). *Principles of Terrestrial*
714 *Ecosystem Ecology*. Springer New York.
- 715 Cowles, J.M., Wragg, P.D., Wright, A.J., Powers, J.S. & Tilman, D. (2016). Shifting
716 grassland plant community structure drives positive interactive effects of
717 warming and diversity on aboveground net primary productivity. *Glob. Change*
718 *Biol.*, 22, 741–749.

719 Craven, D., Eisenhauer, N., Pearse, W.D., Hautier, Y., Isbell, F., Roscher, C., *et al.*
720 (2018). Multiple facets of biodiversity drive the diversity–stability relationship.
721 *Nat. Ecol. Evol.*, 2, 1579–1587.

722 Craven, D., Isbell, F., Manning, P., Connolly, J., Bruelheide, H., Ebeling, A., *et al.*
723 (2016). Plant diversity effects on grassland productivity are robust to both
724 nutrient enrichment and drought. *Philos. Trans. R. Soc. B Biol. Sci.*, 371, Article
725 20150277.

726 De Boeck, H.J., Bloor, J.M.G., Kreyling, J., Ransijn, J.C.G., Nijs, I., Jentsch, A., *et al.*
727 (2018). Patterns and drivers of biodiversity–stability relationships under climate
728 extremes. *J. Ecol.*, 106, 890–902.

729 De Boeck, H.J., Lemmens, C.M.H.M., Zavalloni, C., Gielen, B., Malchair, S., Carnol,
730 M., *et al.* (2008). Biomass production in experimental grasslands of different
731 species richness during three years of climate warming. *Biogeoscience*, 5, 585–
732 594.

733 De Laender, F. (2018). Community- and ecosystem-level effects of multiple
734 environmental change drivers: Beyond null model testing. *Glob. Change Biol.*,
735 24, 5021–5030.

736 De Laender, F., Rohr, J.R., Ashauer, R., Baird, D.J., Berger, U., Eisenhauer, N., *et al.*
737 (2016). Reintroducing Environmental Change Drivers in Biodiversity–
738 Ecosystem Functioning Research. *Trends Ecol. Evol.*, 31, 905–915.

739 Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., *et al.*
740 (2014). Assemblage Time Series Reveal Biodiversity Change but Not Systematic
741 Loss. *Science*, 344, 296–299.

742 Duffy, J.E., Godwin, C.M. & Cardinale, B.J. (2017). Biodiversity effects in the wild
743 are common and as strong as key drivers of productivity. *Nature*, 549, 261–264.

744 Eisenhauer, N., Hines, J., Isbell, F., van der Plas, F., Hobbie, S.E., Kazanski, C.E., *et*
745 *al.* (2018). Plant diversity maintains multiple soil functions in future
746 environments. *eLife*, 7, Article e41228.

747 Eisenhauer, N., Schielzeth, H., Barnes, A.D., Barry, K.E., Bonn, A., Brose, U., *et al.*
748 (2019). Chapter One - A multitrophic perspective on biodiversity–ecosystem
749 functioning research. In: *Advances in Ecological Research*, Mechanisms
750 underlying the relationship between biodiversity and ecosystem function (eds.
751 Eisenhauer, N., Bohan, D.A. & Dumbrell, A.J.). Academic Press, pp. 1–54.

752 Fei, S., Jo, I., Guo, Q., Wardle, D.A., Fang, J., Chen, A., *et al.* (2018). Impacts of
753 climate on the biodiversity-productivity relationship in natural forests. *Nat.*
754 *Commun.*, 9, Article 5436.

755 García, F.C., Bestion, E., Warfield, R. & Yvon-Durocher, G. (2018). Changes in
756 temperature alter the relationship between biodiversity and ecosystem
757 functioning. *Proc. Natl. Acad. Sci.*, 115, 10989–10994.

758 Giling, D.P., Beaumelle, L., Phillips, H.R.P., Cesarz, S., Eisenhauer, N., Ferlian, O.,
759 *et al.* (2019). A niche for ecosystem multifunctionality in global change research.
760 *Glob. Change Biol.*, 25, 763–774.

761 Guerrero-Ramírez, N.R., Craven, D., Reich, P.B., Ewel, J.J., Isbell, F., Koricheva, J.,
762 *et al.* (2017). Diversity-dependent temporal divergence of ecosystem functioning
763 in experimental ecosystems. *Nat. Ecol. Evol.*, 1, 1639–1642.

