

24 **Author Contributions**

25 SX and DL designed this study. SX searched the papers, collected the data, and analyzed the
26 data. SX and EJS wrote the paper. All authors revised and commented on the initial drafts and
27 final manuscript.

28 **Data availability statement**

29 The data set used for the meta-analysis will be made available after acceptance.

30 **Conflict of Interest Statement**

31 The authors declare that they have no conflict of interest.

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47 **Abstract**

48 The impacts of precipitation change on forest carbon (C) storage will have global consequences,
49 as forests play a major role in sequestering anthropogenic CO₂. Although forest soils are one
50 of the largest terrestrial C pools, there is great uncertainty around the response of forest soil
51 organic carbon (SOC) to precipitation change, which limits our ability to predict future forest
52 C storage. To address this, we conducted a meta-analysis to determine the effect of drought and
53 irrigation experiments on SOC pools, plant C inputs and the soil environment based on 161
54 studies across 139 forest sites worldwide. Overall, forest SOC content was not affected by
55 precipitation change, but both drought and irrigation altered plant C inputs and soil properties
56 associated with SOC formation and storage. Drought may enhance SOC stability by altering
57 soil aggregate fractions, but the effect of irrigation on SOC fractions remains unexplored. The
58 apparent insensitivity of SOC to precipitation change can be explained by the short duration of
59 most experiments and by biome-specific responses of C inputs and pools to drought or
60 irrigation. Importantly, we demonstrate that SOC content is more likely to decline under
61 irrigation at drier temperate sites, but that dry forests are currently underrepresented across
62 experimental studies. Thus, our meta-analysis advances research into the impacts of
63 precipitation change in forests by revealing important differences among forest biomes, which
64 are likely linked to plant adaptation to extant conditions. We further demonstrate important
65 knowledge gaps around how precipitation change will affect SOC stability, as too few studies
66 currently consider distinct soil C pools. To accurately predict future SOC storage in forests,
67 there is an urgent need for coordinated studies of different soil C pools and fractions across
68 existing sites, as well as new experiments in underrepresented forest types.

69

70 **Keywords:** precipitation change, drought, irrigation, forest soil organic carbon, plant carbon
71 inputs, SOC fractions.

72 **1. Introduction**

73 Global climate change is modifying precipitation patterns, including the amount, intensity, and
74 frequency of precipitation events (Huang et al., 2020; Kirchmeier-Young and Zhang, 2020),
75 and these changes will possibly continue at a faster rate in the future (Bao et al., 2017; Gampe
76 et al., 2021). Precipitation change, especially in the amount of annual precipitation, is thought
77 to have great impacts on ecosystem processes and functions, such as plant growth, biomass
78 accumulation, and soil carbon (C) cycling and storage (Wilcox et al., 2017; Zhou et al., 2016;
79 Wang et al., 2019; Xu et al., 2020). Thus, in recent decades, many field manipulation
80 experiments have applied drought and irrigation treatments to investigate the effects of
81 precipitation change on ecosystem processes and functions (Hicks et al., 2018; Zhou et al.,
82 2019; Zhang et al., 2020; Sun et al., 2023). In this context, assessing the impact of precipitation
83 change on forest soils is particularly pressing, because forest soils play a critical role in global
84 carbon (C) cycling and climate change mitigation: forest soils account for 16–26% of the global
85 soil C pool (Pan et al., 2011; IPCC, 2013; Wiesmeier et al., 2019) and influence biomass C
86 storage by supporting plant productivity (Schoenholtz et al., 2000; Deluca & Boisvenue., 2012).
87 Recent syntheses have assessed how precipitation change affects soil C dynamics (soil
88 respiration or soil C pools) across terrestrial ecosystems (Zhou et al., 2016; Du et al., 2020;
89 Deng et al., 2021; Chen et al., 2023). However, there remain large knowledge gaps around the
90 effects of precipitation change on soil C storage and stability. In particular, improved
91 understanding of the responses of distinct forest biomes and their soil C pools is critical for
92 predicting the capacity of forests to sequester and store C under future precipitation change.

93 Precipitation change can affect soil C storage by changing plant C inputs, soil C
94 decomposition and soil C stability. Precipitation affects soil water availability (Konapala et al.,
95 2020), and thus becomes an important factor regulating plant growth and biomass under natural
96 conditions, especially in water-limited systems (Maurer et al., 2020; Gampe et al., 2021; Hou

97 et al., 2021). Specifically, plants allocate more carbohydrates to roots to increase uptake
98 resources under drought conditions but allocate more to aboveground to maximize light capture
99 under increased precipitation (Wilcox et al., 2015, 2017). However, the response of plant
100 biomass to precipitation change can differ among forest types (Moser et al., 2014; Li et al.,
101 2021; Wang et al., 2021). For example, Samuelson et al. (2008) found that irrigation had little
102 effect on plant growth and biomass in a temperate plantation, whereas Wang et al. (2019a)
103 observed increased seedling height, basal diameter growth, and biomass production in response
104 to irrigation in a tropical forest. Precipitation change can also alter soil physicochemical and
105 biological properties, such as soil temperature, inorganic nitrogen (N) content (Chen et al.,
106 2019; Li et al., 2021), and microbial communities and activities (Zhou et al., 2018; Xu et al.,
107 2020), thus affecting plant growth and C storage (Zhou et al., 2016). For example, soil N
108 mineralization can increase under irrigation treatments (Cregger et al., 2014; Chen et al., 2017)
109 and greater precipitation generally favors the growth of soil microbes and increases
110 fungal:bacterial ratios in drylands, which can stimulate plant growth (Raczka et al., 2022), soil
111 C cycling and soil C storage (Waring et al., 2013; Nielsen and Ball, 2015). By contrast, although
112 experimental drought treatments have shown little effect on total N supply to plants (Homyak
113 et al., 2017), long-term drought treatments result in reduced plant productivity (Fridley et al.,
114 2016) and a shift towards soil microbial communities characterized by slow-growing, stress-
115 tolerant taxa (Sayer et al., 2017, 2021). Such changes in plant growth and microbial
116 communities under precipitation change will ultimately affect soil C cycling and storage.

117 Changes in precipitation can lead to altered inputs of plant litter and root-derived C
118 (Brunn et al., 2022) due to changes in plant C assimilation and growth (Wu et al., 2011). Such
119 changes in plant growth in turn affect the size of soil organic C (SOC) pool by altering the
120 balance between plant C inputs and soil C outputs (Fröberg et al., 2008; Zhou et al., 2016; Su
121 et al., 2023). In addition, soil respiration is affected by precipitation change both directly by

122 changes in soil moisture (Liu et al., 2016; Du et al., 2020) and indirectly via its impacts on
123 microbial biomass and communities (Zhou et al., 2018; Xu et al., 2020). However, we do not
124 know how SOC in different forest ecosystems responds to precipitation change because its
125 effects on C inputs and outputs depends upon numerous ecosystem characteristics (Zhou et al.,
126 2016; Wangdi et al., 2023). For example, plant C inputs decline under reduced precipitation
127 treatments, but soil respiration also declines, resulting in no net change or even a net gain in
128 SOC content (Zhou et al., 2016; Raczka et al., 2022). By contrast, both plant inputs and
129 respiration increase when precipitation is enhanced (Zhou et al., 2016; Heikkinen et al., 2022)
130 but water-saturated soils can quickly limit microbial activity (Chen et al., 2023). Thus, the
131 impacts of precipitation change on SOC depend largely on the hydrological conditions
132 influencing soil water content, such as mean annual precipitation (MAP) and
133 evapotranspiration rates, as these determine the sensitivity of plant and microbial growth to
134 precipitation change (Zeppel et al., 2014; Giardina et al., 2018; Bennett et al., 2020). As water
135 availability has such a strong influence on both plant growth and SOC, the site aridity is likely
136 an important factor in regulating the relationship between precipitation change and ecosystem
137 C storage (Li et al., 2020).

138 In addition to affecting the biotic processes involved in SOC accumulation, precipitation
139 change can also affect SOC storage by altering the chemical and physical processes
140 underpinning SOC stabilization (Chen et al., 2018; Zhang et al., 2019). The relative proportions
141 of distinct SOC fractions (e.g. soil aggregate and density fractions), can reflect SOC stability
142 and affect both the mineralisation and storage of SOC (John et al., 2005; Lützow et al., 2007;
143 Luo et al., 2017). Specifically, precipitation change can influence associations between organic
144 C and soil minerals by physically destroying soil macroaggregates, and alter amounts of
145 aggregate binding agents produced by plants and microbes (Yang et al., 2018; 2021). Drought
146 can destroy soil macroaggregates both directly through physical effects and indirectly by

147 reducing biological binding agents (Chen et al., 2019c) or altering rhizosphere characteristics
148 (Zhang et al., 2019). Rewetting after drought can also destroy aggregates by physical forces
149 (shrinkage followed by swelling; Deneff et al., 2001). Precipitation change can also indirectly
150 affect the formation of soil particulate and mineral-associated organic matter by altering
151 decomposition processes, soil oxygenation, pH, and soil physical characteristics (Angst et al.,
152 2023). The resulting changes in soil aggregate distributions can affect SOC stability and stocks
153 (Yang et al., 2021) because soil macro-aggregates generally contain large amounts of labile C,
154 whereas micro-aggregates generally contain more stable SOC with longer turnover times
155 (Puget et al., 2000). However, it is unclear how changes in soil aggregate distribution or organic
156 matter fractions might affect SOC stability and storage over the longer-term. In addition, very
157 few studies have measured how forest SOC pools or soil aggregate fractions respond
158 to increased precipitation, although there is evidence that enhanced water availability could
159 increase overall SOC storage (Zhou et al., 2016). Thus, shifts in SOC fractions in response to
160 precipitation change have been largely neglected by field experimental studies (but see Yang
161 et al., 2018; 2021; Angst et al., 2023) and we are currently unable to predict how precipitation
162 change might affect forest SOC stability.

163 Despite the potential for precipitation change to dramatically alter numerous processes
164 involved in SOC storage and stability, few studies have attempted to assess the concerted
165 influence of precipitation changes on soil physical, chemical, and biological properties that
166 underpin plant and SOC storage in forests. Determining how these properties are related can
167 help us understand the mechanisms underlying the responses of forest SOC pools to
168 precipitation change. To achieve this, we conducted a meta-analysis based on 161 field
169 precipitation manipulation experiments across 139 sites. We investigated how precipitation
170 change affects forest SOC pools and the ecosystem characteristics underpinning SOC storage
171 and stability. We hypothesized that:

172 (H1) Precipitation change alters soil C content by affecting plant C inputs and the
173 decomposition environment. Specifically, soil C content will decline in drought treatments, but
174 increase in irrigation treatments; and the change in soil C content will increase with the level
175 of precipitation change.

176 (H2) Soil C stability will decline in drought treatments because of changes in soil
177 aggregate distributions and C density fractions.

178 (H3) The response of soil C to precipitation change is related to changes in soil moisture
179 but dependent on mean annual precipitation (MAP), whereby changes in soil C pools in
180 response to drought or irrigation will be higher at drier than at wetter sites.

181 As precipitation change affects multiple soil physicochemical properties that influence
182 soil C storage, we also investigated the responses of soil pH, inorganic N content and microbial
183 community composition to precipitation manipulation treatments and assessed their
184 relationships to changes in soil C content.

185 Overall, we expected smaller SOC stocks in drought treatments, due to reduced
186 decomposition, lower C inputs, and destruction of macroaggregates. By contrast, we expected
187 larger SOC stocks in irrigation treatments due to greater plant and microbial C inputs and rapid
188 decomposition. We use our findings to expose current gaps in our understanding of the impacts
189 of precipitation change on forest SOC storage and highlight foci for future research.

190 **2. Materials and methods**

191 ***2.1. Data selection***

192 We conducted a comprehensive search of relevant peer-reviewed articles and dissertations in
193 the Web of Science[®] and ProQuest databases using combinations of the following pairs of
194 search string: (“drought” OR “decreased precipitation” OR “increased precipitation” OR
195 “irrigation”) AND (“plant biomass” OR “aboveground biomass” OR “belowground biomass”

196 OR “fine root biomass”); (“drought” OR “decreased precipitation” OR “increased precipitation”
197 OR “irrigation”) AND (“litterfall”); (“drought” OR “decreased precipitation” OR “increased
198 precipitation” OR “irrigation”) AND (“litter decomposition”); (“drought” OR “decreased
199 precipitation” OR “increased precipitation” OR “irrigation”) AND (“soil microbial biomass”
200 OR “soil microbial community”); (“drought” OR “decreased precipitation” OR “increased
201 precipitation” OR “irrigation”) AND (“soil carbon” OR “soil organic carbon” OR “soil
202 characteristics”); (“drought” OR “decreased precipitation” OR “increased precipitation” OR
203 “irrigation”) AND (“soil aggregate” OR “soil carbon fractions”); (“drought” OR “decreased
204 precipitation” OR “increased precipitation” OR “irrigation”) AND (“soil enzyme”); (“drought”
205 OR “decreased precipitation” OR “increased precipitation” OR “irrigation”) AND (“soil
206 biochemical properties” OR “soil chemical properties” OR “soil nutrients”); (“drought” OR
207 “decreased precipitation” OR “increased precipitation” OR “irrigation”) AND (“soil moisture”
208 OR “soil properties”); (“drought” OR “decreased precipitation” OR “increased precipitation”
209 OR “irrigation”) AND (“soil dissolved organic carbon”). We cross-checked the references of
210 the articles to identify other relevant book chapters and peer-reviewed reports. Then we
211 excluded those papers that were meta-analyses or reviews, and those papers not dealing with
212 C cycling and other variables of our interest. When data from the same site and treatments were
213 presented in multiple publications, we used the data from the most recent publication. We only
214 included studies conducted in forest ecosystems, resulting in data from 161 studies across 139
215 sites published between 1992 and May 2023. Treatments that increase water inputs are
216 henceforth referred to as ‘irrigation’ and treatments that reduce water inputs are henceforth
217 referred to as ‘drought’.

