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► **To cite this version:**

Junwei Luan, Siyu Li, Shirong Liu, Yi Wang, Liping Ding, et al.. Biodiversity mitigates drought effects in the decomposer system across biomes. *Proceedings of the National Academy of Sciences of the United States of America*, 2024, 121 (13), pp.e2313334121. 10.1073/pnas.2313334121 . hal-04771105

HAL Id: hal-04771105

<https://hal.science/hal-04771105v1>

Submitted on 7 Nov 2024

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3 **Main Manuscript for**

4 Biodiversity mitigates drought effects in the decomposer system 5 across biomes

6

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29 PNAS strongly encourages authors to supply an ORCID identifier for each author. Do not include
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31 account at www.pnascentral.org. For proper authentication, authors must provide their ORCID at
32 submission and are not permitted to add ORCIDs on proofs.

33 **Author Contributions:** J. Luan and S. Liu designed the experiment, J. Luan and S.
34 Hättenschwiler discussed the statistical analyses and jointly wrote the manuscript, J. Luan
35 conducted the statistical analyses. J. Luan, S. Li, L. Ding, and H. Lu conducted the litter
36 decomposition experiment and analyzed the samples. S. Han and J. Zhang designed, conducted
37 and maintained the rainfall exclusion experiment of temperate Korean pine and broadleaf mixed
38 forest; S. Liu, J. Luan, and Y. Wang designed, conducted and maintained the rainfall exclusion
39 experiment of warm-temperate oak forest and subtropical bamboo forest; S. Liu and L. Chen
40 designed, conducted and maintained the rainfall exclusion experiment of subtropical mixed pine
41 forest; Y. Zhang and W. Zhou designed, conducted and maintained the rainfall exclusion
42 experiment of tropical rainforest.

43 **Competing Interest Statement:** The authors declare no competing interests.

44 **Classification:** Ecology.

45 **Keywords:** Biodiversity; Climate change; Ecosystem functioning; Forest carbon cycling; Litter
46 decomposition; Plant-soil interactions; Soil nutrient cycling; Soil fauna

47

48 **This file includes:**

49 Main Text
50 Caption of Figures 1 to 3

51

52

53 **Abstract**

54 Multiple facets of global change affect the Earth System interactively with complex consequences
55 for ecosystem functioning and stability. Simultaneous climate and biodiversity change are of
56 particular concern, because biodiversity may contribute to ecosystem resistance and resilience
57 and may mitigate climate change impacts. Yet, the extent and generality of how climate and
58 biodiversity change interact, remain insufficiently understood, especially for the decomposition of
59 organic matter, a major determinant of the biosphere – atmosphere carbon feedbacks. With an
60 inter-biome field experiment using large rainfall exclusion facilities, we tested here how drought, a
61 common prediction of climate change models for many parts of the world, and biodiversity in the
62 decomposer system drive decomposition in forest ecosystems interactively. Decomposing leaf
63 litter lost less carbon (C) and especially nitrogen (N) in drier forest floors of five different forest
64 biomes following partial rainfall exclusion compared to conditions without any rainfall exclusion.
65 An increasing complexity of the decomposer community alleviated drought effects with full
66 compensation when large-bodied invertebrates were present. Likewise, mixing leaf litter from
67 different plant species increased diversity effects with increasing litter species richness,
68 counteracting drought effects on C and N loss. Our results show at a relevant spatial scale
69 covering distinct climate zones that both, the diversity of decomposer communities and plant litter
70 in forest floors have a strong potential to mitigate drought effects on C and N dynamics during
71 decomposition. Preserving biodiversity at multiple trophic levels contributes to ecosystem
72 resistance and appears critical to maintain ecosystem processes under ongoing climate change.

73 **Significance Statement**

74 Changing climate and biodiversity modify the functioning of ecosystems. Yet, their interactions
75 remain insufficiently understood, especially for decomposition, a key process for biosphere –
76 atmosphere carbon feedbacks. We tested how drought and the diversity of soil organisms and
77 plant leaf litter interactively drive decomposition in forest ecosystems across distinct climate
78 zones. An increasingly complex decomposer community alleviated negative drought effects on
79 decomposition, with full compensation when large-bodied invertebrates were present. Likewise,

80 plant litter mixing counteracted drought effects with increasing species numbers. Our results
81 show that biodiversity in the decomposer system has a strong potential to mitigate drought effects
82 on biogeochemical cycling. These findings suggest that fostering biodiversity is an important
83 leverage for maintaining critical ecosystem functions under ongoing climate change.

84

85 **Main Text**

86 **Introduction**

87 Climate change profoundly affects ecosystem structure and function (1-3). Ecosystem processes
88 with strong temperature and humidity dependence, such as litter decomposition (4-6) that drives
89 much of the terrestrial carbon (C) and nutrient cycling, may be particularly sensitive (7-9).
90 Decomposition is regulated by a high diversity of soil organisms ranging from prokaryotes to
91 macro-invertebrates that are organized in highly complex food webs (10). Decomposition further
92 depends on the characteristics and diversity of plant-produced organic matter as the primary
93 energy source (11, 12). While all these components of the decomposer system are fundamental
94 for the understanding of biodiversity effects on ecosystem functioning (13, 14), their complexity
95 render the prediction of the consequences of climate change challenging (15, 16). Biodiversity
96 may alleviate adverse climatic conditions because of an increasing probability of more resistant
97 species being present (known as the insurance hypothesis of biodiversity (17, 18)). Such
98 compensatory effects of biodiversity were reported for primary productivity of plant communities
99 (19, 20), but it remains unclear how biodiversity changes across trophic levels affect other
100 ecosystem processes, such as decomposition.

101 Beyond rising temperature, an increasing frequency and intensity of drought events are among
102 the most common and likely predictions of the possible consequences of ongoing climate change,
103 in particular for the Northern Hemisphere (21). Drought leads to water limitation in the activity and
104 ultimately in the abundance and composition of decomposer communities (22-25). Climate
105 change induced shifts in plant community composition and the loss of plant species (26) affects

106 substrate availability to decomposers through altered plant litter production and composition,
107 which can have additional indirect effects on decomposition (12, 27).