764 Guo, Y., Schöb, C., Ma, W., Mohammat, A., Liu, H., Yu, S., *et al.* (2019). Increasing
765 water availability and facilitation weaken biodiversity-biomass relationships in
766 shrublands. *Ecology*, 100, Article e02624.

767 Hautier, Y., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., Hillebrand, H.,
768 *et al.* (2014). Eutrophication weakens stabilizing effects of diversity in natural
769 grasslands. *Nature*, 508, 521–525.

770 Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T. & Reich, P.B. (2015).
771 Anthropogenic environmental changes affect ecosystem stability via biodiversity.
772 *Science*, 348, 336–340.

773 He, Q., Bertness, M.D. & Altieri, A.H. (2013). Global shifts towards positive species
774 interactions with increasing environmental stress. *Ecol. Lett.*, 16, 695–706.

775 Hillebrand, H., Donohue, I., Harpole, W.S., Hodapp, D., Kucera, M., Lewandowska,
776 A.M., *et al.* (2020). Thresholds for ecological responses to global change do not
777 emerge from empirical data. *Nat. Ecol. Evol.*, 4, 1502–1509.

778 Hisano, M. & Chen, H.Y.H. (2020). Spatial variation in climate modifies effects of
779 functional diversity on biomass dynamics in natural forests across Canada. *Glob.*
780 *Ecol. Biogeogr.*, 29, 682–695.

781 Hisano, M., Searle, E.B. & Chen, H.Y.H. (2018). Biodiversity as a solution to
782 mitigate climate change impacts on the functioning of forest ecosystems. *Biol.*
783 *Rev.*, 93, 439–456.

784 Hoek, T.A., Axelrod, K., Biancalani, T., Yurtsev, E.A., Liu, J. & Gore, J. (2016).
785 Resource Availability Modulates the Cooperative and Competitive Nature of a
786 Microbial Cross-Feeding Mutualism. *PLOS Biol.*, 14, Article e1002540.

787 Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich,
788 K.L., *et al.* (2012). A global synthesis reveals biodiversity loss as a major driver
789 of ecosystem change. *Nature*, 486, 105–108.

790 Huang, Y., Chen, Y., Castro-Izaguirre, N., Baruffol, M., Brezzi, M., Lang, A., *et al.*
791 (2018). Impacts of species richness on productivity in a large-scale subtropical
792 forest experiment. *Science*, 362, 80–83.

793 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services,
794 IPBES. (2019). *Summary for policymakers of the global assessment report on*
795 *biodiversity and ecosystem services*. Zenodo.

796 Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., *et al.*
797 (2015). Biodiversity increases the resistance of ecosystem productivity to climate
798 extremes. *Nature*, 526, 574–577.

799 Isbell, F.I., Polley, H.W. & Wilsey, B.J. (2009). Biodiversity, productivity and the
800 temporal stability of productivity: patterns and processes. *Ecol. Lett.*, 12, 443–
801 451.

802 Jessup, C.M., Kassen, R., Forde, S.E., Kerr, B., Buckling, A., Rainey, P.B., *et al.*
803 (2004). Big questions, small worlds: microbial model systems in ecology. *Trends*
804 *Ecol. Evol.*, 19, 189–197.

805 Jiang, L. & Morin, P.J. (2004). Temperature-dependent interactions explain
806 unexpected responses to environmental warming in communities of competitors.
807 *J. Anim. Ecol.*, 73, 569–576.

808 Jiang, M., Medlyn, B.E., Drake, J.E., Duursma, R.A., Anderson, I.C., Barton, C.V.M.,
809 *et al.* (2020). The fate of carbon in a mature forest under carbon dioxide
810 enrichment. *Nature*, 580, 227–231.

811 Koricheva, J., Gurevitch, J. & Mengersen, K. (2013). *Handbook of meta-analysis in*
812 *ecology and evolution*. Princeton University Press, Princeton.

813 Lajeunesse, M.J. (2011). On the meta-analysis of response ratios for studies with
814 correlated and multi-group designs. *Ecology*, 92, 2049–2055.

815 Lajeunesse, M.J. (2015). Bias and correction for the log response ratio in ecological
816 meta-analysis. *Ecology*, 96, 2056–2063.