218 We extracted data for the following variables in the topsoil (0-30 cm depth of mineral soil):
219 aboveground biomass (g m^{-2}); fine root biomass (g m^{-2}); microbial biomass carbon (MBC; g
220 kg^{-1}), total soil carbon or soil organic carbon (given as % or g kg^{-1}) converted to a single unit

221 (g kg⁻¹), soil C fractions, including soil macroaggregates (>250 μm), microaggregates (<250
222 μm), and the density-based light fraction organic carbon (LFOC) and mineral-associated
223 organic carbon (MAOC); soil pH, soil water content (%) and soil dissolved organic carbon
224 (DOC; g kg⁻¹); soil microbial data based on phospholipid fatty acids (PLFAs), including fungal
225 biomass, bacterial biomass, and the fungal to bacterial biomass ratio (F:B ratio). We also
226 extracted information for treatment levels as described in the papers, whereby the increase
227 (irrigation) or decrease (drought) in water input was expressed as a percentage of mean annual
228 precipitation (%MAP; Supplement B). We also extracted data for site information, including
229 latitude and longitude of the site, mean annual temperature (MAT, °C), mean annual
230 precipitation (MAP, mm), ecosystem type, and the time between the start of precipitation
231 change treatments and sampling for biomass or soil properties. If MAT and MAP were not
232 given in the publications, we extracted them from the CHELSA bioclimate dataset version 1.2
233 (Karger et al., 2017; <http://chelsa-climate.org/downloads/>) using the *raster* package (Hijmans,
234 2020) in R version 3.5.1 (R Development Core Team 2018). We collated data from the main
235 text, tables, and figures. Numerical values were extracted from graphically presented data by
236 digitizing the figures using Engauge Digitizer (Free Software Foundation, Inc., Boston, USA).

237 The duration of treatments ranged from <1 year to 21 years (Supplement B). The
238 geographical distribution of the sites included in our study was -37.42 N to 64.12 N, and -
239 111.971 E to 150.98 E and the biomes included subtropical and tropical forest, boreal forest,
240 Mediterranean forest, and temperate forest. Given the paucity of studies in subtropical and
241 tropical biomes, data from these biomes were combined into a single (sub-)tropical forest type
242 in our study. The distribution of the experimental sites considered is shown in Figure S1, which
243 was generated using R version 3.5.1 (R Development Core Team 2018) using the packages
244 *ggsm* (Baquero, 2017) and *legendMap* (Gallic, 2016). Detailed information of the studies
245 included in the meta-analysis is provided in Supplement B.

246 2.2. Meta-analysis

247 We conducted a meta-analysis, as described by Hedges et al. (1999). The data were analysed
248 using effect sizes for each observation calculated as the natural log of the response ratio (RR):
249 $RR = \ln(\overline{X}_t / \overline{X}_c)$, where \overline{X}_c is the control mean, and \overline{X}_t is the treatment mean. The
250 variance of the mean effect size was calculated using resampling techniques (Adams et al.,
251 1997). If the lower bound of the 95 % CI of RR was larger than 1, then the response was
252 significantly positive at $P < 0.05$. If the upper bound of the 95 % CI of RR was smaller than 1,
253 then the response was significantly negative at $P < 0.05$. For each investigated parameter, a
254 subgroup analysis was conducted to assess whether the magnitudes of treatment effects differed
255 across forest biome. Although there is no accepted minimum number of studies that are
256 required for a meta-analysis, we adopted the criteria for systematic review by Fu et al. (2011)
257 in which each subgroup should have a minimum of four studies. We therefore present results
258 by subgroup only where sufficient observations were available in more than one subgroup. As
259 there were fewer than four studies in Boreal forests, we were unable to perform subgroup
260 analysis for this biome. Total heterogeneity (Q_T) was partitioned into within-group (Q_W) and
261 between-group (Q_B) heterogeneities. According to Hedges et al. (1999), a significant Q_B
262 indicates that the response ratios differ among groups. Subgroup means were considered
263 significantly different if their 95% CI did not overlap. The publication bias was estimated by
264 the *dnorm* function (Fig. S1 in the Supplement A), and the frequency distributions of all RR
265 values for the target variables followed a normal distribution, indicating no significant
266 publication bias in our study for any of the response variables (Koricheva and Gurevitch, 2014).
267 All statistical analyses for the meta-analysis were conducted in Metawin 2.0 (Rosenberg et al.,
268 2000).

269 2.3. Aridity index

270 To aid interpretation and compare the level of aridity among sites, we calculated the De
271 Martonne aridity index (AI; de Martonne et al., 1926; Liu et al., 2016) for each site as follows:

$$272 \quad AI = \text{MAP} / (\text{MAT} + 10)$$

273 Where MAP is mean annual precipitation, and MAT is mean annual temperature. To aid
274 interpretation, we expressed aridity as 100-AI, such that high values indicate arid sites and low
275 values indicate humid sites (Sanaei et al., 2023).

276 ***2.4. Meta-regression analyses of potential modulators***

277 To assess how experimental or site characteristics might influence changes in C inputs and
278 pools, we analyzed the relationships between treatment level (% MAP) or treatment duration
279 and the magnitude of changes in other relevant response variables (soil moisture, aboveground
280 biomass, litterfall, litter mass loss, fine root biomass, DOC, and MBC in response to drought
281 and irrigation treatments), as well as the relationships between changes in SOC and latitude,
282 aridity index, soil clay content, soil moisture content, treatment level, treatment duration or plot
283 size. All meta-regressions were done in Sigmaplot 15 (Systat Software Inc., San Jose,
284 California, USA).

285 **3. Results**

286 ***3.1. The effect of precipitation change on soil moisture***

287 Across all sites, soil moisture was 24% lower in drought treatments compared to controls
288 (n=102; Fig. 1a). When data were divided into different forest biomes, soil moisture was
289 significantly 24%, 25% and 23% lower in Mediterranean forest (n=16), (sub-)tropical forest
290 (n=35) and temperate forest (n=51), respectively (Fig. 1a). The reduction in soil moisture
291 increased with the proportion of mean annual precipitation excluded by drought treatments
292 (%MAP; $R^2=0.33$, $P<0.0001$; Fig. 1b). When data were divided into different forest biomes,
293 the same soil moisture response to treatment level was observed in (sub-)tropical forest

294 ($R^2=0.49, P<0.0001$) and temperate forest ($R^2=0.33, P<0.0001$) but not in Mediterranean forest
295 (Fig. 1b).

296 In irrigation treatments, soil moisture was 16% higher compared to controls across all sites
297 ($n=44$; Fig. 1c). When the data were divided into different forest biomes, soil moisture was
298 significantly 15% and 17% higher in (sub-)tropical forest and temperate forest, respectively
299 (Fig. 1c) but there were insufficient data to evaluate the response in Mediterranean forest ($n =$
300 1). Across all sites, and for temperate and (sub-)tropical forests, there was no relationship
301 between the increase in soil moisture in response to irrigation and the amount of water added
302 in the treatments (%MAP; Fig. 1d) but there were insufficient data to evaluate the relationship
303 for Mediterranean forest (Fig. 1d).

304 ***3.2. Impacts of precipitation change effect on carbon inputs and SOC pools***

305 Surprisingly, drought treatments had no discernable overall impact on DOC ($n=38$), SOC
306 content ($n=68$) or litterfall ($n=34$; Fig. 2a). By contrast, aboveground biomass ($n=15$), litter
307 mass loss ($n=50$) and fine root biomass ($n=51$) were 24%, 18% and 20% lower, respectively,
308 in drought treatments compared to controls (Fig. 2a). Total microbial biomass C ($n=90$) was
309 significantly 19% lower in drought treatments compared to controls, but there was no change
310 in fungal biomass ($n=25$), bacterial biomass ($n=23$), or the F:B ratio ($n=27$; Fig. 2a). However,
311 drought treatments altered SOC fractions: the soil macroaggregate fraction was 6% smaller in
312 drought treatments compared to controls ($n=8$), but the soil microaggregate fraction was 29%
313 greater ($n=8$). Less SOC was associated with the light fraction in drought treatments than in
314 controls ($n=3$), and although there was more mineral-associated soil C under drought ($n=2$; Fig.
315 2a), there were too few studies to determine statistical significance of changes in either C
316 density fraction.

317 Subgroup analysis revealed somewhat variable effects of drought on C pools and inputs
318 across forest biomes (Table 1). Aboveground and root biomass declined in response to drought

319 in (sub-)tropical forests (n=8 and n=27, respectively) but not in temperate forest (n=6 and n=24,
320 respectively); there were too few datapoints to evaluate the response of either biomass pool in
321 Mediterranean forest. Litterfall only increased under drought in temperate forest (n=8) but litter
322 mass loss declined in all three forest biomes (Table 1). Microbial biomass C was lower under
323 drought in both temperate (n=35) and (sub-)tropical (n=49) but not Mediterranean forest (n=5)
324 but there were no discernable effects of drought on fungal biomass, bacterial biomass, or DOC
325 in any forest biome (Table 1). Soil aggregate distribution changed in response to drought in
326 both temperate and tropical forests, with fewer macroaggregates (n=5 and n=3 respectively)
327 and more microaggregates (n=5 and n=3 respectively), but there were too few studies to
328 evaluate the response of soil aggregate fractions in Mediterranean forests (Table 1) or to
329 perform subgroup analysis of SOC density fractions.

330 Overall, irrigation treatments had no significant effect on DOC concentrations (n=8) or
331 SOC content (n=46; Fig. 2b). There was a marginally significant trend towards higher
332 aboveground biomass (n=13) and litterfall (n=15) in irrigation treatments compared to controls,
333 and fine root biomass was significantly 24% higher (n=55; Fig. 2b) but litter mass loss (n=11)
334 was not affected by irrigation (Fig. 2b). Bacterial biomass (n=14) was higher in irrigation
335 treatments, but the increase was only marginally significant, and total microbial biomass
336 (n=56), fungal biomass (n=14), and the F:B ratio (n=12) were not affected by irrigation
337 treatments (Fig. 2b). We found no studies that assessed the effects of irrigation on SOC
338 fractions (Fig. 2b).

339 Subgroup analysis revealed variable effects of irrigation on C pools and inputs across forest
340 biomes (Table 1). Both aboveground and root biomass increased in response to irrigation in
341 temperate forests (n=8 and n=28, respectively) but only root biomass increased in
342 Mediterranean forest (n=4 and n=13, respectively). By contrast, root biomass in (sub-)tropical
343 forest was unaffected by irrigation (n=14) and there were too few datapoints to evaluate the

344 response of aboveground biomass (Table 1). Litterfall was not affected by irrigation in
345 temperate forest (n=9) and there were too few datapoints to assess the response of litterfall in
346 (sub-)tropical forest or Mediterranean forest (n=3). Litter mass loss was unaffected by
347 irrigation treatments in temperate and (sub-)tropical forest but there were too few datapoints to
348 evaluate litter mass loss in Mediterranean forest (Table 1). Total microbial biomass increased
349 in response to irrigation treatments in (sub-)tropical (n=21) but not in temperate (n=29) or
350 Mediterranean forest (n=5). However, fungal biomass declined with irrigation in
351 Mediterranean forest (n=7), whereas both fungal biomass and bacterial biomass increased with
352 irrigation in (sub-)tropical forest (n=5), and there were too few datapoints to evaluate the
353 response of fungal or bacterial biomass in temperate forest (Table 1). There were no discernable
354 effects of irrigation on DOC in temperate or (sub-)tropical forest and insufficient data on DOC
355 in Mediterranean forest (Table 1).

356 ***3.3. The response of soil properties to precipitation change***

357 Experimental drought affected few soil properties related to SOC storage. In drought treatments,
358 soil total N (n=58) was 7% lower compared to controls, but there was no significant effect of
359 drought on soil pH (n=69), soil ammonium-N (n=33) or nitrate-N content (n=31; Fig. 2a). Of
360 the three investigated soil enzymes related to C turnover, only β -glucosidase activity (n=15)
361 was significantly 12% lower in drought treatments; cellobiohydrolase activity (n=7) was not
362 affected by drought and there were too few datapoints to evaluate the response of polyphenol
363 oxidase (n=3; Fig. 2a). Subgroup analysis revealed declines in total soil N under drought in
364 Mediterranean (n=11) and (sub-)tropical (n=25) but not in temperate forests (n=22), whereas
365 pH increased in temperate (n=31) and Mediterranean (n=4), but not in (sub-)tropical forests
366 (n=33). The decline in β -glucosidase was not significant when Mediterranean (n=9) and
367 (sub-)tropical forests (n=5) were analysed separately, and there were too few datapoints to
368 assess the response of β -glucosidase to drought in temperate forest, or the response of

369 cellobiohydrolase activity in any forest biome (Table 1).