108 The limited number of existing studies indicate that increasing litter diversity may mitigate slower
109 decomposition under drought (24, 28, 29), but these effects can be very small (28) and were not
110 supported by others (30). Decomposers on the other hand show body-size dependent drought
111 resistance (31) that can also vary among taxa (32). Detritivores of relatively large body size may
112 be less drought sensitive than microorganisms (27), and they can considerably increase overall
113 decomposition either directly through litter consumption and fragmentation (33), or indirectly
114 through cascading effects on microbial decomposers by the transformation of litter to faeces (34).
115 Increasing litter diversity and decomposer community complexity can interactively change carbon
116 (C) and nitrogen (N) fluxes during litter decomposition in a variety of ecosystems (12), but it is
117 presently unknown how increasing drought intensity predicted for the near future modifies these
118 interactions, which critically limits the understanding of the consequences of concomitantly
119 changing climatic conditions and biodiversity for biogeochemical cycling.

120 We addressed this question in the present study across different forest biomes ranging from the
121 temperate to the tropical climate zone across China. We manipulated forest floor humidity with a
122 series of rainfall exclusion experiments and the complexity of decomposer communities and the
123 richness of plant leaf litter in the field (SI Appendix, Table S1 and Fig. S1, Methods). We
124 hypothesized that 1) reductions in the amount of rainfall, followed by lower soil moisture, will
125 decrease carbon (C) and nitrogen (N) fluxes during decomposition and that 2) higher litter
126 diversity and more complex decomposer communities alleviate the negative drought effects.

127

128 **Results and Discussion**

129 Partial rainfall exclusion reduced topsoil moisture by an average of 20.6 ± 4.1 % across the five
130 different forest biomes, but soil temperature did not change (SI Appendix, Table S1). As
131 expected, total litter mass loss proceeded less rapidly under drought (46.8 ± 7.8 % on average)

132 compared to control conditions (57.8 ± 7.2 % on average) (SI Appendix, Table S2). Accordingly,
133 there was 17.9 ± 4.4 % less C and 27.4 ± 4.2 % less N lost from decomposing litter in drought
134 compared to control plots (Fig. 1, Table 1; SI Appendix, Fig. S2). Slower decomposition under
135 drought was reported in earlier studies, both including soil invertebrates (24) or solely microbial
136 driven (35), and confirms the important role of climate control over decomposition (4-6). An
137 increasing complexity of the decomposer communities, which is likely associated with higher
138 functional diversity, increased C and N loss from decomposing litter, regardless of the treatment-
139 induced differences in soil moisture (Table 1, Fig. 1), underpinning the critical role of a diverse
140 decomposer community in the C and N cycle (12). Across all sites, the presence of mesofauna
141 (e.g. springtails and mites) in the decomposer community increased C and N loss on average by
142 15.4 ± 2.0 % and 15.9 ± 12.9 %, respectively (Fig. 1, Table 1), and the complete decomposer
143 community, additionally including macrofauna (e.g. millipedes and isopods), increased C and N
144 loss by 35.2 ± 2.3 % and 51.9 ± 17.1 %, respectively (compared to the treatment without access
145 of these two groups of organisms). These differences in C and N loss due to an increasing
146 decomposer community complexity are comparable to previous studies (12, 36) and are within
147 the range of a former global meta-analysis (37) that, however, showed some differences among
148 biomes. They reported for example somewhat higher fauna effects in tropical wet forests than in
149 deciduous forests on average (37). Our experimental design with replicated partial rainfall
150 exclusion plots and control plots in one forest of each biome, does not allow to thoroughly test
151 biome-specific differences (Methods). The effects of the complete decomposer community
152 appeared to vary little among the distinct forest ecosystems in five different biomes, but seemed
153 to be comparatively larger in the temperate Korean pine mixed broadleaf forest (the climatically
154 least favorable northernmost location) and the subtropical mixed pine forest (the second most
155 southern and climatically rather favorable location) and lowest in the bamboo forest (intermediate
156 latitudinal position) (SI Appendix, Tables S2-S4).

157

158 The relative difference between the drought and the control treatment was smaller the more
159 complex the decomposer community, in particular for C loss (Fig. 1a). In fact, the drought effect
160 size on C loss was significantly smaller (less negative) when all decomposer organisms were
161 present compared to when larger size invertebrates were absent (Fig. 1c). Marginally significant
162 interactions between drought and decomposer complexity were also observed for net diversity
163 effects of C and N loss (Table 2). Most importantly, the average C and N losses tended to be
164 even higher (statistically not significantly different) under drought with the full decomposer
165 complexity compared to the control treatment with the simplest decomposer community
166 (excluding meso- and macrofauna, see dashed line in Fig. 1a, b). These results indicate that
167 larger invertebrates can fully compensate drought effects on microbial dominated decomposition.
168 Soil fauna activity was only little affected by reduced precipitation in previous studies (38, 39),
169 and much less than the considerably reduced activity of microbial decomposers (38). Such
170 contrasting responses in activity to drought can result in strong negative effects on microbial
171 driven litter C loss without any change in detritivore-driven litter C loss (27). Drought mitigating
172 effects on decomposition by soil fauna were reported during the extreme El Niño year in 2015-16
173 in a Bornean tropical rainforest (33). Fauna effects could also have longer lasting ecosystem
174 consequences via changes in nutrient dynamics (33) and through fauna-induced translocation of
175 organic matter into deeper and more humid soil layers (40), which could be particularly relevant in
176 a future climate with less precipitation. However, in the longer term, potentially counteracting
177 effects through changes in the abundance of certain groups of soil fauna are also possible (23,
178 24), which can lead to altered food web structure and indirect drought effects through modified
179 trophic interactions (41).

180

181 Nitrogen loss during decomposition increased with the number of litter types in the litter
182 mixtures (SI Appendix, Fig. S2; Table 1), showing that tree species diversity modifies N cycling
183 via a mixed litter layer decomposing on the forest floor across substantially different forest types.