817 Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., *et al.* (2016).
818 Positive biodiversity-productivity relationship predominant in global forests.
819 *Science*, 354, Article aaf8957.

820 Loreau, M. (1998). Biodiversity and ecosystem functioning: A mechanistic model.
821 *Proc. Natl. Acad. Sci.*, 95, 5632–5636.

822 Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in
823 biodiversity experiments. *Nature*, 412, 72–76.

824 Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009). Refining the
825 stress-gradient hypothesis for competition and facilitation in plant communities.
826 *J. Ecol.*, 97, 199–205.

827 Metz, J. & Tielbörger, K. (2016). Spatial and temporal aridity gradients provide poor
828 proxies for plant–plant interactions under climate change: a large-scale
829 experiment. *Funct. Ecol.*, 30, 20–29.

-
- 830 van Moorsel, S.J., Hahl, T., Wagg, C., Deyn, G.B.D., Flynn, D.F.B.,
831 Zuppinger-Dingley, D., *et al.* (2018). Community evolution increases plant
832 productivity at low diversity. *Ecol. Lett.*, 21, 128–137.
- 833 Mori, A.S. (2018). Environmental controls on the causes and functional consequences
834 of tree species diversity. *J. Ecol.*, 106, 113–125.
- 835 Mori, A.S., Furukawa, T. & Sasaki, T. (2013). Response diversity determines the
836 resilience of ecosystems to environmental change. *Biol. Rev.*, 88, 349–364.
- 837 Naeem, S., Bunker, D.E., Hector, A., Loreau, M. & Perrings, C. (2009). *Biodiversity,*
838 *ecosystem functioning, and human wellbeing: an ecological and economic*
839 *perspective*. Oxford biology. Oxford Univ. Press, Oxford; New York.
- 840 Nakagawa, S., Noble, D.W.A., Senior, A.M. & Lagisz, M. (2017). Meta-evaluation of
841 meta-analysis: ten appraisal questions for biologists. *BMC Biol.*, 15, Article 18.
- 842 Nakagawa, S. & Santos, E.S.A. (2012). Methodological issues and advances in
843 biological meta-analysis. *Evol. Ecol.*, 26, 1253–1274.
- 844 Olsen, S.L., Töpper, J.P., Skarpaas, O., Vandvik, V. & Klanderud, K. (2016). From
845 facilitation to competition: temperature-driven shift in dominant plant
846 interactions affects population dynamics in seminatural grasslands. *Glob.*
847 *Change Biol.*, 22, 1915–1926.
- 848 Parain, E.C., Rohr, R.P., Gray, S.M. & Bersier, L.-F. (2019). Increased Temperature
849 Disrupts the Biodiversity–Ecosystem Functioning Relationship. *Am. Nat.*, 193,
850 227–239.
- 851 Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., *et al.*
852 (2018). Biodiversity increases and decreases ecosystem stability. *Nature*, 563,
853 109–112.
- 854 Piccardi, P., Vessman, B. & Mitri, S. (2019). Toxicity drives facilitation between 4
855 bacterial species. *Proc. Natl. Acad. Sci.*, 116, 15979–15984.

856 Pires, A.P.F., Srivastava, D.S. & Farjalla, V.F. (2018). Is Biodiversity Able to Buffer
857 Ecosystems from Climate Change? What We Know and What We Don't.
858 *BioScience*, 68, 273–280.

859 Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen,
860 K., *et al.* (2017). Biodiversity and ecosystem functioning relations in European
861 forests depend on environmental context. *Ecol. Lett.*, 20, 1414–1426.

862 Reich, P.B., Hobbie, S.E., Lee, T.D., Rich, R., Pastore, M.A. & Worm, K. (2020).
863 Synergistic effects of four climate change drivers on terrestrial carbon cycling.
864 *Nat. Geosci.*, 13, 787–793.

865 Reich, P.B., Knops, J., Tilman, D., Craine, J., Ellsworth, D., Tjoelker, M., *et al.*
866 (2001). Plant diversity enhances ecosystem responses to elevated CO₂ and
867 nitrogen deposition. *Nature*, 410, 809–810.

868 Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F.B., *et al.*
869 (2012). Impacts of Biodiversity Loss Escalate Through Time as Redundancy
870 Fades. *Science*, 336, 589–592.