370 Few soil properties changed under irrigation treatments. Soil pH (n=24) was 2% higher in
371 irrigation treatments than in controls (Fig. 2b) but there was no significant effect of irrigation
372 on soil total N (n=20), soil ammonium-N (n=13) or soil nitrate-N content (n=14; Fig. 2b). Soil
373 enzyme activity was also unaffected by irrigation treatments, as neither β -glucosidase (n=8)
374 nor polyphenol oxidase activity (n=4) was altered by irrigation, and there were too few
375 datapoints to evaluate the response of cellobiohydrolase (n=1, Fig. 2b). Subgroup analysis
376 revealed that the increase in soil pH with irrigation was consistent across Mediterranean (n=4)
377 and (sub-)tropical (n=11) forest, but pH did not respond to irrigation in temperate forests (n=8).
378 Total soil N and nitrate-N did not respond to irrigation in any forest biome, but ammonium-N
379 increased with irrigation in (sub-)tropical forest (n=7; Table 1). There were too few datapoints
380 to evaluate the response of extracellular enzyme activities in any biome.

381 ***3.4. Relationships between SOC content and abiotic or treatment characteristics***

382 Across biomes, the magnitude of change in SOC content in response to drought treatments was
383 not explained by latitude, aridity, soil clay content, treatment level, treatment duration or plot
384 area (Fig. 3a-f). In addition, across biomes, the magnitude of change in SOC content in
385 response to irrigation treatments was not explained by latitude, aridity, treatment level,
386 treatment duration or plot area (Fig. 3g-k). Surprisingly, the change in SOC content was not
387 related to the change in soil moisture in either drought or irrigation treatments across all studies
388 (Fig. 4c,d).

389 Subgroup analysis by forest biome (Mediterranean forest, (sub-)tropical forest and
390 temperate forest) revealed no significant overall effect of drought on SOC content in any of the
391 three forest types (Fig. 4a). In (sub-)tropical forests, the magnitude of change in SOC content
392 in response to drought treatments was not affected by any of the variables investigated in this
393 study. By contrast, in temperate forest, the decline in SOC in response to drought became more

394 pronounced with increasing %MAP excluded by treatments ($R^2=0.24$, $P=0.03$, Fig. 3d), i.e. the
395 more severe the drought treatment, the greater the decline in SOC content. Similarly, in
396 (sub-)tropical forest, the magnitude of change in SOC was related to the magnitude of change
397 in soil moisture ($R^2=0.27$, $P=0.005$, Fig. 4c), with greater declines in SOC content when
398 drought treatments resulted in a larger reduction in soil water content.

399 Irrigation treatments had no significant effect on SOC content in Mediterranean forest or
400 temperate forest (Fig. 4b) but SOC content in (sub-)tropical forest was lower in irrigation
401 treatments compared to controls (Fig. 4b). In temperate forest, the decline in SOC content in
402 response to irrigation became more pronounced with increasing aridity (Fig. 3h), and therefore
403 irrigation had a greater negative impact on SOC content at drier sites in temperate forest. In
404 addition, the magnitude of change in SOC content weakened with increasing %MAP added in
405 irrigation treatments in (sub-)tropical forest ($R^2=0.17$, $P=0.03$, Fig. 3i). There were too few
406 datapoints for individual biomes to evaluate the relationship between the magnitude of change
407 in SOC and the magnitude of change in soil moisture (Fig. 4d).

408 **3.5. Relationships between C inputs and treatment level or duration**

409 The %MAP excluded in drought treatments did not explain the magnitude of change in
410 aboveground biomass, litterfall or DOC (Fig. 5a,b,e). However, the declines in litter mass, fine
411 root biomass and MBC all became more pronounced with increasing %MAP excluded in
412 drought treatments (Fig. 5c,d,f). By contrast, the %MAP added in irrigation treatments did not
413 explain changes in any C inputs. Surprisingly, the duration of drought or irrigation treatments
414 did not explain the magnitude of change for any C inputs (Fig. S4).

415 **4. Discussion**

416 Our global meta-analysis revealed that forest SOC content appears largely resistant to drought
417 and irrigation treatments in manipulative field experiments. Our findings demonstrate that this

418 resilience is likely due to the distinct effects of precipitation change on plant C inputs to the
419 soil and on the decomposition environment, which largely controls outputs. However, the
420 responses of individual SOC pools indicate that precipitation change could affect SOC stability
421 and thus alter SOC storage over the longer-term. Importantly, our study demonstrates that the
422 lack of a global response of SOC content to precipitation change can be attributed to differences
423 in the responses of SOC inputs and pools among forest biomes. In addition, the response of
424 SOC inputs and pools depended on site aridity and the severity of precipitation changes. Here,
425 we discuss how precipitation change could influence SOC storage and stability by altering the
426 balance between C inputs and decomposition processes in different forest biomes (Fig. 6).

427 ***4.1. SOC fractions, but not SOC content, respond to precipitation change***

428 In contrast to our first hypothesis, forest SOC content was not strongly influenced by
429 precipitation change (Fig. 2). Similar insensitivity of SOC has previously been reported for
430 increased precipitation (Zhou et al., 2016; Yue et al., 2017) and drought (Zhou et al., 2016)
431 across multiple ecosystem types. This apparent insensitivity of SOC content to precipitation
432 change is likely due to the short duration of most experiments (<6 years), as it can take many
433 years or decades to detect changes in SOC (Hungate et al., 1996). However, our results reveal
434 that changes in individual C pools and inputs could affect overall SOC content and stability
435 under long-term precipitation change. For example, lower C inputs from root biomass and
436 litterfall under drought (Moser et al., 2014; Liu et al., 2015) might be offset by reduced
437 microbial biomass C and β -glucosidase activity (Sardans and Peñuelas, 2005; Ren et al., 2017;
438 Xu et al., 2020), which could in turn reduce SOC mineralization as well as litter mass loss (Fig.
439 6). By contrast, under irrigation, increased fine root and bacterial biomass could eventually
440 enhance SOC content over the longer-term. Thus, to predict change in forest SOC stocks in
441 response to precipitation change we not only need longer-term experiments (Deng et al., 2021)
442 but we must also consider how precipitation change influences multiple C inputs and outputs

443 (Zhou et al., 2016).

444 Given the difficulties in assessing change in total SOC content, many studies instead focus
445 on changes in SOC stability using particle size distributions and density fractions to represent
446 functional pools of C (e.g. Lavallee et al., 2020). Indeed, shifts in C storage among different
447 fractions can result in no apparent overall change in SOC (Schwendenmann and Pendall, 2007).
448 Soil macro-aggregates and light density fractions are generally associated with C that is
449 susceptible to microbial mineralization, whereas micro-aggregates and mineral-associated
450 organic matter are thought to contain more stable SOC with longer turnover times (Puget et al.,
451 2000; Lavallee et al., 2020). We therefore hypothesised that drought would reduce soil C
452 stability via changes in soil aggregate distributions and C density fractions (H2). Although we
453 only had eight data-points for the response of soil aggregate fractions to drought, we found a
454 consistent pattern of a smaller lower macroaggregate fraction, but a larger microaggregate
455 fraction (Fig. 2). Hence, in contrast to our hypothesis, changes in soil aggregate distributions
456 in response to drought could increase SOC stability (Yang et al., 2021), which might offset
457 lower C inputs through decomposition. Multiple mechanisms could underpin these changes in
458 the distribution of soil aggregate fractions under drought. Besides physical disruption by drying
459 rewetting cycles (REF), reduced microbial biomass C and root biomass (Fig. 2) could also
460 reduce biological binding agents (Chen et al., 2019c) and alter other rhizosphere characteristics
461 (Zhang et al., 2019) that contribute to aggregate formation. The corresponding shifts in C
462 associated with different density fractions, from LFOC to MAOC (Fig. 2) support an increase
463 in stable C (Lavallee et al., 2020) under drought. However, so few studies have assessed soil
464 density fractions that the meta-analytical results for LFOC and MAOC are only indicative (Fu
465 et al., 2011). Furthermore, we found no data on forest soil aggregate distribution or SOC density
466 fractions in irrigation experiments. Many more studies of soil C fractions are needed to
467 determine how precipitation changes will affect soil C stability. However, as changes in SOC

468 fractions can indicate the resistance of SOC to perturbations (Schwendenmann and Pendall,
469 2006; Lavallee et al., 2020), such studies will be critical to predict future forest SOC stocks.

470 *4.2. Precipitation change effects on plant C inputs*

471 Although aboveground biomass is a major reservoir of C in forests (Houghton, 2005;
472 Keith et al., 2009), few studies have reported results for forest aboveground biomass in
473 precipitation change experiments (n=15). The lack of data on changes in aboveground biomass
474 could be because it is difficult to estimate forest aboveground biomass (Zhang et al., 2014;
475 Vafaei et al., 2018). However, as most precipitation change experiments to date have lasted <
476 6 years, it is more likely that the experimental duration was insufficient to measure or detect
477 changes in tree growth. Nonetheless, we found consistent declines in aboveground biomass in
478 response to drought treatments consistent across studies (Fig. 2a), although our biome-level
479 analyses showed that the decline in aboveground biomass was only significant in (sub-)tropical
480 forest (Table 1). Clearly, long-term measurements of tree growth responses to drought are
481 needed to estimate and model changes in aboveground C stocks in different forest biomes.

482 Despite lower aboveground biomass in drought treatments, we found no consistent
483 response in litterfall (Fig. 2a). Variable effects of drought on litterfall are likely because drought
484 can reduce litter production, but also often encourage leaf fall (Peñuelas et al., 2007), with
485 studies reporting lower, higher or no changes in litterfall (Peñuelas et al., 2007; Moser et al.,
486 2014; Liu et al., 2015). Our analyses demonstrate that differences among biomes can explain
487 these discrepancies, as litterfall increased in temperate forests but did not change in
488 Mediterranean or (sub-)tropical forests. These biome-level differences likely reflect adaptation
489 of the trees to extant conditions. For example, many (sub-)tropical forests experience a distinct
490 dry season, and Mediterranean tree species have numerous physiological adaptations to
491 minimize water loss without shedding their leaves (e.g. Sardans and Peñuelas, 2013). We note
492 that, given the paucity of data, our analysis does not consider differences in tree functional

493 types, which differ greatly in their responses to water availability (Beard et al., 2005; McCluney
494 et al., 2011). Future consideration of tree life history strategies could therefore greatly improve
495 our ability to predict the responses of forest plant C inputs to precipitation change. However,
496 consistently lower litter mass loss in drought treatments across studies (Fig. 2a) can be
497 attributed to declining litter quality (Aerts, 1997; Cornwell et al., 2008) or water limitation of
498 decomposer activity (Ren et al., 2017; Xu et al., 2020). Taken together, these results suggest
499 that drought could lead to a decline in soil C inputs from aboveground litter.

500 Our results showed that aboveground C inputs were less responsive to irrigation
501 compared to drought (Fig. 2b), regardless of the amount of water added in the treatments (Fig.
502 5g,h,i). Such limited changes in forest aboveground productivity to irrigation likely reflects the
503 distribution of forests in regions with sufficient rainfall to support woody plant growth (Pan et
504 al., 2013). We therefore expected greater effects of irrigation on plant C inputs in Mediterranean
505 forests, but there were surprisingly few such experiments (n=7) and only three or four of those
506 studies had measured the response of aboveground biomass or litterfall, respectively (Table 1).
507 However, Mediterranean forests have been experiencing declines in precipitation (Peñuelas et
508 al., 2017; Cramer et al., 2018), making irrigation experiments less valuable for determining the
509 impacts of climate changes in this biome.

510 Root biomass was highly sensitive to precipitation change. Our results showed
511 substantial changes in fine root biomass in the topsoil (0-30 cm) in response to both drought
512 (20% decline) and irrigation (24% increase; Fig. 2a,b), which suggests that precipitation change
513 could have large effects on SOC pools via changes in root growth and rhizosphere activity.
514 Under drought, declines in root biomass, but not aboveground biomass or litterfall, are
515 consistent with the theory that trees will maintain competitiveness for light as long as possible
516 under moderate drought (Brunner et al., 2015). Indeed, higher root biomass in response to
517 irrigation in temperate and Mediterranean forest suggests that tree investment in root biomass

518 is determined by water availability (Table 1). Biome-level differences in biomass allocation
519 above- vs belowground under precipitation change likely reflect tree adaptations to water
520 availability (Brunner et al., 2015), which will also result in distinct responses of SOC stocks.
521 In particular, greater aboveground and root biomass in response to irrigation in temperate forest
522 indicate that increased precipitation could enhance plant C storage. Unfortunately, there were
523 too few studies to evaluate root biomass responses to drought in Mediterranean forests. Given
524 that Mediterranean forests are experiencing more frequent and severe droughts (Peñuelas et al.,
525 2017; Cramer et al., 2018), field experiments investigating the effects of drought on rhizosphere
526 processes are urgently needed to understand the impacts of precipitation change on forest C
527 storage.