184 While this positive litter richness effect is broadly in agreement with recent meta-analyses on litter
185 diversity effects beyond two litter species (42, 43), they were comparatively modest, and the litter
186 richness effects on C loss further depended on partial rainfall exclusion (significant drought x litter
187 type richness effect, Table 1). This interaction with drought was mostly driven by smaller
188 differences in C loss between drought and control conditions from two- and four-species mixtures
189 (SI Appendix, Fig. S2). The litter type richness effect on N loss was more consistent across
190 treatments with overall increasing N losses with increasing litter species number. At the highest
191 richness level of four litter species, for example, this resulted in 9.4 % and 33.7 % higher N loss
192 compared to one-species litter treatments in control and drought conditions, respectively,
193 indicating a stronger litter richness effect under drought. During the initial stage of decomposition,
194 N can also be immobilized possibly leading to net increases in litter N rather than net N losses
195 (44). Although we measured net N loss across all treatment combinations, there was some
196 apparent net N immobilization in the two northernmost sites of the temperate Korean pine and
197 broadleaf mixed forest (KBF) and the warm-temperate oak forest (OF) (SI Appendix, Table S4).
198 This N immobilization was driven entirely by the pine species at these two sites, *Pinus koraiensis*
199 (at KBF) with an average net N increase of 113%, and *Pinus armandii* (at OF) with an average
200 net N increase of 19% across all treatment combinations.

201

202 For a more detailed evaluation of the litter diversity effects we used the additive partitioning
203 approach (45) based on the data of individual litter species C and N loss within all litter mixtures
204 (Methods). Additive partitioning allows to separate the overall net diversity effect into
205 complementarity and selection effects (the details of the applied formulae for these calculations
206 are presented in Loreau and Hector's paper (45)). The complementarity effect quantifies the part
207 of the diversity effect that is driven by interactions among species. For example, if decomposition
208 mutually increases when species A and species B are mixed together (for example through
209 nutrient transfer (12)) compared to when they decompose alone, a positive complementarity

210 effect would result. On the other hand, if species C slows decomposition of admixed species, for
211 example via inhibiting compounds, a negative complementarity effect would result. The selection
212 effect quantifies the part of the net diversity effect that is driven by the presence of a particular
213 species dominating the decomposition of the mixture as a whole, for example a very slowly
214 decomposing species. Our results showed that the overall mean positive net diversity effects on
215 C and N loss were largely driven by complementarity effects (Fig. 2, Table 2; SI Appendix, Fig.
216 S2 and S3), corroborating previous findings (12, 46). The fact that selection effects were overall
217 unimportant is a noteworthy result, in particular with the distinct functional litter types chosen here
218 at all five locations. We expected that specific traits of some of the included litter types such as
219 conifer needle litter or litter from N-fixing plant species could trigger negative or positive selection
220 effects due to their presence within a litter mixture. The dominant role of complementarity effects
221 rather suggests that litter diversity effects were determined by interactions among distinct litter
222 types, for example by providing more diverse and complementary resources or more suitable
223 habitats to decomposers possibly allowing the establishment of a more active, more diverse or
224 more abundant decomposer community (47, 48). These complementarity-driven interactions
225 among litter types increased significantly with increasing litter type richness (Fig. 2, Table 2; SI
226 Appendix, Fig. S3), clearly showing that a higher diversity of litter functional types within litter
227 mixtures improve mixture decomposition with higher C and N turnover rates. This important result
228 for the understanding of the role of biodiversity in biogeochemical cycling, appeared to be robust
229 across five distinct forest types from contrasting biomes (SI Appendix, Table S5 and S6), but
230 again, a thorough test for potential biome-specific responses would require multiple study sites
231 within each biome.

232

233 Although drought reduced net diversity and complementarity effects overall, they remained
234 significantly positive (Fig. 2, Table 2; SI Appendix, Fig. S3), and kept increasing with increasing
235 litter type richness, although at a somewhat lower rate (significant drought x litter type richness

236 interaction, Table 2). This sustained increase in complementarity effects under drought with
237 increasing litter type richness, indicates that higher litter diversity can counteract negative drought
238 effects on litter C and N loss. For example, net diversity effects of three- and four-species
239 mixtures under drought were up to two times higher compared to those of two-species mixtures
240 under control conditions (Fig. 2c, d). Maintaining similar diversity effects with the exclusion of
241 substantial amounts of rainfall suggests that the mechanisms underlying complementarity effects
242 are largely the same and remain operational under drought. Interestingly, the generally higher net
243 diversity effects with increasing decomposer community complexity, tended to be stronger under
244 drought (Fig. 3, marginally significant drought x decomposer complexity interaction for both C and
245 N loss, Table 2). Accordingly, the negative drought effects were fully compensated by the most
246 complex decomposer community (Fig. 3), suggesting that complementarity under drought
247 became particularly important when litter feeding macrofauna had access. This supports the
248 critical importance of larger soil fauna for decomposition when conditions are becoming drier (27,
249 33, 38) as discussed above.

250

251 **Implications**

252 Our study underscores the importance of functional tree diversity and decomposer community
253 complexity, in particular the presence of litter feeding macrofauna, in maintaining ecosystem
254 functioning under ongoing climate change. We provide strong evidence for drought mitigation
255 effects of litter diversity and decomposer community complexity on biogeochemical cycling across
256 a wide variety of distinct forest types. However, in the longer term, species distribution, and hence
257 community composition and relative species abundances will be affected by climate change (49).
258 The associated changes in litterfall composition and decomposer community complexity may then
259 modify the drought mitigation effects of litter diversity and detritivore macrofauna on C and N
260 cycling we reported here. Depending on how litter functional diversity and decomposer
261 communities are altered, the resulting changes may lead to stronger or weaker mitigation effects.

262 This may also provide the possibility for potential management decisions in managed forests for
263 example, by fostering a functionally diverse litter layer and favoring litter detritivores and complex
264 decomposer communities towards maintaining ecosystem functioning under more constraining
265 future climatic conditions.