871 Rillig, M.C., Ryo, M., Lehmann, A., Aguilar-Trigueros, C.A., Buchert, S., Wulf, A.,
872 *et al.* (2019). The role of multiple global change factors in driving soil functions
873 and microbial biodiversity. *Science*, 366, 886–890.

874 Song, J., Wan, S., Piao, S., Knapp, A.K., Classen, A.T., Vicca, S., *et al.* (2019). A
875 meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling
876 responses to global change. *Nat. Ecol. Evol.*, 3, 1309–1320.

877 Spaak, J.W., Baert, J.M., Baird, D.J., Eisenhauer, N., Maltby, L., Pomati, F., *et al.*
878 (2017). Shifts of community composition and population density substantially
879 affect ecosystem function despite invariant richness. *Ecol. Lett.*, 20, 1315–1324.

880 Steudel, B., Hallmann, C., Lorenz, M., Abrahamczyk, S., Prinz, K., Herrfurth, C., *et*
881 *al.* (2016). Contrasting biodiversity–ecosystem functioning relationships in
882 phylogenetic and functional diversity. *New Phytol.*, 212, 409–420.

-
- 883 Steudel, B., Hautier, Y., Hector, A. & Kessler, M. (2011). Diverse marsh plant
884 communities are more consistently productive across a range of different
885 environmental conditions through functional complementarity: Productivity in
886 different environments. *J. Appl. Ecol.*, 48, 1117–1124.
- 887 Steudel, B., Hector, A., Friedl, T., Löffke, C., Lorenz, M., Wesche, M., *et al.* (2012).
888 Biodiversity effects on ecosystem functioning change along environmental stress
889 gradients. *Ecol. Lett.*, 15, 1397–1405.
- 890 Tabi, A., Petchey, O.L. & Pennekamp, F. (2019). Warming reduces the effects of
891 enrichment on stability and functioning across levels of organisation in an
892 aquatic microbial ecosystem. *Ecol. Lett.*, 22, 1061–1071.
- 893 Thakur, M.P., Milcu, A., Manning, P., Niklaus, P.A., Roscher, C., Power, S., *et al.*
894 (2015). Plant diversity drives soil microbial biomass carbon in grasslands
895 irrespective of global environmental change factors. *Glob. Change Biol.*, 21,
896 4076–4085.
- 897 Tilman, D., Isbell, F. & Cowles, J.M. (2014). Biodiversity and Ecosystem
898 Functioning. *Annu. Rev. Ecol. Evol. Syst.*, 45, 471–493.
- 899 Tilman, D., Lehman, C.L. & Thomson, K.T. (1997). Plant diversity and ecosystem
900 productivity: Theoretical considerations. *Proc. Natl. Acad. Sci.*, 94, 1857–1861.
- 901 Tilman, D., Reich, P.B. & Isbell, F. (2012). Biodiversity impacts ecosystem
902 productivity as much as resources, disturbance, or herbivory. *Proc. Natl. Acad.*
903 *Sci.*, 109, 10394–10397.
- 904 Urban, M.C. (2015). Accelerating extinction risk from climate change. *Science*, 348,
905 571–573.
- 906 Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown,
907 C.D., *et al.* (2013). Global meta-analysis reveals no net change in local-scale
908 plant biodiversity over time. *Proc. Natl. Acad. Sci.*, 110, 19456–19459.
- 909 Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the **metafor** Package. *J.*
910 *Stat. Softw.*, 36, 1–48.

911 Wagg, C., O'Brien, M.J., Vogel, A., Scherer-Lorenzen, M., Eisenhauer, N., Schmid,
912 B., *et al.* (2017). Plant diversity maintains long-term ecosystem productivity
913 under frequent drought by increasing short-term variation. *Ecology*, 98, 2952–
914 2961.

915 Wang, Y., Cadotte, M.W., Chen, Y., Fraser, L.H., Zhang, Y., Huang, F., *et al.* (2019).
916 Global evidence of positive biodiversity effects on spatial ecosystem stability in
917 natural grasslands. *Nat. Commun.*, 10, Article 3207.

918 Wright, A., Schnitzer, S.A. & Reich, P.B. (2014). Living close to your neighbors: the
919 importance of both competition and facilitation in plant communities. *Ecology*,
920 95, 2213–2223.