528 ***4.3. Precipitation change alters the decomposition environment, i.e. site and experimental*** 529 ***characteristics***

530 We hypothesized that changes in soil C content would be related to decomposition processes,
531 soil properties and environmental conditions. Although few soil properties responded to
532 precipitation change, soil moisture, soil N and pH were all affected by drought or irrigation
533 (Fig. 1). Reduced litter mass loss, microbial biomass C and β -glucosidase activity under
534 drought can all be directly attributed to inhibition of biological activity at low soil water content
535 (Manzoni et al., 2012; Deng et al., 2021), whereas lower total soil N under drought could either
536 be a cause or a consequence of reduced decomposition. Overall, drought creates an
537 unfavourable environment for decomposition, which could explain the observed shifts in SOC
538 fractions and ultimately enhance SOC accumulation. By contrast, irrigation treatments only
539 affected soil pH (Fig. 2b), which could affect decomposition processes via changes in microbial
540 communities (Sun et al., 2020). However, we found no changes in litter mass loss, microbial
541 biomass, the F:B ratio or enzyme activities in response to irrigation.

542 We expected several sites or experimental characteristics to regulate SOC responses to

543 precipitation change in forest, including latitude, climate, soil clay content, treatment level,
544 treatment duration, and plot area. Surprisingly, across biomes, the magnitude of change in SOC
545 content in response to drought or irrigation treatments was not explained by latitude, aridity,
546 soil clay content, treatment level, treatment duration or plot area (Fig. 3). However, in
547 temperate forest, the decline in SOC content in response to irrigation became more pronounced
548 with increasing aridity (Fig. 3h), and therefore irrigation had a greater negative impact on SOC
549 content at drier sites in temperate forest. Previous meta-analyses studies found higher
550 sensitivity of SOC responsive to drought at drier sites across different ecosystem types (Deng
551 et al., 2021; Wang et al., 2021; Chen et al., 2023). However, we also found that SOC content
552 tended to decline with irrigation at drier sites in temperate forest (Fig. 3h), perhaps because
553 irrigation alleviated water limitation of biological activity, resulting in mineralization of SOC
554 (Liu et al., 2016). Our results therefore suggest that SOC in temperate forest at dry sites could
555 be particularly sensitive to irrigation. Given that relatively fewer studies have been conducted
556 at arid sites, the responses of dry forest C stocks to precipitation change should be a future
557 research priority.

558 **5. Conclusion**

559 Despite apparent insensitivity of forest SOC content to precipitation change, our meta-
560 analysis revealed changes in C inputs and pools that are likely to affect long-term forest SOC
561 storage. We demonstrate that the response of forest biomes to both drought and irrigation
562 involves concerted changes in plant C inputs, microbial communities and activity, and the
563 decomposition environment. These changes to C cycle processes, alongside shifts in soil
564 fractions representing SOC stability suggest that forest SOC storage will be affected over
565 timeframes that exceed the duration of most existing experiments. Importantly, our meta-
566 analysis exposed three key knowledge gaps that impede our ability to predict how SOC stocks
567 in forests might respond to precipitation change: First, drought could enhance SOC stability by

568 altering the distribution of C among soil aggregate or density fractions. Second, differences
569 among forest biomes account for the lack of a global response of C pools in response to
570 precipitation change, which is likely due to plant adaptation to regional growing conditions.
571 Finally, the response of forest C pools to irrigation depends upon the extant climate conditions
572 at the site (aridity) in temperate forest. Our study exposes a current lack of experimental data
573 to address these knowledge gaps, especially from irrigation experiments, which hampers our
574 ability to fully assess potential consequences for SOC storage. We call for future work linking
575 the response of tree functional groups to processes underpinning SOC formation, distribution,
576 and storage. We further call for a concerted effort to include standard measurements of multiple
577 C pools at existing sites, and the establishment of experimental networks to capture the
578 responses of forest C along natural rainfall gradients. Thus, our findings provide novel insights
579 into the responses of SOC storage and stability that will advance research into precipitation
580 change in forest ecosystems worldwide.

581

582 **References**

- 583 Adams, D.C., Gurevitch, J., Rosenberg, M.S., 1997. Resampling tests for meta-analysis of
584 ecological data. *Ecology* 78, 1277-1283. [https://doi.org/10.1890/0012-9658\(1997\)078\[1277:RTFMAO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1277:RTFMAO]2.0.CO;2).
- 586 Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial
587 ecosystems: a triangular relationship. *Oikos* 79, 439 – 449. <https://doi.org/10.2307/3546886>.
- 588 Angst, G., Mueller, K.E., Castellano, M.J. et al. 2023. Unlocking complex soil systems as
589 carbon sinks: multi-pool management as the key. *Nat. Commun.* 14, 2967.
590 <https://doi.org/10.1038/s41467-023-38700-5>.
- 591 Bao, J., Sherwood, S.C., Alexander, L.V., Evans, J.P., 2017. Future increases in extreme

592 precipitation exceed observed scaling rates. *Nat. Clim. Change* 7, 128–132.
593 <https://doi.org/10.1038/nclimate3201>.

594 Baquero, O.S., 2017. Ggsn: North Symbols and Scale Bars for Maps Created with ‘ggplot2’ or
595 ‘ggmap’. Available at <https://CRAN.R-project.org/package=ggsn>.

596 Beard, K. H., Vogt, K. A., Vogt, D. J., Scatena, F. N., Covich, A. P., Sigurdardottir, R., ...
597 Crowl, T. A., 2005. Structural and functional responses of a subtropical forest to 10 years
598 of hurricanes and droughts. *Ecol. Monogr.* 75, 345-361. <https://doi.org/10.1890/04-1114>.

599 Beier, C., Beierkuhnlein, C., Wohlgemuth, T., Penuelas, J., Emmett, B., Korner, C., et al. 2012.
600 Precipitation manipulation experimes-challenges and recommendations for the future.
601 *Ecol. Lett.* 15(8), 899-911. <https://doi.org/10.1111/j.1461-0248.2012.01793.x>.

602 Bennett, A.C., Penman, T.D., Arndt, S.K., Roxburgh, S.H., Bennett, L.T., 2020. Climate more
603 important than soils for predicting forest biomass at the continental scale. *Ecography* 43,
604 1692-1705. <https://doi.org/10.1111/ecog.05180>.

605 Berg, A., Sheffield, J., 2018. Climate Change and Drought: the Soil Moisture Perspective. *Curr.*
606 *Clim. Change Rep.* 4, 180–191. <https://doi.org/10.1007/s40641-018-0095-0>.

607 Brunn M, Hafner BD, Zwetsloot MJ, Weikl F, Pritsch K, Hikino K, Rühr NK, Sayer EJ, Bauerle
608 TL, 2022. Carbon allocation to root exudates is sustained in mature temperate tree species
609 under drought. *New Phytol.* 235, 965-977. <https://doi.org/10.1111/nph.18157>.

610 Chen, J., Xiao, G., Kuzyakov, Y., Jenerette, G. D., Ma, Y., Liu, W., Wang, Z., Shen, W., 2017.
611 Soil nitrogen transformation responses to seasonal precipitation changes are regulated by
612 changes in functional microbial abundance in a subtropical forest. *Biogeosciences* 14,
613 2513–2525. <https://doi.org/10.5194/bg-14-2513-2017>.

614 Chen, X., Deng, Q., Lin, G., Lin, M., Wei, H., 2018. Changing rainfall frequency affects soil
615 organic carbon concentrations by altering non-labile soil organic carbon concentrations in
616 a tropical monsoon forest. *Sci. Total Environ.* 644, 762–769.

617 <https://doi.org/10.1016/j.scitotenv.2018.07.035>.

618 Chen, J., Kuzyakov, Y., Jenerette, G. D., Xiao, G., Liu, W., Wang, Z., Shen, W., 2019.

619 Intensified Precipitation Seasonality Reduces Soil Inorganic N Content in a Subtropical

620 Forest: Greater Contribution of Leaching Loss Than N₂O Emissions. *Journal of*

621 *Geophysical Research: Biogeosciences* 124, 494-508.

622 <https://doi.org/10.1029/2018JG004821>.

623 Chen, Z., Wei, X., Ni, X., Wu, F., Liao, S., 2023. Changing precipitation effect on forest soil

624 carbon dynamics is driven by different attributes between dry and wet areas. *Geoderma*

625 429, 116279. <https://doi.org/10.1016/j.geoderma.2022.116279>.

626 Chen Z., Zhou X., Geng S., Miao Y., Cao Y., Chen Z., Zhang J., Han S., 2019. Interactive

627 effect of nitrogen addition and throughfall reduction decreases soil aggregate stability

628 through reducing biological binding agents. *Forest Ecol. Manag.* 445, 13–19.

629 <https://doi.org/10.1016/j.foreco.2019.04.057>.

630 Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O.,

631 Hobbie, S.E., Hoorens, B., Kurokawa, H., Perez-Harguindeguy, N., Queded, H.M.,

632 Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P.,

633 Brovkin, V., Chatain, A., Callaghan, T.V., Diaz, S., Garnier, E., Gurvich, D.E., Kazakou,

634 E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Victoria Vaieretti, M., Westoby,

635 M., 2008. Plant species traits are the predominant control on litter decomposition rates

636 within biomes worldwide. *Ecol. Lett.* 11, 1065 – 1071. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2008.01219.x)

637 [0248.2008.01219.x](https://doi.org/10.1111/j.1461-0248.2008.01219.x).

638 Cramer, W., Guiot, J., Fader, M., Garrabou, J., Gattuso, J. P., Iglesias, A., ... & Xoplaki, E.

639 (2018). Climate change and interconnected risks to sustainable development in the

640 Mediterranean. *Nature Climate Change*, 8(11), 972-980.

641 Cregger, M.A., McDowell, N.G., Pangle, R.E., Pockman, W.T., Classen, A.T., Niu, S., 2014.

642 The impact of precipitation change on nitrogen cycling in a semi-arid ecosystem. *Funct.*
643 *Ecol.* 28, 1534-1544. <https://doi.org/10.1111/1365-2435.12282>.

644 de Martonne, E., 1926. Une nouvelle fonction climatologique: l ' indice d ' aridite. *La*
645 *Meteorologie* 2, 449 – 458.

646 Deneff, K., Six, J., Paustian, K., Merckx, R., 2001. Importance of macroaggregate dynamics
647 in controlling soil carbon stabilization: short-term effects of physical disturbance induced
648 by dry-wet cycles. *Soil Biol. Biochem.* 33, 2145–2153. [https://doi.org/10.1016/S0038-](https://doi.org/10.1016/S0038-0717(01)00153-5)
649 [0717\(01\)00153-5](https://doi.org/10.1016/S0038-0717(01)00153-5).

650 Deng, L., Peng, C., Kim, D.G., Li, J., Liu, Y., Hai, X., et al. 2021. Drought effects on soil
651 carbon and nitrogen dynamics in global natural ecosystems. *Earth Sci. Rev.* 214, 103501.
652 <https://doi.org/10.1016/j.earscirev.2020.103501>.

653 Du, Y., Wang, Y.P., Su, F., Jiang, J., Wang, C., Yu, M., Yan, J., 2020. The response of soil
654 respiration to precipitation change is asymmetric and differs between grasslands and
655 forests. *Glob. Chang. Biol.* 26, 6015-6024. <https://doi.org/10.1111/gcb.15270>.

656 Fridley, J.D., Lynn, J.S., Grime, J.P., Askew, A.P., 2016. Longer growing seasons shift
657 grassland vegetation towards more-productive species. *Nat. Clim. Change* 6, 865-868.
658 <https://doi.org/10.1038/nclimate3032>.

659 Fröberg, M., Hanson, P.J., Todd, D.E., Johnson, D.W., 2008. Evaluation of effects of sustained
660 decadal precipitation manipulations on soil carbon stocks. *Biogeochemistry* 89, 151-161.
661 <https://doi.org/10.1007/s10533-008-9205-8>.

662 Fu, R., Gartlehner, G., Grant, M. et al. 2011. Conducting quantitative synthesis when
663 comparing medical interventions: AHRQ and the Effective Health Care Program. *J. Clin.*
664 *Epidemiol.* 64, 1187–1197. <https://doi.org/10.1016/j.jclinepi.2010.08.010>.

665 Gallic, E. 2016. legendMap: North arrow and scale bar for ggplot2 graphics. R package version
666 1.0.

667 Gampe, D., Zscheischler, J., Reichstein, M., O’Sullivan, M., Smith, W.K., Sitch, S., Buermann,
668 W., 2021. Increasing impact of warm droughts on northern ecosystem productivity over
669 recent decades. *Nat. Clim. Change*. 11, 772–779. [https://doi.org/10.1038/s41558-021-](https://doi.org/10.1038/s41558-021-01112-8)
670 01112-8.

671 Giardina, F., Konings, A.G., Kennedy, D., Alemohammad, S. H., Oliveira, R.S., Uriarte, M.,
672 Gentine, P., 2018. Tall Amazonian forests are less sensitive to precipitation variability. *Nat.*
673 *Geosci.* 11, 405-409. <https://doi.org/10.1038/s41561-018-0133-5>.

674 Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in
675 experimental ecology. *Ecology* 80, 1150–1156. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2)
676 9658(1999)080[1150:TMAORR]2.0.CO;2.