266

267 **Materials and Methods**

268

269 ***Experimental sites and design***

270 The experiments were set up in five distinct forest ecosystems across a broad latitudinal gradient
271 spanning from the temperate to the tropical climatic zone (see SI Appendix, Fig. S1 and Table
272 S1). Accordingly, there were marked differences in climatic conditions with mean annual
273 temperatures ranging between 3.8 °C and 22.5 °C and mean annual precipitation between 745
274 mm and 1428 mm (SI Appendix, Table S1). At each of the five sites increased drought was
275 simulated using partial rain exclusion beneath the tree canopies at about 1.5~2 m above the soil
276 surface. Partial rain exclusion removed 50% of total precipitation except of the Korean pine and
277 broadleaf mixed forest site with 30% removal (SI Appendix, Table S1, Fig. S1). Detailed
278 descriptions for the partial rain exclusion experiments at the different sites were published
279 previously (50-54). At all sites, rainfall exclusion was applied using a pairwise design with three
280 replicated pairs of 20 x 20 m plots, except for the bamboo forest with four replicated plot pairs, the
281 Korean pine and broadleaf mixed forest with larger plots of 25 x 50 m, and the tropical rainforest
282 with five replicated smaller plots of 10 x 10 m. The paired plots were separated by at least a 15 m
283 wide buffer strip and with buried PVC boards (down to 100 cm of soil depth) along the
284 circumference of each plot to avoid lateral water movement, except for the Korean pine and
285 broadleaf mixed forest, where this additional plot separation was unnecessary with a rather flat
286 topography. Partial rainfall exclusion was applied all year round, except for the two temperate
287 sites (Korean pine and broadleaf mixed forest and oak forest) where the exclusion panels were
288 removed during the winter to avoid snow damage. The precipitation received as snowfall in the

289 partial exclusion plots during winter was less than 20% and 10% of the total annual rainfall at
290 Korean pine and broadleaf mixed forest and oak forest, respectively. Partial rainfall exclusion
291 significantly reduced moisture within the topsoil by an average of $20.6 \pm 4.1\%$ across all sites (SI
292 Appendix, Table S1), but there were no significant differences in soil temperature.

293

294 At each location, the decomposition experiment included leaf litter from the most common site-
295 specific native tree species from each of the same four distinct functional types, including different
296 N acquisition strategies (N fixer versus not N fixer), C allocation strategies (deciduous versus
297 evergreen), leaf type of evergreen (broadleaved versus coniferous), and litter recalcitrance of
298 deciduous non-N-fixers (rapidly decomposing versus slowly decomposing leaf litter). See SI
299 Appendix Fig. S1 for tree species selected from each site, their initial litter C to N ratio, and their
300 C loss rate. Since there were no conifer tree species in the tropical rainforest, we used leaf litter
301 from *Castanopsis echidnocarpa* instead, which shares similar traits with conifers (evergreen,
302 slowly decomposing and needle-shaped leaves). We used three different mesh sizes (0.05 mm, 1
303 mm, 5 mm) for litterbag construction. The different mesh sizes were chosen to allow access to an
304 increasingly complex community of decomposer organisms. The smallest mesh width of 0.05 mm
305 allowed access to microorganisms and microfauna (e.g. nematodes and protists), the
306 intermediate mesh width of 1 mm additionally allowed access to mesofauna (e.g. collembolans
307 and mites), and the largest mesh width of 5 mm also let pass macrofauna (e.g. isopods and
308 smaller earthworms). The bottom side of all litterbags was made uniformly of 0.05 mm nylon
309 mesh to prevent gravitational loss of small litter particles. All three types of litterbags (i.e. three
310 different mesh sizes) contained litter from either of the four tree species individually or from the
311 mixtures of all possible combinations of these four species (a total of 11 mixtures). Litterbags of
312 all mesh sizes and all litter combinations were placed in each control plot and in each plot with
313 rainfall exclusion at all five locations ($n = 5$ locations \times 2 precipitation treatments \times 15 litter
314 combinations \times 3 mesh sizes \times 5 replicates for tropical rainforest and 4 replicates for bamboo

315 forest and 3 replicates for the other sites = 1620). In some of the locations there were two
316 litterbags per treatment combination and per plot, but we always used plot means for the
317 statistical analysis.

318

319 ***Leaf litter collection and field incubations***

320 We collected the leaf litter with litter traps underneath the trees from the four target species (at
321 least and often more than 10 individuals per species) at each site close to the experimental plots
322 and created one common pool of litter for each litter species. We filled the 20 cm x 20 cm
323 litterbags with a total of 8 g oven dried (at 65°C) litter for each litter treatment with equal amounts
324 of different species in mixed litterbags. The litterbags were placed at each plot avoiding edge
325 effects of the rain exclusion structures and with at least 0.5 m distance among individual
326 litterbags. Each litterbag was properly held in place by fixing the corners of the litterbag with
327 stings, while the bottom mesh was in intimate contact with the soil surface (natural litter layer
328 removed before litterbag placement). The initial litter characteristics of each litter species were
329 determined from five samples randomly taken from the well-mixed litter pool per species. The
330 samples were oven dried to constant mass at 65°C and then ground with a ball mill to a fine
331 homogeneous powder, with aliquots then analyzed for C, N, and P concentrations. Initial litter C
332 and N concentrations were analyzed using an elemental analyzer (Costech ECS 4010, Valencia,
333 Italy). Initial phosphorus (P) concentration was determined by an automatic chemical analyzer
334 (Smartchem 300, AMS, Italy).

335

336 ***Mass, C and N loss from litterbags***

337 The litterbags were left in the field for 254 to 368 days depending on the site (SI Appendix, Table
338 S1). After litterbag retrieval from the field, we dried samples to constant mass at 65 °C, then
339 separating into individual species (for mixed species litterbags) by gently cleaning litter by
340 brushing off any dirt without using water (to prevent nutrient leaching) before measuring dry mass
341 for each constituent species. Mass loss, and C and N concentrations (using the same method as

342 described above for initial litter characteristics) of the litter were determined for each individual
343 litter species sorted from each litterbag. Litter C and N loss (%) was calculated as $100 \times [(M_i \times CN_i) -$
344 $(M_f \times CN_f)] / (M_i \times CN_i)$, where M_i and M_f are the initial and final litter dry mass, respectively, and
345 CN_i and CN_f are the initial and final C or N concentrations (% of litter dry mass).