921 Wright, A.J., Mommer, L., Barry, K. & Ruijven, J. van. (2021). Stress gradients and
922 biodiversity: monoculture vulnerability drives stronger biodiversity effects
923 during drought years. *Ecology*, 102, Article e03193.

924 Wright, A.J., Wardle, D.A., Callaway, R. & Gaxiola, A. (2017). The Overlooked Role
925 of Facilitation in Biodiversity Experiments. *Trends Ecol. Evol.*, 32, 383–390.

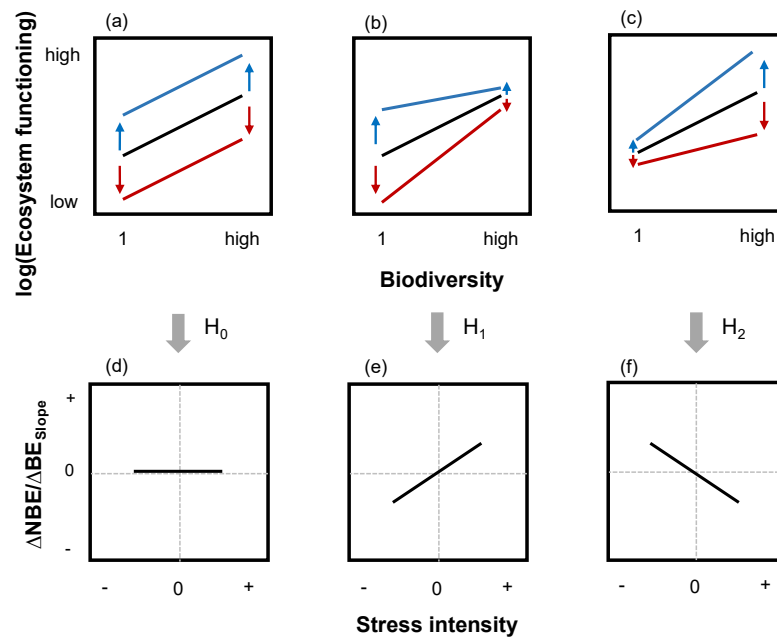
926 Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a
927 fluctuating environment: The insurance hypothesis. *Proc. Natl. Acad. Sci.*, 96,
928 1463–1468.

929 Yuan, Z., Jiao, F., Shi, X., Sardans, J., Maestre, F.T., Delgado-Baquerizo, M., *et al.*
930 (2017). Experimental and observational studies find contrasting responses of soil
931 nutrients to climate change. *eLife*, 6, Article e23255.

932 Yvon-Durocher, G., Allen, A.P., Cellamare, M., Dossena, M., Gaston, K.J., Leitaó,
933 M., *et al.* (2015). Five Years of Experimental Warming Increases the
934 Biodiversity and Productivity of Phytoplankton. *PLOS Biol.*, 13, Article
935 e1002324.