677 Heikkinen, J., Keskinen, R., Kostensalo, J., Nuutinen, V., 2022. Climate change induces carbon
678 loss of arable mineral soils in boreal conditions. *Global Change Biology* 28, 3960–3973.
679 <https://doi.org/10.1111/gcb.16164>.

680 Hertel, D., Strecker, T., Müller-Haubold, H., Leuschner, C., Guo, D., 2013. Fine root biomass
681 and dynamics in beech forests across a precipitation gradient – is optimal resource
682 partitioning theory applicable to water-limited mature trees? *J. Ecol.* 101, 1183-1200.
683 <https://doi.org/10.1111/1365-2745.12124>.

684 Hicks, L.C., Rahman, M.M., Carnol, M., Verheyen, K., Rousk, J., 2018. The legacy of mixed
685 planting and precipitation reduction treatments on soil microbial activity, biomass and
686 community composition in a young tree plantation. *Soil Biol. Biochem.* 124, 227–235.
687 <https://doi.org/10.1016/j.soilbio.2018.05.027>

688 Hijmans, R.J., 2020. raster: Geographic Data Analysis and Modeling. R package version 3.4-
689 5. <https://CRAN.R-project.org/package=raster>.

690 Homyak, P. M., Allison, S. D., Huxman, T. E., Goulden, M. L., Treseder, K. K., 2017.
691 Effects of drought manipulation on soil nitrogen cycling: A meta-analysis. *Journal of*

692 Geophysical Research: Biogeosciences 122, 3260– 3272.
693 <https://doi.org/10.1002/2017JG004146>.

694 Hou, E., Litvak, M. E., Rudgers, J. A., Jiang, L., Collins, S. L., Pockman, W. T., et al. 2021.
695 Divergent responses of primary production to increasing precipitation variability in global
696 drylands. *Glob. Chang. Biol.* 27, 5225-5237. <https://doi.org/10.1111/gcb.15801>.

697 Houghton, 2005. Aboveground Forest Biomass and the Global Carbon Balance. *Glob. Chang.*
698 *Biol.* 11, 945–958. <https://doi:10.1111/j.1365-2486.2005.00955.x>.

699 Huang, X., Swain, D.L., Hall, A.D., 2020. Future precipitation increase from very high
700 resolution ensemble downscaling of extreme atmospheric river storms in California. *Sci.*
701 *Adv.* 6, 1-13. <https://doi:10.1126/sciadv.aba1323>.

702 Hungate, B. A., Jackson, R. B., Field, C. B., Chapin, III, F. S., 1996. Detecting changes in soil
703 carbon in CO₂ enrichment experiments. *Plant Soil* 187, 135–145.
704 <https://doi.org/10.1007/BF00017086>.

705 Jing, Y., Wang, Y., Liu, S., Zhang, X., Wang, Q., Liu, K., Yin, Y., Deng, J., 2019. Interactive
706 effects of soil warming, throughfall reduction, and root exclusion on soil microbial
707 community and residues in warm-temperate oak forests. *Appl. Soil Ecol.* 142, 52–58.
708 <https://doi.org/10.1016/j.apsoil.2019.05.020>.

709 John, B., Yamashita, T., Ludwig, B., Flessa, H., 2005. Storage of organic carbon in aggregate
710 and density fractions of silty soils under different types of land use. *Geoderma* 128, 63–
711 79. <https://doi.org/10.1016/j.geoderma.2004.12.013>.

712 Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W. et al. 2017.
713 Climatologies at high resolution for the Earth land surface areas. *Sci. Data* 4, 170122.
714 <https://doi.org/10.1038/sdata.2017.122>.

715 Keith, H., Mackey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon
716 stocks and lessons from the world’s most carbon-dense forests. *Proc. Natl. Acad. Sci. U.*

717 S. A. 106, 11635–11640. <https://doi.org/10.1073/pnas.0901970106>.

718 Kirchmeier-Young, M.C., Zhang, X., 2020. Human influence has intensified extreme
719 precipitation in North America. *Proc. Natl. Acad. Sci. U. S. A.* 117, 13308–13313.
720 <https://doi.org/10.1073/pnas.1921628117>.

721 Konapala, G., Mishra, A. K., Wada, Y., Mann, M. E., 2020. Climate change will affect global
722 water availability through compounding changes in seasonal precipitation and
723 evaporation. *Nat. Commun.* 11, 3044. <https://doi.org/10.1038/s41467-020-16757-w>.

724 Koricheva, J., Gurevitch, J. 2014. Uses and misuses of meta-analysis in plant ecology. *Journal*
725 *of Ecology* 102, 828–844. <https://doi.org/10.1111/1365-2745.12224>.

726 Lavalley, J.M., Soong, J.L., Cotrufo, M.F., 2020. Conceptualizing soil organic matter into
727 particulate and mineral-associated forms to address global change in the 21st century. *Glob.*
728 *Chang. Biol.* 26, 261–273. <https://doi.org/10.1111/gcb.14859>.

729 Li, X., Zhang, C., Zhang, B., Wu, D., Zhu, D., Zhang, W., et al. 2021. Nitrogen deposition and
730 increased precipitation interact to affect fine root production and biomass in a temperate
731 forest: Implications for carbon cycling. *Sci. Total Environ.* 765, 144497.
732 <https://doi.org/10.1016/j.scitotenv.2020.144497>.

733 Li, Z. et al. 2020. Climatic humidity mediates the strength of the species richness – biomass
734 relationship on the Mongolian Plateau steppe. *Sci. Total Environ.* 718, 137252.
735 <https://doi.org/10.1016/j.scitotenv.2020.137252>.

736 Liu, D., Ogaya, R., Barbeta, A., Yang, X., Peñuelas, J., 2015. Contrasting impacts of
737 continuous moderate drought and episodic severe droughts on the aboveground-biomass
738 increment and litterfall of three coexisting Mediterranean woody species. *Glob. Chang.*
739 *Biol.* 21, 4196-4209. <https://doi.org/10.1111/gcb.13029>.

740 Liu, L., Wang, X., Lajeunesse, M. J., Miao, G., Piao, S., Wan, S., et al. 2016. A cross-biome
741 synthesis of soil respiration and its determinants under simulated precipitation changes.

742 Glob. Chang. Biol. 22, 1394-1405. <https://doi.org/10.1111/gcb.13156>.

743 Lützw, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner,
744 E., Marschner, B., 2007. SOM fractionation methods: Relevance to functional pools and
745 to stabilization mechanisms. Soil Biol. Biochem. 39, 2183–2207.
746 <https://doi.org/10.1016/j.soilbio.2007.03.007>.

747 Luo, Z., Feng, W., Luo, Y., Baldock, J., Wang, E., 2017. Soil organic carbon dynamics jointly
748 controlled by climate, carbon inputs, soil properties and soil carbon fractions. Glob.
749 Change Biol. 23, 4430 – 4439. <https://doi.org/10.1111/gcb.13767>.

750 Manzoni, S., Schimel, J. P., Porporato, A. 2012. Responses of soil microbial communities to
751 water stress: results from a meta-analysis. Ecology 93, 930-938.
752 <https://doi.org/10.1890/11-0026.1>.

753 Maurer, G.E., Hallmark, A.J., Brown, R.F., Sala, O.E., Collins, S.L., 2020. Sensitivity of
754 primary production to precipitation across the United States. Ecol. Lett. 23, 527-536.
755 <https://doi.org/10.1111/ele.13455>.

756 McCluney, K.E., Belnap, J., Collins, S.L., González, A.L., Hagen, E.M., Nathaniel H., J., ...
757 Wolf, B.O., 2012. Shifting species interactions in terrestrial dryland ecosystems under
758 altered water availability and climate change. Biol. Rev. 87, 563-582.
759 <https://doi.org/10.1111/j.1469-185X.2011.00209.x>.

760 McColl, K., Alemohammad, S., Akbar, R. et al. 2017. The global distribution and dynamics of
761 surface soil moisture. Nature Geosci. 10, 100–104. <https://doi.org/10.1038/ngeo2868>.

762 Moser, G., Schuldt, B., Hertel, D., Horna, V., Coners, H., Barus, H., Leuschner, C., 2014.
763 Replicated throughfall exclusion experiment in an Indonesian perhumid rainforest: wood
764 production, litter fall and fine root growth under simulated drought. Glob. Change Biol.
765 20, 1481-1497. <https://doi.org/10.1111/gcb.12424>.

766 Nielsen, U.N., Ball, B.A., 2015. Impacts of altered precipitation regimes on soil communities

767 and biogeochemistry in arid and semi-arid ecosystems. *Glob. Change Biol.* 21, 1407-1421.
768 <https://doi.org/10.1111/gcb.12789>.

769 Pan, Y., Birdsey, R.A., Phillips, O.L., Jackson, R.B., 2013. The structure, distribution, and
770 biomass of the world's forests. *Annu. Rev. Ecol. Evol. Syst.* 44, 593-622.
771 <https://doi.org/10.1146/annurev-ecolsys-110512-135914>.

772 Penuelas, J., Prieto, P., Beier, C., et al. 2007. Response of plant species richness and primary
773 productivity in shrublands along a north–south gradient in Europe to seven years of
774 experimental warming and drought: reductions in primary productivity in the heat and
775 drought year of 2003. *Glob. Change Biol.* 13, 2563–2581, [http://doi: 10.1111/j.1365-](http://doi:10.1111/j.1365-2486.2007.01464.x)
776 [2486.2007.01464.x](http://doi:10.1111/j.1365-2486.2007.01464.x).

777 Peñuelas, J., Sardans, J., Filella, I., Estiarte, M., Llusà, J., Ogaya, R., ... & Terradas, J. (2017).
778 Impacts of global change on Mediterranean forests and their services. *Forests*, 8(12), 463.
779 <https://doi.org/10.5194/cp-6-245-2010>.

780 Puget, P., Chenu, C., Balesdent, J., 2000. Dynamics of soil organic matter associated with
781 particle-size fractions of water-stable aggregates. *Eur. J. Soil Sci.* 51, 595 – 605.
782 <https://doi.org/10.1111/j.1365-2389.2000.00353.x>.

783 Raczka, N.C., Carrara, J.E., Brzostek, E.R., 2022. Plant–microbial responses to reduced
784 precipitation depend on tree species in a temperate forest. *Glob. Change Biol.* 28, 5820-
785 5830. <https://doi.org/10.1111/gcb.16340>.

786 Ren, C., Zhao, F., Shi, Z., Chen, J., Han, X., Yang, G., Feng, Y., Ren, G., 2017. Differential
787 responses of soil microbial biomass and carbon-degrading enzyme activities to altered
788 precipitation. *Soil Biol. Biochem.* 115, 1-10. <https://doi.org/10.1016/j.soilbio.2017.08.002>.

789 Rosenberg, M.S., Adams, D.C., and Gurevitch, J., 2000. *Meta-Win: statistical software for*
790 *meta-analysis, v. 2.0.* Sunderland, MA: Sinauer.

791 Sanaei, A., Sayer, E.J., Delgado-Baquerizo, M., Seabloom, E., Yaun, Z., Ali, A., Wang, X.,
792 2023. Grazing intensity alters the diversity-carbon storage relationship in rangelands
793 across topographic and climate gradients. *Funct. Ecol.* <http://doi:10.1111/1365->
794 2435.14270

795 Sardans, J., Peñuelas, J., 2005. Drought decreases soil enzyme activity in a Mediterranean
796 *Quercus ilex* L. forest. *Soil Biol. Biochem.* 37, 455–461.
797 <https://doi.org/10.1016/j.soilbio.2004.08.004>.

798 Sardans, J., Peñuelas, J., 2013. Plant-soil interactions in Mediterranean forest and shrublands:
799 impacts of climatic change. *Plant Soil* 365, 1-33. <https://doi.org/10.1007/s11104-013->
800 1591-6.

801 Sayer, E.J., Crawford, J.A., Edgerley, J., Askew, A.P., Hahn, C.A., Whitlock, R., Dodd, I.C.,
802 2021. Adaptation to chronic drought modifies soil microbial community responses to
803 phytohormones. *Commun. Biol.* 4, 516. <https://doi.org/10.1038/s42003-021-02037-w>.

804 Sayer, E.J., Oliver, A.E., Fridley, J.D., Askew, A., Mills, R.T.E., Grime, J.P. 2017. Long-term
805 drought affects soil microbial communities via plant functional traits. *Ecol. Evol.* 7, 855–
806 862.

807 Schlesinger, W.H., Dietze, M.C., Jackson, R.B., Phillips, R.P., Rhoades, C.C., Rustad, L.E.,
808 Vose, J.M., 2016. Forest biogeochemistry in response to drought. *Glob. Change Biol.* 22,
809 2318-2328. <https://doi.org/10.1111/gcb.13105>.

810 Schwendenmann, L., Pendall, E., 2006. Effects of forest conversion into grassland on soil
811 aggregate structure and carbon storage in Panama: evidence from soil carbon fractionation
812 and stable isotopes. *Plant Soil* 288, 217-232. <https://doi.org/10.1007/s11104-006-9109-0>.

813 Silver, W.L., Lugo, A.E., Keller, M., 1999. Soil oxygen availability and biogeochemistry along
814 rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry* 44,
815 301–328. <https://doi.org/10.1007/BF00996995>.