346

347 ***Calculations and statistical analysis***

348 The separation of all individual litter types at the end of the decomposition experiment allowed us
349 to use the additive partitioning approach to tease apart the two alternative mechanisms of the
350 complementarity and the selection effect, which both contribute to the net diversity effect (45) for
351 both C and N loss from litter mixtures. The complementarity effect refers to any biotic interactions
352 among individual species within mixtures. These can be positive, for example when transfer of
353 elements such as N or C among litter types increase decomposition of the mixture compared to
354 when individual litter types decompose singly. Complementarity effects can also be negative,
355 although this is less frequently observed, when for example a specific species is rich in inhibiting
356 compounds, such as phenolics, which then also slows decomposition of admixed litter types. The
357 selection effect on the other hand quantifies a dominance effect of a particular species, for
358 example for a litter type that decomposes much less rapidly than others and may then dominate
359 the decomposition of the mixture. The calculations are explained in detail in Loreau and Hector's
360 paper (45). Briefly, the net biodiversity effect was measured as the difference between the
361 observed loss of the element in the mixture during the experiment and the expected loss in the
362 mixture based on the measured element loss of individual litter types decomposing singly, that is
363 $\Delta Y = Y_O - Y_E$, where $Y_O = \sum_i Y_{O,i}$ is total observed element loss of the mixture, $Y_{O,i}$ = observed
364 element loss of species i in the mixture, $Y_E = \sum_i Y_{E,i} = \sum_i RY_{E,i} \times M_i$ is the total expected element loss
365 of the mixture, $Y_{E,i} = RY_{E,i} \times M_i$ = expected element loss of species i in the mixture, M_i is the
366 element loss of species i in single species litterbags, $\Delta RY_i = RY_{O,i} - RY_{E,i}$ is the deviation from
367 expected relative element loss of species i in the mixture, $RY_{O,i} = Y_{O,i} / M_i$ = observed relative

368 element loss of species i in the mixture, and $RY_{E,i}$ = expected relative element loss of species i in
369 the mixture.

370

371 The net biodiversity effect is the sum of the complementarity effect and the selection effect, that
372 is:

$$373 \Delta Y = N_s \overline{\Delta RY\bar{M}} + N_s \text{cov}(\Delta RY, M)$$

374 with $N_s \overline{\Delta RY\bar{M}}$ quantifying the complementarity effect, and $N_s \text{cov}(\Delta RY, M)$ quantifying the
375 selection effect.

376 N_s is the number of species in the mixture.

377 To meet the assumptions for the analysis of variance of net diversity, complementarity and
378 selection effects, all data of C and N loss were square-root transformed but the original negative
379 and positive signs for the transformed values were kept.

380

381 We used the natural logarithm of the response ratio (R) as a metric of effect size (55) on C loss, a
382 metric that reflects a relative change in the variable due to partial rainfall exclusion:

$$383 \ln R = \ln (X_T/X_C)$$

384 where X_T is the treatment mean and X_C is the control mean. If the treatment increased or
385 decreased the target variable the effect size $\ln R$ was greater or smaller than zero, respectively.

386 And we used Hedges d as a metric of effect size on N loss because there are negative values
387 (56).

$$388 d = \frac{Y_e - Y_c}{\sqrt{\frac{(N_e - 1)S_e^2 + (N_c - 1)S_c^2}{N_e + N_c - 2}}} J$$

$$389 J = 1 - \frac{3}{4(N_e + N_c - 2) - 1}$$

390 Y_e and Y_c are the treatment mean and control mean; N_e and N_c are the treatment sample number
391 and control sample number, S_e and S_c are the variance for the treatment and control,
392 respectively.

393

394 Analysis of variance were conducted to assess the effects of drought, the richness of plant litter
395 functional types, the complexity of the decomposer community, and their interactions on litter C
396 and N loss, and diversity effects (net diversity effect, complementarity effect, and selection effect)
397 of plant litter mixtures on C and N loss. We included the location (the experimental site within
398 each biome) as a random effect in the mixed models, because we had no *a priori* hypothesis for
399 the drought effects among the different sites. Also, the sites were not replicated within biomes
400 because of the very heavy workload to keep five rain exclusion facilities running simultaneously.
401 Although the experiments were well replicated within each of the five biome-specific sites, each
402 biome is represented by one single forest site, which does not allow to thoroughly test biome-
403 specific responses. Analysis of variance was also performed to assess the effects of decomposer
404 complexity or plant litter functional type richness on the response ratio ($\ln R$) of litter C loss and
405 multiple comparisons were conducted with least significant difference (LSD) method. We further
406 assessed the drought effect on net diversity effect of plant litter mixtures on C and N loss for each
407 level of decomposer complexity or plant litter functional type richness, where location was
408 considered as random effect using the same type of the mixed models mentioned above. All the
409 statistical analyses were conducted using IBM SPSS Statistics 21.0 (IBM SPSS Statistics Inc.,
410 USA).

411

412 **Acknowledgments**

413 We would like to thank Drs. Dapao Yu, Guanhua Dai, Xinwei Guo, Jinglei Zhang for their help in
414 experiment implementation and field sampling. Thanks go to Professor Joann K. Whalen for her
415 valuable comments on the early stage of the manuscript. This study was jointly funded by the
416 National Key R&D Program of China (2021YFD2200403, 2021YFD2200405), Science and
417 technology cooperation projects between governments of China and the European Union
418 (2023YFE0105100), the National Natural Science Foundation of China (No. 31930078,
419 31971461, 31670450, 32101500, 42073080), and the Fundamental Research Funds for ICBR
420 (1632021023; 1632019006; 1630032023002).

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555 **Figure captions**

556

557 **Figure 1. Litter C (a) and N (b) loss and drought effect size for C loss (c) and N loss (d) with**

558 **increasing complexity of decomposer communities.** Decomposer community complexity was

559 manipulated by using litterbags of 0.05 mm mesh size (allowing the presence of microorganisms

560 and microfauna (e.g., nematodes and protists) only), litterbags of 1 mm mesh size (allowing

561 additionally the access by mesofauna (e.g., springtails and mites)), and litterbags of 5 mm mesh

562 size (allowing access by the full complexity of decomposers communities including macrofauna

563 (e.g., millipedes and isopods)). Mean values of all litter treatments across the five locations are

564 shown for control plots (light blue) and for partial rainfall exclusion plots (orange) in panels a) and

565 b) ($n = 15$ litter combinations \times 18 replicated plots per treatment (control vs. drought) for the five

566 locations = 270, see Table 1 for statistics). The numbers on top of each pair of columns show the

567 relative difference between the mean values in the control and the drought treatment for each

568 level of decomposer complexity. Dashed lines in panels a) and b) indicate average values of litter