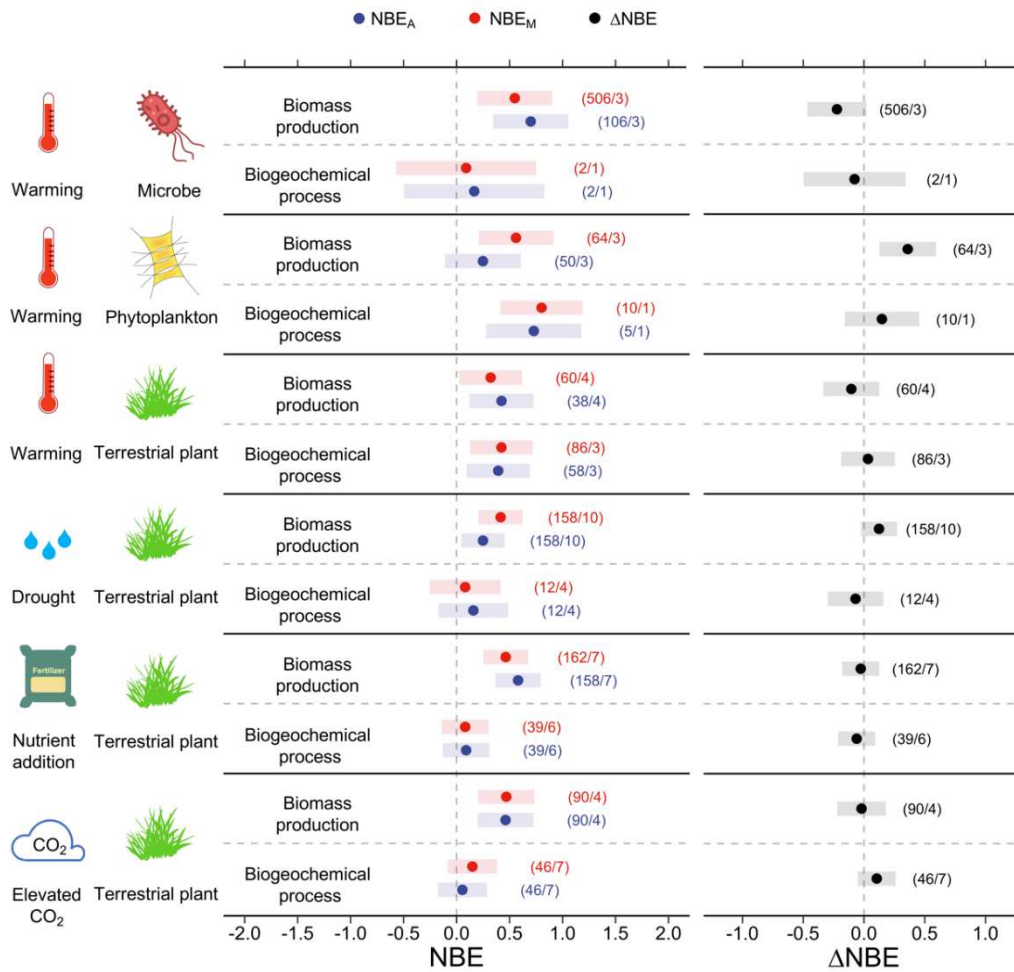
936 Zhou, J., Xue, K., Xie, J., Deng, Y., Wu, L., Cheng, X., *et al.* (2012). Microbial
937 mediation of carbon-cycle feedbacks to climate warming. *Nat. Clim. Change*, 2,
938 106–110.

939 Zuppinger-Dingley, D., Schmid, B., Petermann, J.S., Yadav, V., De Deyn, G.B. &
 940 Flynn, D.F.B. (2014). Selection for niche differentiation in plant communities
 941 increases biodiversity effects. *Nature*, 515, 108–111.
 942
 943