816 Su, X., Su, X., Zhou, G., Du, Z., Yang, S., Ni, M., Qin, H., Huang, Z., Zhou, X., Deng, J., 2020.
817 Drought accelerated recalcitrant carbon loss by changing soil aggregation and microbial
818 communities in a subtropical forest. *Soil Biol. Biochem.* 148, 107898.
819 <https://doi.org/10.1016/j.soilbio.2020.107898>.

820 Sun, S., Liu, X., Lu, S., Cao, P., Hui, D., Chen, J., Guo, J., Yang, Y., 2023. Depth-dependent
821 response of particulate and mineral-associated organic carbon to long-term throughfall
822 reduction in a subtropical natural forest. *Catena* 223, 106904.
823 <https://doi.org/10.1016/j.catena.2022.106904>.

824 Tarnocai, C., Canadell, J.G., Schuur, E.A.G., Kuhry, P., Mazhitova, G., Zimov, S., 2009. Soil
825 organic carbon pools in the northern circumpolar permafrost region. *Glob. Biogeochem.*
826 *Cycle* 23. <https://doi.org/10.1029/2008GB003327>.

827 Vafaei, S., Soosani, J., Adeli, K., Fadaei, H., Naghavi, H., Pham, T. D., & Tien Bui, D. (2018).
828 Improving accuracy estimation of Forest Aboveground Biomass based on incorporation
829 of ALOS-2 PALSAR-2 and Sentinel-2A imagery and machine learning: A case study of
830 the Hyrcanian forest area (Iran). *Remote Sensing*, 10(2), 172.
831 <https://doi.org/10.3390/rs10020172>.

832 Wang, J., Hui, D., Lu, H., Wang, F., Liu, N., Sun, Z., Ren, H., 2019a. Main and interactive
833 effects of increased precipitation and nitrogen addition on growth, morphology, and
834 nutrition of *Cinnamomum burmanni* seedlings in a tropical forest. *Glob. Ecol. Conserv.* 20,
835 e00734. <https://doi.org/10.1016/j.gecco.2019.e00734>.

836 Wang, P., Huang, K., Hu, S., 2019b. Distinct fine-root responses to precipitation changes in
837 herbaceous and woody plants: a meta-analysis. *New Phytol.* 225, 1491–1499.
838 <https://doi.org/10.1111/nph.16266>.

839 Wang, C., Sun, Y., Chen, H.Y.H., Yang, J., Ruan, H., 2021. Meta-analysis shows non-uniform
840 responses of above- and belowground productivity to drought. 782, 146901.

841 <https://doi.org/10.1016/j.scitotenv.2021.146901>.

842 Wangdi, N., Ahmed, I.U., Mayer, M., Nirola, M.P., Orong, K., Zangmo, N., Godbold, D.L.,
843 Gratzer, G., Schindlbacher, A., 2023. Estimating the response of Himalayan old-growth
844 mountain forests to decreased monsoon precipitation. *Agric. For. Meteorol.* 336, 109471.
845 <https://doi.org/10.1016/j.agrformet.2023.109471>.

846 Waring, B.G., Averill, C., Hawkes, C.V., 2013. Differences in fungal and bacterial physiology
847 alter soil carbon and nitrogen cycling: insights from meta-analysis and theoretical models.
848 *Ecol. Lett.* 16, 887–894. <https://doi.org/10.1111/ele.12125>.

849 Wilcox, K.R., Shi, Z., Gherardi, L.A., Lemoine, N.P., Koerner, S.E., Hoover, D.L., et al. 2017.
850 Asymmetric responses of primary productivity to precipitation extremes: A synthesis of
851 grassland precipitation manipulation experiments. *Glob. Change Biol.* 23, 4376-4385.
852 <https://doi.org/10.1111/gcb.13706>.

853 Wilcox, K.R., von Fischer, J.C., Muscha, J.M., Petersen, M.K., Knapp, A.K., 2015. Contrasting
854 above- and belowground sensitivity of three Great Plains grasslands to altered rainfall
855 regimes. *Glob. Change Biol.* 21, 335-344. <https://doi.org/10.1111/gcb.12673>.

856 Wu, W., Geller, M.A., Dickinson, R.E., 2002. The Response of Soil Moisture to Long-Term
857 Variability of Precipitation. *J. Hydrometeorol.* 3, 604–613. [https://doi.org/10.1175/1525-7541\(2002\)003<0604:TROSMT>2.0.CO;2](https://doi.org/10.1175/1525-7541(2002)003<0604:TROSMT>2.0.CO;2).

859 Wu, Z., Dijkstra, P., Koch, G.W., Penuelas, J., Hungate, B.A., 2011. Responses of terrestrial
860 ecosystems to temperature and precipitation change: a meta-analysis of experimental
861 manipulation. *Glob. Change Biol.* 17, 927-942. <https://doi.org/10.1111/j.1365-2486.2010.02302.x>.

863 Xu, S., Geng, W., Sayer, E.J., Zhou, G., Zhou, P., Liu, C., 2020. Soil microbial biomass and
864 community responses to experimental precipitation change: A meta-analysis. *Soil Ecol.*
865 *Lett.* 2, 93-103. <https://doi.org/10.1007/s42832-020-0033-7>.

866 Yang, Y.J., Liu, S.R., Wang, H., Chen, L., Lu, L.H., Cai, D.X., 2018. Reduction in throughfall
867 reduces soil aggregate stability in two subtropical plantations. *Eur. J. Soil Sci.* 70, 301-
868 310. <https://doi.org/10.1111/ejss.12734>.

869 Yang, Y., Liu, S., Schindlbacher, A., Wang, J., Li, Z., Wang, H., et al. 2021. Topsoil organic
870 carbon increases but its stability declines after five years of reduced throughfall. *Soil Biol.*
871 *Biochem.* 156, 108221. <https://doi.org/10.1016/j.soilbio.2021.108221>.

872 Yaseef, N.R., Yakir, D., Rotenberg, E., Schiller, G., Cohen, S., 2010. Ecohydrology of a semi-
873 arid forest: partitioning among water balance components and its implications for
874 predicted precipitation changes. *Ecohydrology* 3, 143–154. <https://doi.org/10.1002/eco.65>.

875 Yue, K., Fornara, D. A., Yang, W., Peng, Y., Peng, C., Liu, Z., Wu, F., 2017. Influence of
876 multiple global change drivers on terrestrial carbon storage: additive effects are common.
877 *Ecol. Lett.* 20, 663-672. <https://doi.org/10.1111/ele.12767>.

878 Zeppel, M.J.B., Wilks, J.V., Lewis, J.D., 2014. Impacts of extreme precipitation and seasonal
879 changes in precipitation on plants. *Biogeosciences* 11, 3083-3093.
880 <https://doi.org/10.5194/bg-11-3083-2014>.

881 Zhang, G., Ganguly, S., Nemani, R. R., White, M. A., Milesi, C., Hashimoto, H., ... & Myneni,
882 R. B. (2014). Estimation of forest aboveground biomass in California using canopy height
883 and leaf area index estimated from satellite data. *Remote Sensing of Environment*, 151,
884 44-56. <https://doi.org/10.1016/j.rse.2014.01.025>.

885 Zhang, H., Shi, L., Lu, H., Shao, Y., Liu, S., Fu, S., 2020. Drought promotes soil phosphorus
886 transformation and reduces phosphorus bioavailability in a temperate forest. *Sci. Total*
887 *Environ.* 732, 139295. <https://doi.org/10.1016/j.scitotenv.2020.139295>.

888 Zhang, Q., Shao, M., Jia, X., Wei, X., 2019. Changes in soil physical and chemical properties
889 after short drought stress in semi-humid forests. *Geoderma* 338, 170–177.
890 <https://doi.org/10.1016/j.geoderma.2018.11.051>.

891 Zhou, M., Yan, G., Xing, Y., Chen, F., Zhang, X., Wang, J., Zhang, J., Dai, G., Zheng X., Sun,
892 W., Wang, Q., Liu, T., 2019. Nitrogen deposition and decreased precipitation does not
893 change total nitrogen uptake in a temperate forest. *Sci. Total Environ.* 651, 32–41.
894 <https://doi.org/10.1016/j.scitotenv.2018.09.166>.

895 Zhou, X., Zhou, L., Nie, Y., Fu, Y., Du, Z., Shao, J., et al. 2016. Similar responses of soil carbon
896 storage to drought and irrigation in terrestrial ecosystems but with contrasting
897 mechanisms: A meta-analysis. *Agr. Ecosyst. Environ.* 228, 70-81.
898 <https://doi.org/10.1016/j.agee.2016.04.030>.

899 Zhou, Z., Wang, C., Luo, Y., 2018. Response of soil microbial communities to altered
900 precipitation: A global synthesis. *Global Ecol. Biogeogr.* 27, 1121 – 1136.
901 <https://doi.org/10.1111/geb.12761>.

902

903 **Acknowledgement**

904 This study was financially supported by the Research Grants Council of the Hong Kong Special
905 Administrative Region, China (Grant No. CUHK14302014, CUHK14305515 and
906 CUHK14122521), the Chinese University of Hong Kong (4052228).
907 This work was also supported by the National Natural Science Foundation of China (4212205
908 4 and 42192513).

909

910

911

912

913 **Table 1** The effects of drought and irrigation on plant carbon inputs, soil carbon pools and soil organic carbon (SOC) content, soil microbial and
 914 physicochemical properties, and soil enzymes related to carbon degradation in three forest biomes: Mediterranean forest, (sub-)tropical forest and
 915 temperate forest. DOC is dissolved organic carbon; N is nitrogen; NH₄⁺ is ammonium-N; NO₃⁻ is nitrate-N; MBC is microbial biomass carbon;
 916 F:B ratio is the fungal to bacterial ratio. Effect sizes are shown as natural log-response ratios for *n* studies per response variable. Confidence
 917 intervals (CI) of an effect size overlapping 1 indicate no change relative to controls, whereas effects are significant when confidence intervals do
 918 not overlap with 1 (shown in bold type); *n* represents the number of observations for each parameter.

Variable	Drought				Variable	Irrigation			
	Forest biome	Effect size	Bootstrap CI	<i>n</i>		Forest biome	Effect size	Bootstrap CI	<i>n</i>
Aboveground biomass	Mediterranean	--	--	--	Aboveground biomass	Mediterranean	0.918	0.809-1.073	4
	(sub-)tropical	0.861	0.781-0.946	8		(sub-)tropical	--	--	--
	temperate	0.801	0.595-1.097	6		temperate	1.339	1.049-1.738	8
Litterfall	Mediterranean	0.995	0.863-1.146	12	Litterfall	Mediterranean	1.298	1.063-1.476	3
	(sub-)tropical	0.946	0.880-1.010	13		(sub-)tropical	--	--	--
	temperate	1.105	1.050-1.159	8		temperate	1.002	0.958-1.072	9
Litter mass loss	Mediterranean	0.883	0.872-0.894	19	Litter mass loss	Mediterranean	--	--	--
	(sub-)tropical	0.859	0.772-0.955	5		(sub-)tropical	1.031	0.956-1.126	4
	temperate	0.770	0.684-0.855	26		temperate	1.056	0.939-1.197	7
Fine root biomass	Mediterranean	--	--	--	Fine root biomass	Mediterranean	1.298	1.099-1.526	13
	(sub-)tropical	0.823	0.746-0.908	27		(sub-)tropical	1.061	0.868-1.266	14
	temperate	0.770	0.553-1.010	24		temperate	1.303	1.175-1.453	28
DOC	Mediterranean	1.180	0.766-1.506	5	DOC	Mediterranean	--	--	--
	(sub-)tropical	1.124	0.991-1.294	19		(sub-)tropical	0.979	0.917-1.029	3
	temperate	0.941	0.828-1.061	14		temperate	0.917	0.797-1.022	5
SOC	Mediterranean	0.977	0.749-1.262	12	SOC	Mediterranean	1.031	0.741-1.562	7
	(sub-)tropical	0.959	0.889-1.034	26		(sub-)tropical	0.918	0.864-0.975	12
	temperate	1.016	0.977-1.057	30		temperate	0.963	0.891-1.030	27
Macroaggregate	Mediterranean	--	--	--	Macroaggregate	Mediterranean	--	--	--