569 C or N loss in the control treatment with the simplest decomposer community. The drought effect

570 size (lnR) of C loss (panel c) and N loss (Hedges d , panel d) are shown for each level of

571 decomposer complexity, with different capital letters indicating significant decomposer complexity

572 differences at $P < 0.05$ (no significant differences for drought effect size on N loss). Dashed lines

573 in panels c) and d) indicate the zero line (negative effects sizes below and positive effect sizes

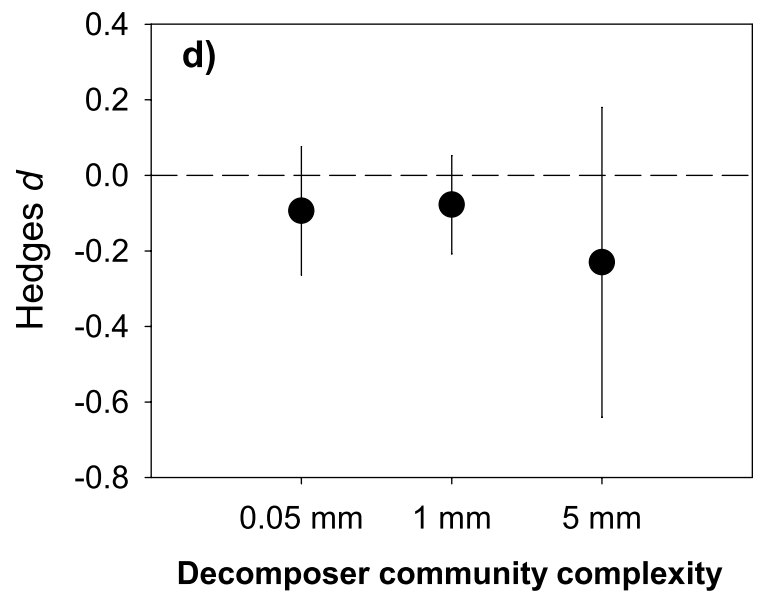
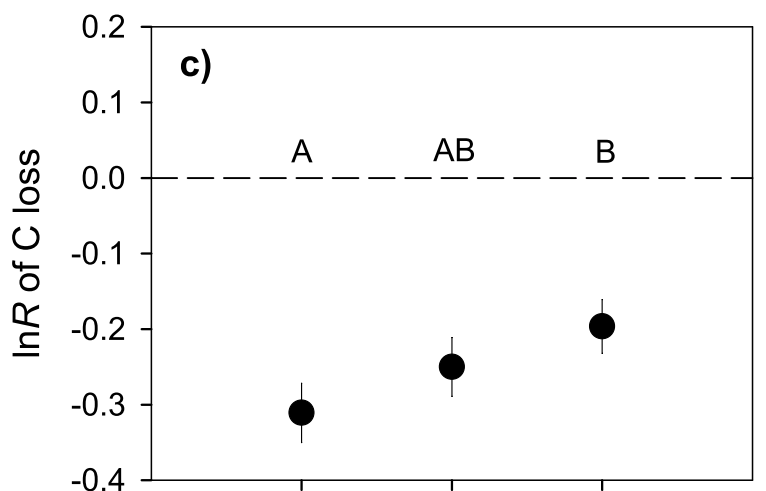
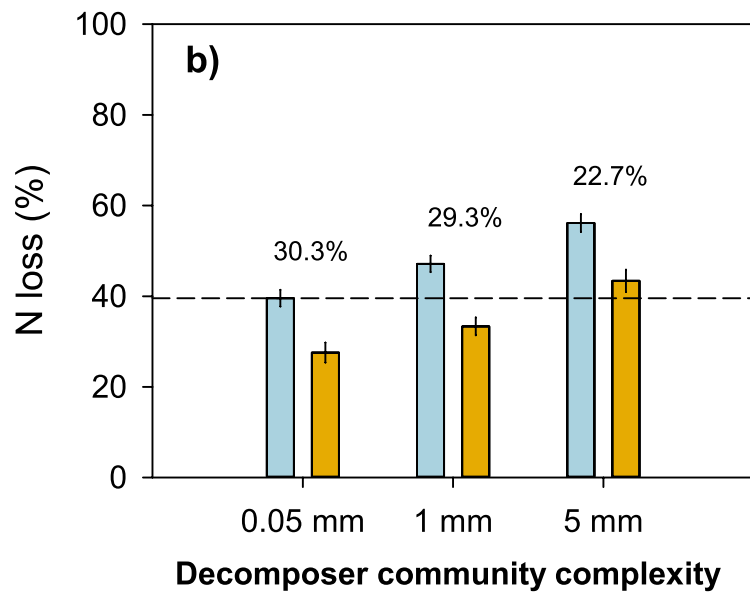
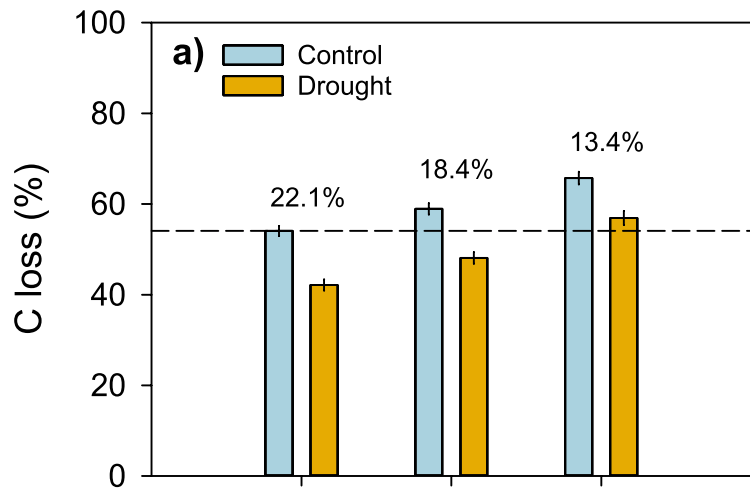
574 above the zero line). Linear mixed models, where location was considered as random effect were