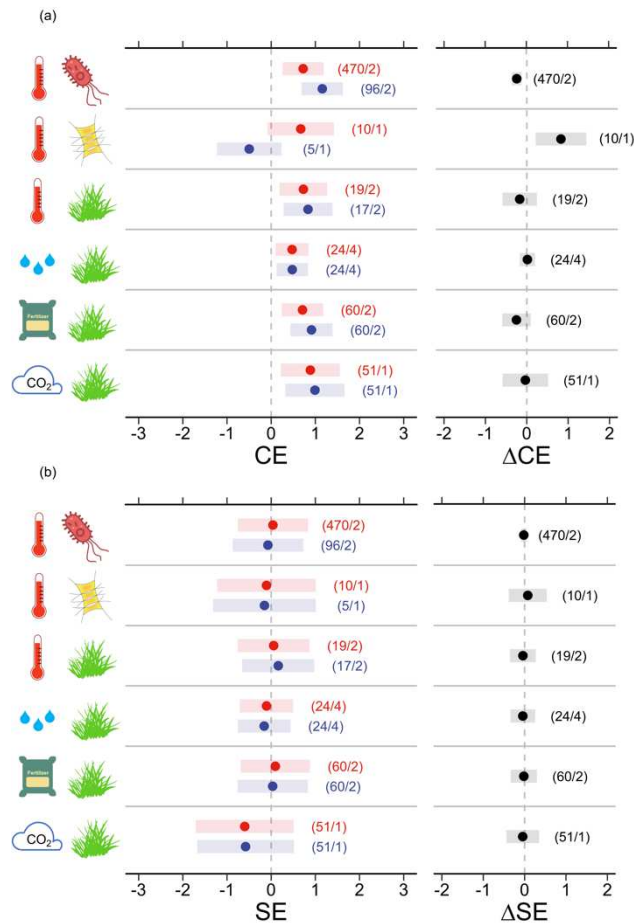


944
 945 **Figure 1** Scenarios underlying the responses of biodiversity–ecosystem functioning
 946 relationships to stress intensity (a–c) and the resulting relationship between changes in
 947 biodiversity effects (ΔNBE , $\Delta\text{BE}_{\text{Slope}}$) and stress intensity (e–f). Global change drivers
 948 can either increase or decrease ecosystem functioning and thus result in a more
 949 favorable or stressful environment for ecological communities. Under the null
 950 scenario (H_0) where mixtures are similarly influenced by global change driver as
 951 monocultures, biodiversity effects are not altered by global change drivers and we
 952 will observe no relationship between stress intensity and ΔNBE or $\Delta\text{BE}_{\text{Slope}}$. Under
 953 the scenario (H_1) where mixtures are less influenced by global change drivers
 954 compared with monocultures, biodiversity effects are enhanced in more stressful
 955 environments but weakened in more favorable environments, and we will observe a
 956 positive relationship between ΔNBE or $\Delta\text{BE}_{\text{Slope}}$ and stress intensity. Under the
 957 scenario (H_2) where mixtures are more influenced by global change drivers compared
 958 with monocultures, biodiversity effects are weakened in more stressful environments

959 but enhanced in more favorable environments, and we will observe a negative
 960 relationship between ΔNBE or $\Delta\text{BE}_{\text{slope}}$ and stress intensity.