	(sub-)tropical	0.935	0.924-0.948	3		(sub-)tropical	--	--	--
	temperate	0.948	0.910-0.979	5		temperate	--	--	--
Microaggregate	Mediterranean	--	--	--	Microaggregate	Mediterranean	--	--	--
	(sub-)tropical	1.310	1.019-1.624	3		(sub-)tropical	--	--	--
	temperate	1.272	1.118-1.491	5		temperate	--	--	--
Soil pH	Mediterranean	1.027	1.001-1.054	4	Soil pH	Mediterranean	1.088	1.022-1.178	4
	(sub-)tropical	1.257	0.986-1.794	33		(sub-)tropical	1.011	1.004-1.018	11
	temperate	2.289	1.197-4.593	31		temperate	1.010	0.996-1.024	8
Soil total N	Mediterranean	0.788	0.616-0.999	11	Soil total N	Mediterranean	0.905	0.652-1.236	5
	(sub-)tropical	0.936	0.886-0.985	25		(sub-)tropical	0.945	0.867-1.022	11
	temperate	0.993	0.958-1.029	22		temperate	1.019	0.957-1.090	4
Soil NH4+	Mediterranean	0.855	0.767-0.953	2	Soil NH4+	Mediterranean	--	--	--
	(sub-)tropical	0.985	0.829-1.171	18		(sub-)tropical	1.484	1.169-1.845	7
	temperate	1.177	0.989-1.559	13		temperate	0.868	0.690-1.066	6
Soil NO3-	Mediterranean	1.646	1.409-1.923	2	Soil NO3-	Mediterranean	--	--	--
	(sub-)tropical	0.933	0.752-1.123	18		(sub-)tropical	0.896	0.774-1.042	7
	temperate	0.830	0.602-1.121	11		temperate	0.906	0.693-1.079	7
MBC	Mediterranean	1.024	0.835-1.187	5	MBC	Mediterranean	1.147	0.923-1.406	5
	(sub-)tropical	0.769	0.692-0.855	49		(sub-)tropical	1.145	1.051-1.243	21
	temperate	0.829	0.710-0.945	35		temperate	0.923	0.819-1.050	29
Fungal biomass	Mediterranean	0.822	0.578-1.204	10	Fungal biomass	Mediterranean	0.869	0.787-0.966	7
	(sub-)tropical	0.899	0.730-1.107	8		(sub-)tropical	1.436	1.190-1.764	5
	temperate	1.005	0.799-1.312	7		temperate	1.040	0.745-1.450	2
Bacterial biomass	Mediterranean	0.921	0.757-1.175	10	Bacterial biomass	Mediterranean	1.066	0.804-1.407	7
	(sub-)tropical	0.860	0.690-1.043	5		(sub-)tropical	1.425	1.229-1.606	5
	temperate	0.952	0.802-1.149	7		temperate	--	--	--
F: B ratio	Mediterranean	0.804	0.594-1.206	6	F: B ratio	Mediterranean	0.977	0.695-1.350	7
	(sub-)tropical	0.935	0.795-1.105	8		(sub-)tropical	1.022	0.882-1.205	4
	temperate	1.561	1.242-1.946	12		temperate	0.971	0.851-1.046	3
β -glucosidase	Mediterranean	0.864	0.709-1.041	9	β -glucosidase	Mediterranean	--	--	--
	(sub-)tropical	0.889	0.742-1.063	5		(sub-)tropical	1.048	1.000-1.099	2
	temperate	--	--	--		temperate	1.056	0.937-1.199	6
Cellobiohydrolase	Mediterranean	--	--	--	Polyphenol oxidase	Mediterranean	--	--	--
	(sub-)tropical	1.116	0.813-1.622	4		(sub-)tropical	1.124	1.108-1.141	2
	temperate	--	--	--		temperate	0.878	0.685-1.125	2

920 **Figure legends**

921 **Figure 1** The effects of drought (a,b) and irrigation treatments (c,d) on soil moisture, showing
922 (a,c) the magnitude of change in response to drought or irrigation treatments and (b,d) the
923 relationships between treatment level, expressed as a proportion of mean annual precipitation
924 (%MAP) across forest biomes. Pink symbols represent drought and blue symbols represent
925 irrigation. Effect sizes are shown as natural log-response ratios (LnRR). Confidence intervals
926 overlapping 1 (dashed line) indicate no change relative to controls, whereas effects are
927 significant when confidence intervals do not overlap 1. Numbers in parentheses represent the
928 number of observations (*n*) for each parameter. Regression lines are shown for relationships
929 significant at $P < 0.05$.

930 **Figure 2** The effects of drought (a) and irrigation treatments (b) on forest plant carbon (C)
931 inputs, soil dissolved organic carbon (DOC) and soil organic carbon (SOC), soil aggregate and
932 density fractions, soil physicochemical properties, microbial characteristics and extracellular
933 enzyme activities across forest biomes, where LFOC is light fraction organic C, MAOC is
934 mineral associated organic C; N is nitrogen; NH_4^+ is ammonium-N; NO_3^- is nitrate-N; MBC is
935 microbial biomass carbon; F:B ratio is the fungal to bacterial ratio. Effect sizes are shown as
936 natural log-response ratios for *n* studies per response variable. Confidence intervals of an effect
937 size overlapping 1 (dashed line) indicate no change relative to controls, whereas effects are
938 significant when confidence intervals do not overlap 1. Numbers in parentheses represent the
939 number of observations (*n*) for each parameter.

940 **Figure 3** Relationships between the magnitude of change in soil organic carbon (SOC) in
941 response to drought (a-f) or irrigation (g-k) treatments and (a) latitude, (b) aridity, (c) soil clay
942 content, (d) precipitation treatment level, (e) precipitation treatment duration, and (f) plot area;
943 where %MAP is the amount of water excluded or added by drought (pink symbols) and
944 irrigation treatments (blue symbols), respectively. The magnitude of change is indicated by the

945 effect size shown as the natural log response ratio (LnRR). Regression lines are shown for
946 significant relationships at $P < 0.05$.

947 **Figure 4** The effects of drought (a,c) and irrigation (b,d) treatments on soil organic carbon
948 (SOC) content in forests, showing (a,b) the magnitude of change in SOC in Mediterranean
949 forest (circles), (sub-)tropical forest (squares) and temperate forest (triangles); and the
950 relationships between the change in SOC content and (c,d) the change in soil moisture under
951 drought (pink symbols) or irrigation (blue symbols), respectively. The magnitude of change is
952 indicated by the effect size shown as the natural log response ratio (LnRR) for n studies per
953 response variable. Confidence intervals of an effect size overlapping 1 (a,b) or 0 (c,d), shown
954 as dashed lines, indicate no change relative to controls, whereas effects are significant when
955 confidence intervals do not overlap with 1 or 0, respectively. In (a,b), numbers in parentheses
956 represent the number of observations (n) for each parameter. In (c,d), regression lines are shown
957 for significant relationships at $P < 0.05$.

958 **Figure 5** Changes in plant or soil carbon pools in response to drought (a-f; pink symbols) or
959 irrigation (g-l; blue symbols) treatments, and their relationship with precipitation treatment
960 level, expressed as the proportion of mean annual precipitation (%MAP) excluded or added by
961 the treatments, respectively; showing the magnitude of change as effect sizes expressed as the
962 natural log response ratio (LnRR) for (a,g) aboveground biomass (AB), (b,h) litterfall, (c,i)
963 litter mass loss, (d,j) fine root biomass, (e,k) dissolved organic carbon (DOC), and (f,l)
964 microbial biomass carbon (MBC). Regression lines are shown for significant relationships at
965 $P < 0.05$.

966 **Figure 6** Conceptual model depicting the potential pathways by which precipitation change
967 could influence soil organic carbon (SOC) storage, showing the effects of drought (pink) and
968 irrigation (blue) on dissolved organic carbon (DOC); microbial biomass carbon (MBC); fungal
969 to bacterial ratio (F:B ratio); ammonium-N (NH_4^+); nitrate-N (NO_3^-); light fraction organic

970 carbon (LFOC); mineral-associated organic carbon (MAOC); soil respiration (CO₂, not
971 considered in this study). A minus symbol indicates a negative effect, a plus symbol indicates
972 a positive effect, and n.s. indicates non-significant effects, based on the present meta-analysis.