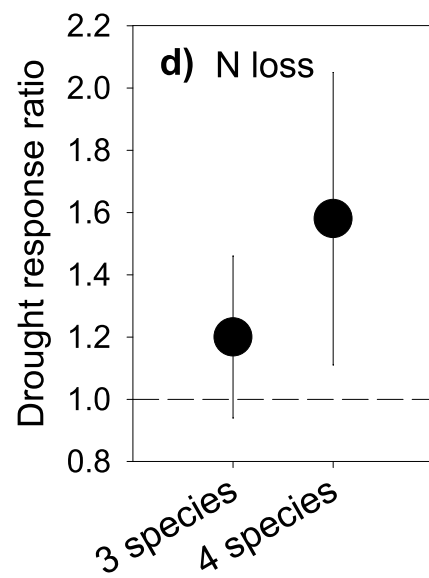
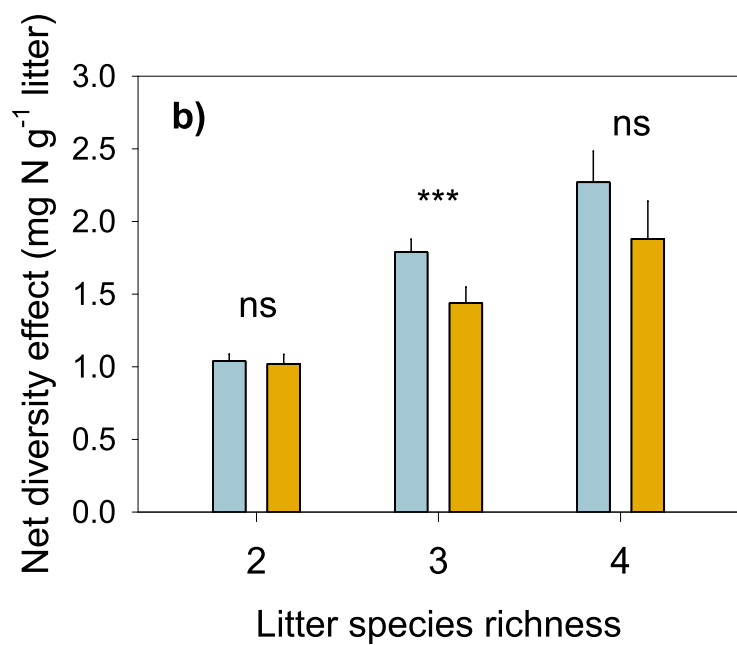
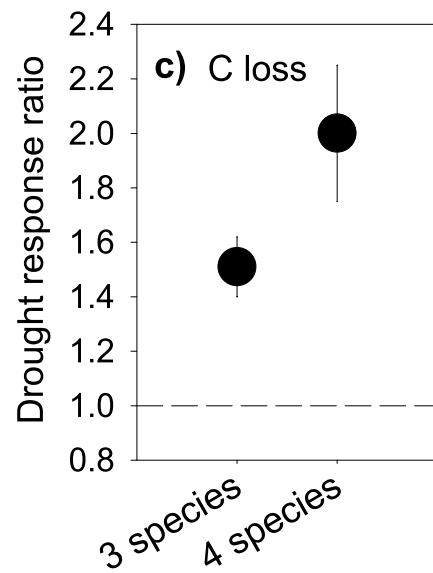
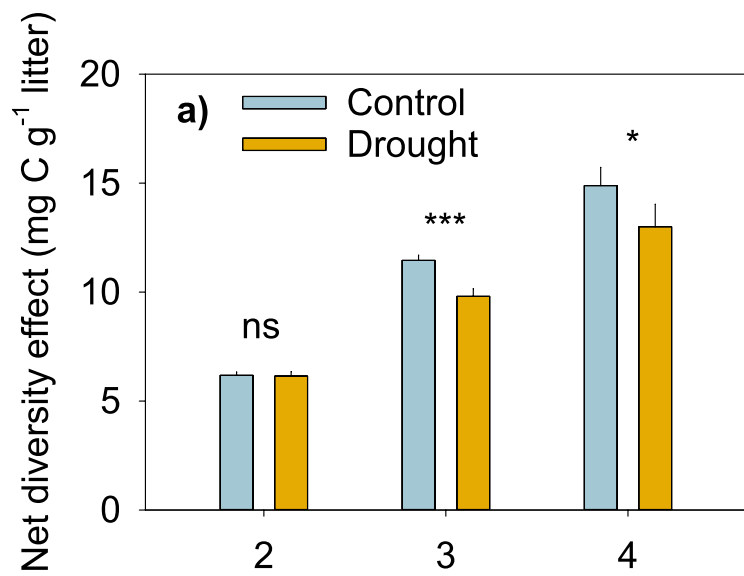
575 used for statistical testing and comparisons were done by the least square significant (LSD)

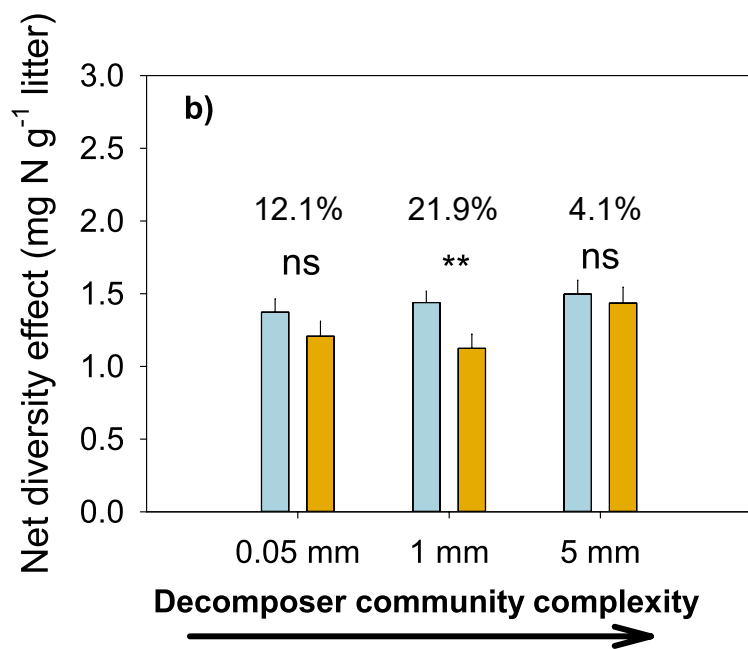
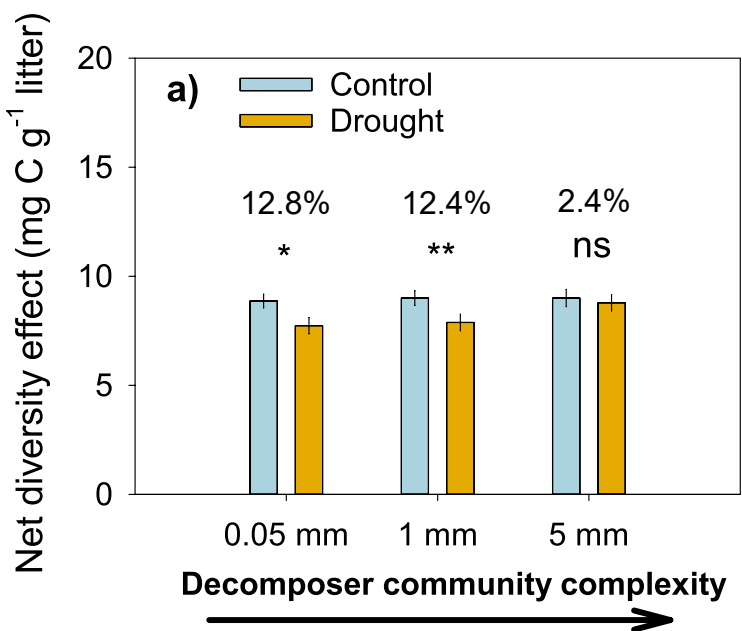
576 method.