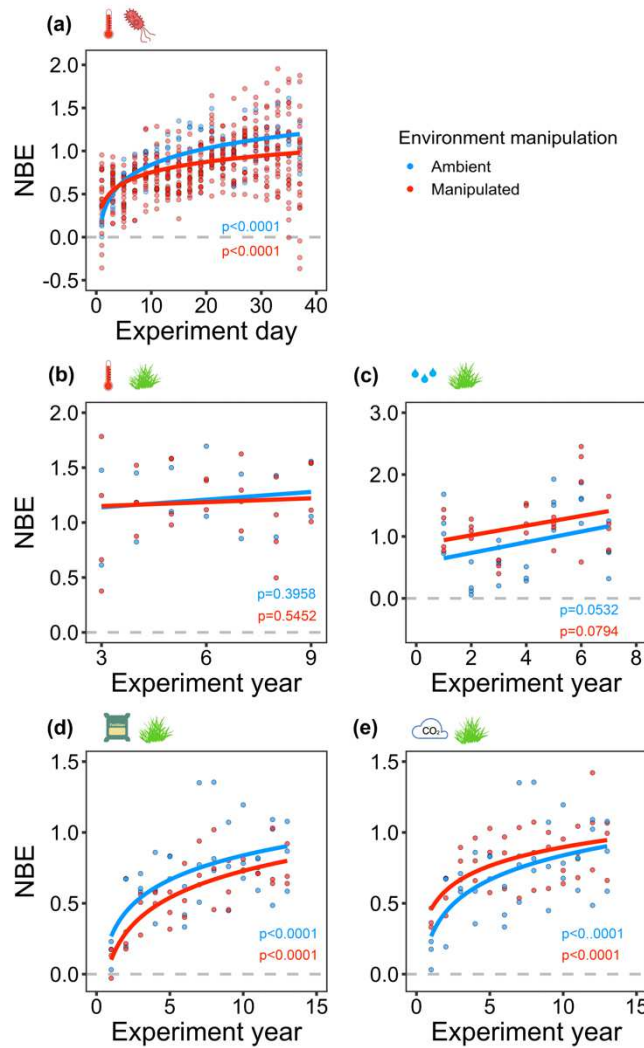


961
 962 **Figure 2** Net biodiversity effects (NBE) on ecosystem functioning under ambient
 963 (NBE_A , blue) and manipulated environmental conditions (NBE_M , red), and the
 964 difference between them ($\Delta\text{NBE} = \text{NBE}_M - \text{NBE}_A$, black) across different
 965 combinations of types of global change drivers (warming, drought, nutrient addition
 966 or elevated CO_2), taxonomic groups (microbes, phytoplankton or plants) and
 967 ecosystem functions (biomass production or biogeochemical process). The numbers in
 968 brackets show the number of effect sizes and studies. The points and shades represent
 969 the estimated mean and confidence interval, respectively, from linear mixed-effects
 970 models (see Methods). Confidence intervals (95%) not overlapping with the dashed
 971 line (i.e. 0) indicate statistical significance ($p < 0.05$).
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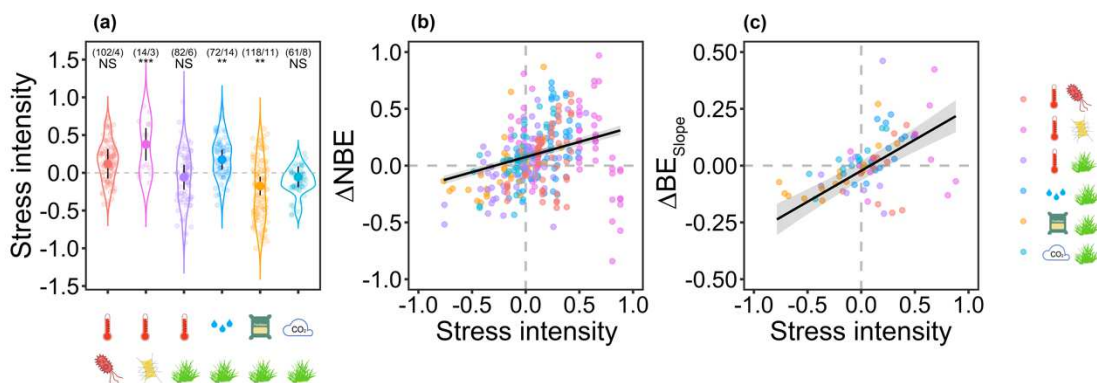
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974 **Figure 3** Complementarity (CE) (a) and selection (SE) (b) effects on biomass
 975 production under ambient (CE_A and SE_A , respectively, blue) and manipulated
 976 environmental conditions (CE_M and SE_M , respectively, red) and the difference
 977 between them ($\Delta CE = CE_M - CE_A$, $\Delta SE = SE_M - SE_A$, black), across different
 978 combinations of types of global change drivers (warming, drought, nutrient addition
 979 or elevated CO_2) and taxonomic groups (microbes, phytoplankton and plants). The
 980 numbers in brackets show the number of effect sizes and studies. Analyses were based
 981 on 12 experiments with raw data of monocultures, and CE and SE were square-root
 982 transformed (restoring the sign after transformation; see Methods). The points and
 983 shades represent the estimated means and confidence intervals, respectively, from
 984 linear mixed-effects models (see Methods). Confidence intervals (95%) not
 985 overlapping with the dashed line (i.e. 0) indicate statistical significance ($p < 0.05$).



986

987 **Figure 4** Net biodiversity effect (NBE) as a function of experimental duration across
 988 different types of environmental manipulations and taxonomic groups: (a) warming
 989 on microbes (Pennekamp *et al.* 2018); (b) warming on plants (Cowles *et al.* 2016); (c)
 990 drought on plants (Wagg *et al.* 2017); (d) nutrient addition on plants (Reich *et al.*
 991 2001); (e) CO₂ enrichment on plants (Reich *et al.* 2001).



992

993 **Figure 5** Distribution of environmental stress intensity for each combination of types
 994 of environmental manipulations and taxonomic group (a), and relationship between

995 changes in biodiversity effects (ΔNBE , $\Delta\text{BE}_{\text{slope}}$) and stress intensity (b, c). In (a),
996 light-colored points represent the distribution of stress intensity, which was calculated
997 as the relative difference under ambient vs. manipulated environmental conditions in
998 each study. Positive (negative) values mean lower (higher) monoculture functions in
999 manipulated environments. Colored points represent their averages with 95%
1000 confidence intervals (black bars), and numbers on the top represent sample sizes. The
1001 numbers in brackets show the number of effect sizes and studies. In (b) and (c),
1002 changes in biodiversity effects between manipulated and ambient environmental
1003 conditions were calculated in two ways: the difference in net biodiversity effect
1004 (ΔNBE ; $N = 327$, $n = 46$, $p < 0.0001$) (b) and the difference in the log-log slope
1005 between ecosystem functioning and species richness ($\Delta\text{BE}_{\text{slope}}$; $N = 76$, $n = 46$, $p =$
1006 0.0003) (c). Trendlines and 95% confidence intervals are given. NS, not significant
1007 ($p > 0.1$); *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.