973

974

975

976

977

978

979

980

981

982

983

984

985

986

987

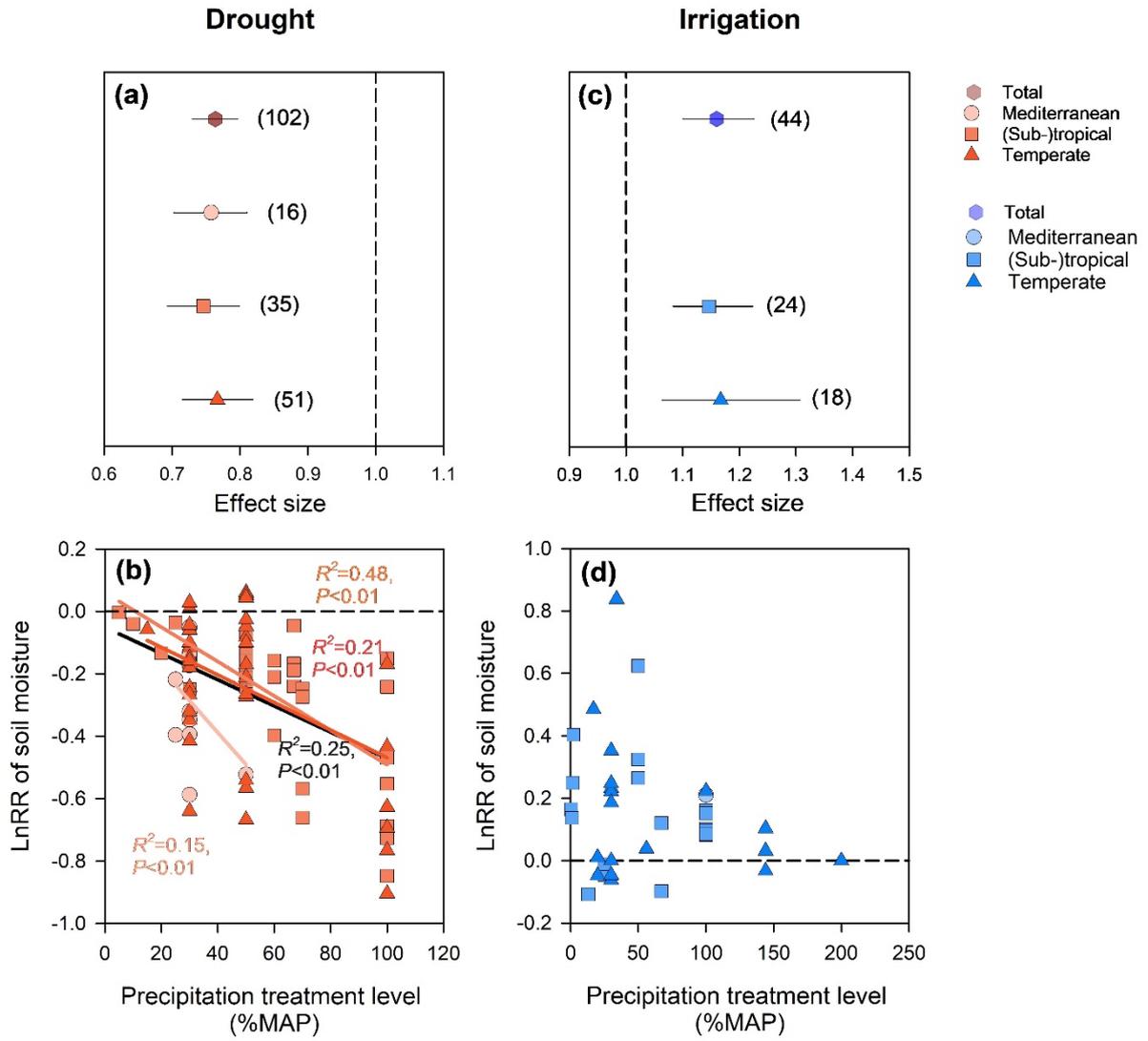
988

989

990

991

Figure 1



993

994

995

996

997

998

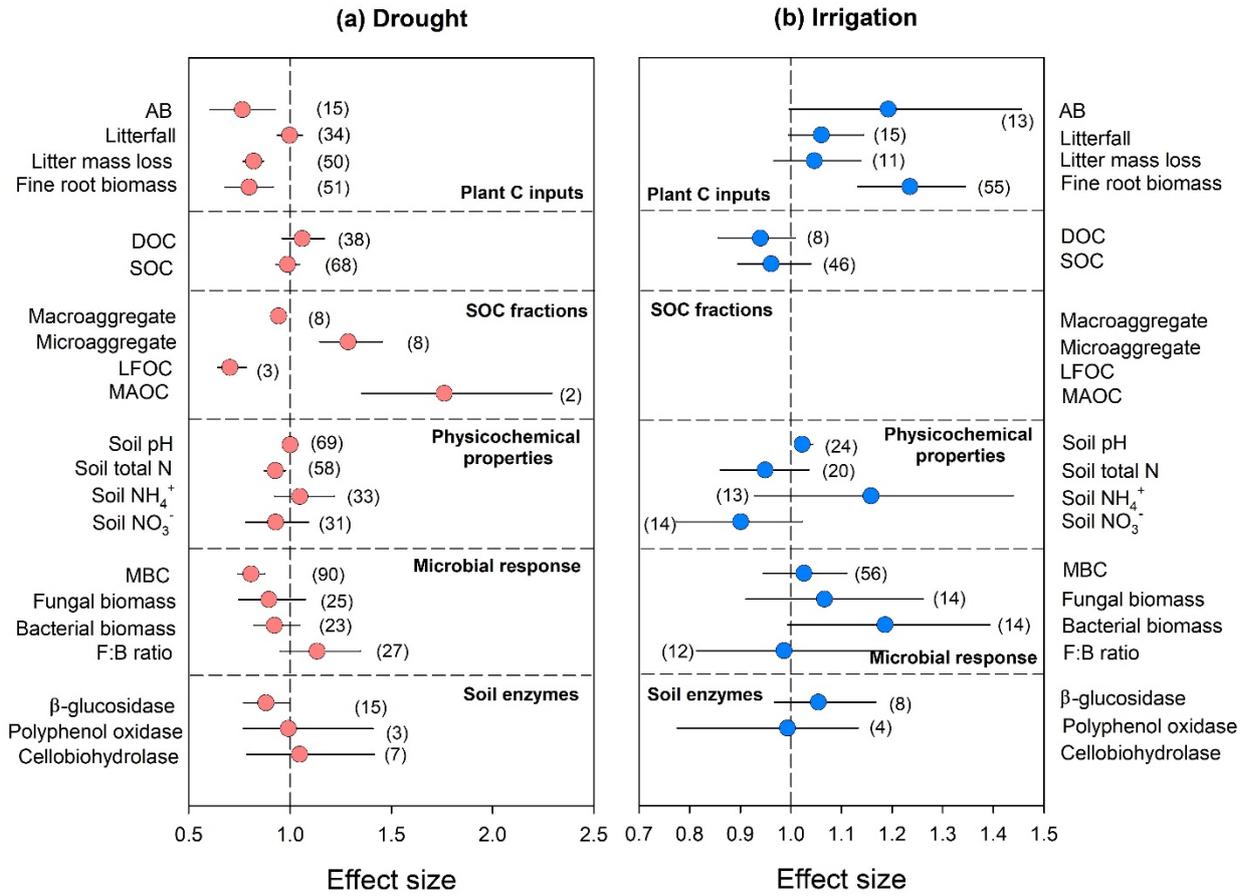
999

1000

1001

1002

Figure 2



1004

1005

1006

1007

1008

1009

1010

1011

1012

1013

1014

1015

1016

Figure 3

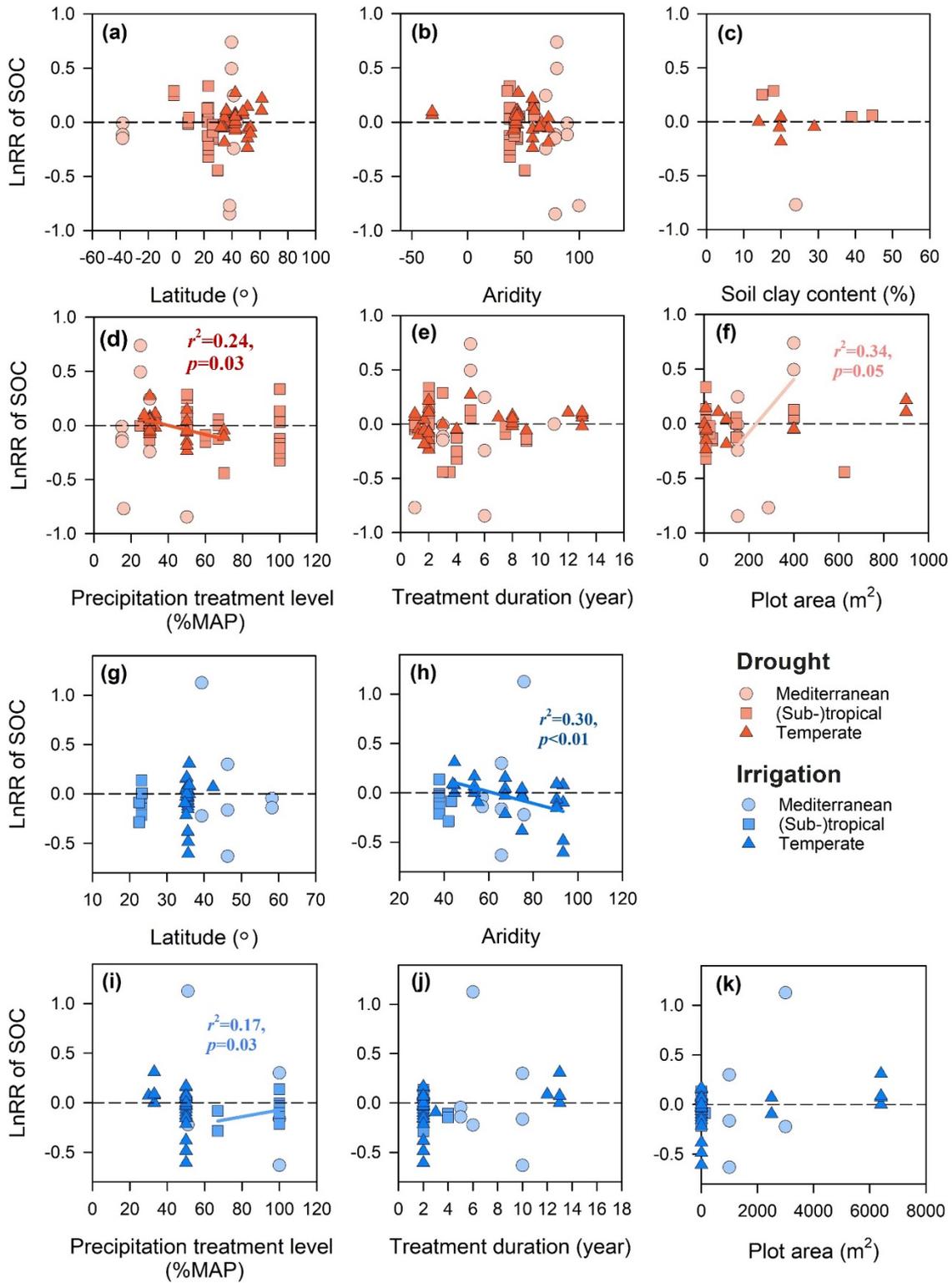
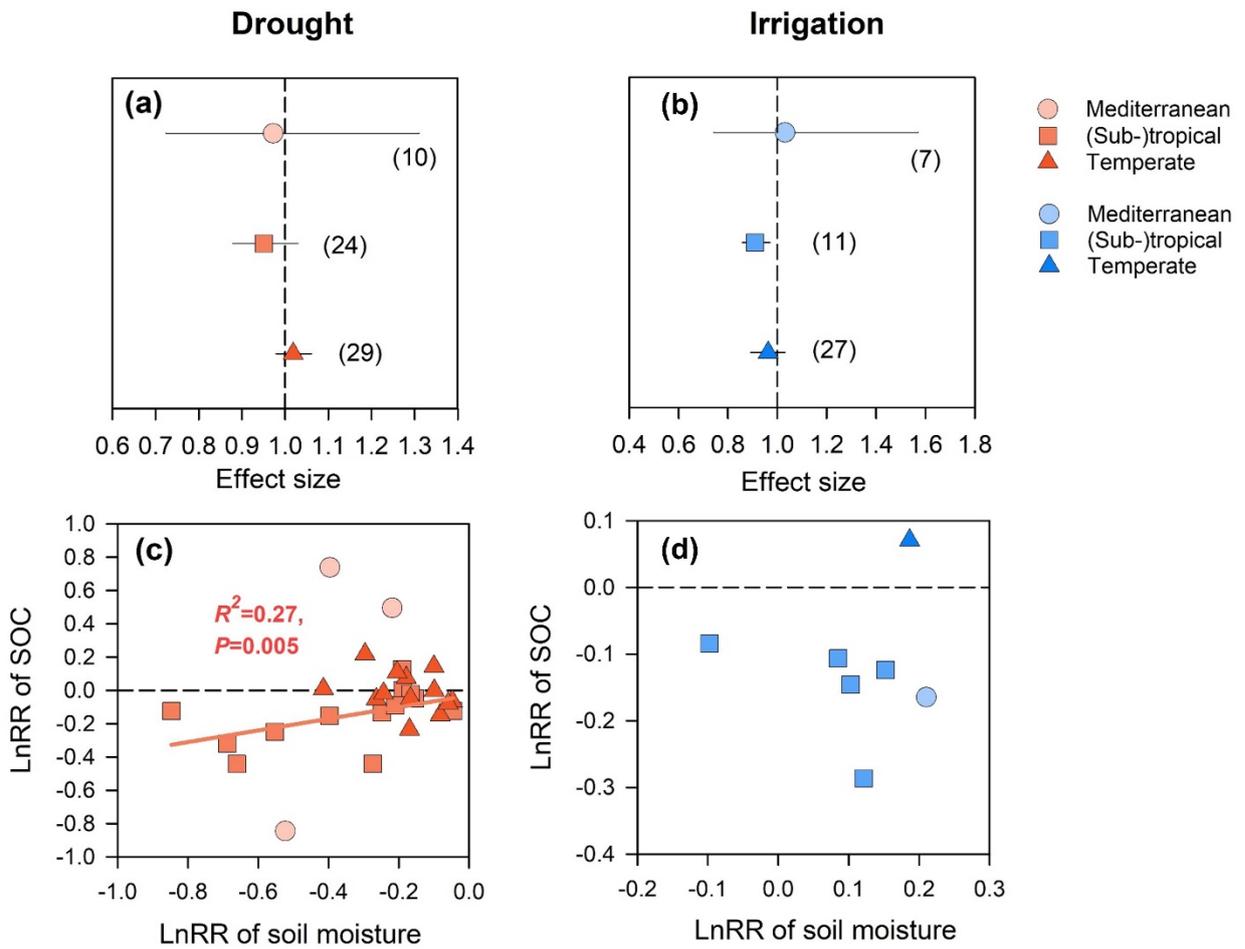


Figure 4



1023

1024

1025

1026

1027

1028

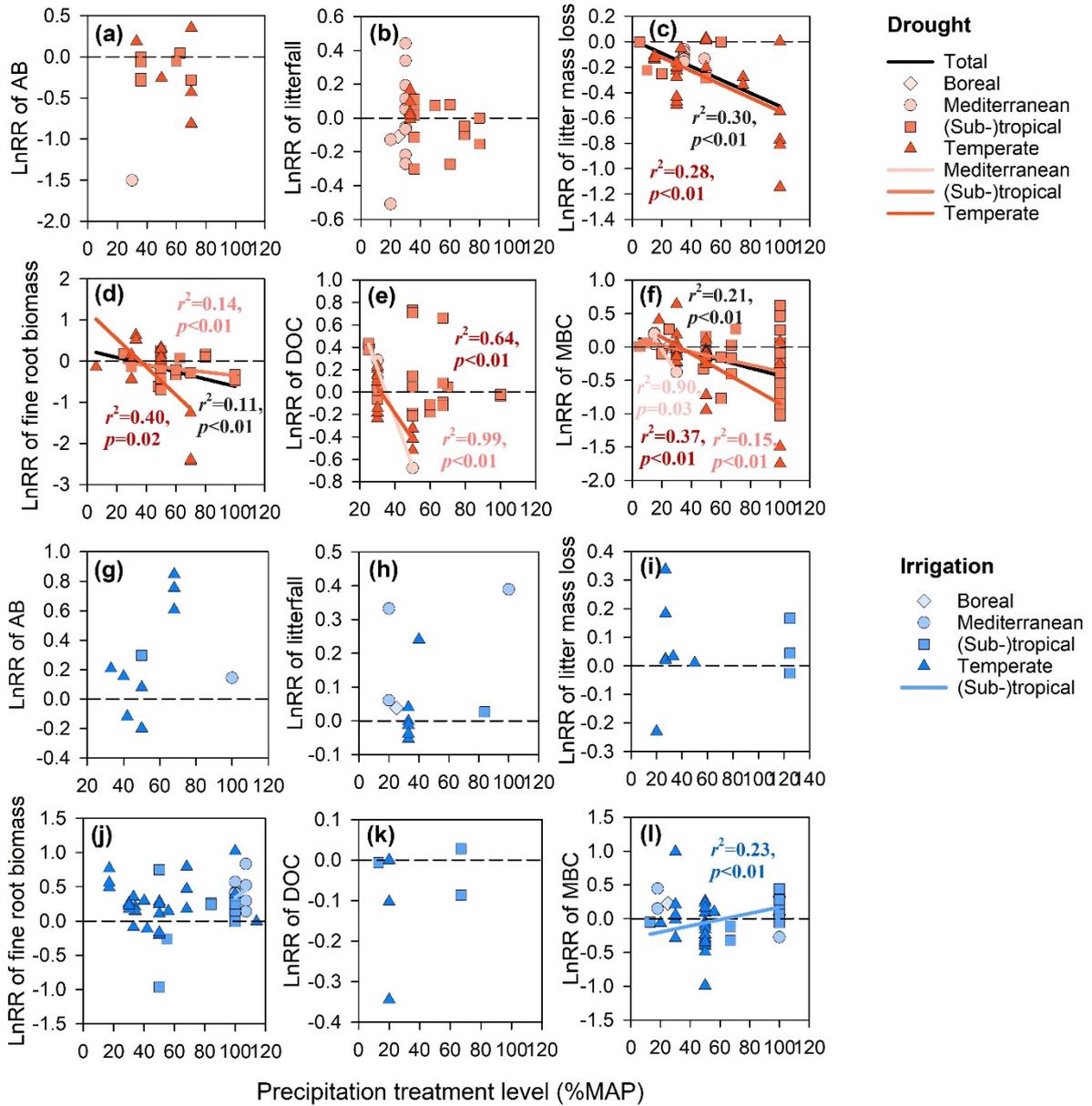
1029

1030

1031

1032

Figure 5



1034

1035

1036

1037

Figure 6