577 **Figure 2. Net diversity effects in two-, three-, and four-species litter mixtures on C loss (a)**
578 **and N loss (b) and drought response ratios on C loss (c) and N loss (d).** Mean values of all
579 litter mixture treatments (single litter species treatments were used to calculate net diversity
580 effects) across the five locations are shown for control plots (light blue) and for partial rainfall
581 exclusion plots (orange) (n = 6, 4, and 1 litter combinations x 3 mesh sizes x 18 replicated plots
582 per treatment (control vs. drought) for the five locations = 324, 216, and 54 for two, three, and
583 four species mixtures, respectively., see Table 2 for statistics). Asterisks indicate significant
584 differences between control and drought treatments for each species richness level separately (*,
585 **, and *** denote significant effects at $P < 0.05$, $P < 0.01$, and $P < 0.001$, and ns = not statistically
586 significant). Panels (c) and (d) show the response ratios of the net diversity effects under drought
587 in three- and four-species litter mixtures compared to the two-species mixtures under control
588 conditions for C loss (c) and N loss (d).

589 **Figure 3. Net diversity effects with increasing decomposer community complexity (from**
590 **left (0.05 mm mesh) to right (5 mm mesh)) on C loss (a) and N loss (b).** Mean values of all
591 litter mixture treatments (single litter species treatments were used to calculate net diversity
592 effects) across the five locations are shown for control plots (light blue) and for partial rainfall
593 exclusion plots (orange) (n = 11 litter mixtures x 18 replicated plots per treatment (control vs.
594 drought) for the five locations = 198, see Table 2 for statistics). The numbers on top of each pair
595 of columns indicate the relative difference between the mean values in the control and the
596 drought treatment followed by asterisks for statistical significance (* and ** denote significant
597 effects at $P < 0.05$ and $P < 0.01$, and ns = not statistically significant) for each level of
598 decomposer complexity.







1

2

3 **Tables for**

4 Biodiversity mitigates drought effects in the decomposer system
5 across biomes

6

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9

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12

13 **This file includes:**

14 Tables 1 to 2

15

16 **Tables**

17

18 **Table 1. Variance in C and N loss associated with drought treatment, diversity, and their**
 19 **interactions.**

Source of variance	df	C loss		N loss	
		F	P	F	P
Drought	1	206.8	<0.001	70.4	<0.001
Leaf litter type richness (LR)	3	1.33	0.26	8.55	<0.001
Decomposers complexity (DC)	2	112.8	<0.001	41.2	<0.001
Drought * LR	3	2.96	0.03	0.86	0.46
Drought * DC	2	1.27	0.28	0.22	0.80
LR * DC	6	0.44	0.86	0.45	0.84
Drought * LR * DC	6	0.49	0.82	0.45	0.85

20 Analysis of variance was conducted by linear mixed models (LMM), where location was
 21 considered as random effect. Bold values are used for *P*-values indicating statistically significant
 22 effects at *P*<0.05.

23

24 **Table 2. Variance in net diversity effects, complementarity effects, and selection effects of**
 25 **litter mixtures on C and N loss associated with drought, litter type richness, decomposer**
 26 **community complexity, and their interactions.**

Source of variance	Net diversity			Complementarity		Selection	
	df	F	<i>P.</i>	F	<i>P.</i>	F	<i>P.</i>
C loss							
Drought	1	23.0	<0.001	12.8	<0.001	1.01	0.314
Leaf litter type richness (LR)	2	330.2	<0.001	260.1	<0.001	0.73	0.482
Decomposers complexity (DC)	2	8.30	<0.001	7.89	<0.001	0.88	0.415
Drought * LR	2	7.28	0.001	4.35	0.013	0.29	0.744
Drought * DC	2	2.57	0.077	2.59	0.076	2.16	0.116
LR * DC	4	1.01	0.399	0.81	0.517	0.10	0.982
Drought * LR * DC	4	1.28	0.276	1.04	0.388	0.23	0.919
N loss							
Drought	1	10.5	0.001	6.35	0.012	0.30	0.584
LR	2	52.5	<0.001	35.8	<0.001	1.99	0.137
DC	2	6.08	0.002	0.18	0.838	5.76	0.003
Drought * LR	2	2.69	0.068	2.24	0.107	0.96	0.384
Drought * DC	2	2.73	0.065	0.23	0.796	2.25	0.106
LR * DC	4	0.87	0.479	0.44	0.780	1.25	0.289
Drought * LR * DC	4	1.51	0.197	0.76	0.552	0.98	0.420

27 Analysis of variance was conducted using linear mixed models (LMM), where location was
 28 considered as random effect. Bold values are used for *P*-values indicating statistically significant
 29 effects at *P*<0.05.