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1 **Rainfall frequency, not quantity, controls isopod effect on litter decomposition**

2
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11 **Abstract**

12 Increasing climate variability is one of the dominant components of climate change, resulting
13 particularly in altered rainfall patterns. Yet, the consequences of rainfall variability on
14 biogeochemical processes that contribute to greenhouse gas emissions has received far less
15 attention than have changes in long-term mean rainfall. In particular, it remains unclear how leaf
16 litter decomposition responds to changes in rainfall frequency compared to changes in
17 cumulative rainfall quantity, and if changes in rainfall patterns will differentially affect
18 organisms in the decomposer food web (e.g., microbial decomposers that break down leaf litter
19 through saprotrophic processes versus detritivores that directly ingest leaf litter). To address this
20 knowledge gap, we disentangled the relative importance of cumulative rainfall quantity and
21 rainfall frequency on both microbial- and detritivore-driven litter decomposition, using the
22 isopod *Armadillidium vulgare* as a model macro-detritivore species and simulating rainfall in a
23 full-factorial microcosm experiment. We found that microbially-driven decomposition was

24 positively related to cumulative rainfall quantity, but tended to saturate with increasing
25 cumulative rainfall quantity when rainfall events were large and infrequent. This saturation
26 appeared to result from two mechanisms. First, at high level of cumulative rainfall quantity, large
27 and infrequent rainfall events induce lower litter moisture compared to smaller but more frequent
28 ones. Second, microbial activity saturated with increasing litter moisture, suggesting that water
29 was no longer limiting. In contrast, isopod-driven decomposition was unaffected by cumulative
30 rainfall quantity, but was strongly controlled by the rainfall frequency, with higher isopod-driven
31 decomposition at low rainfall frequency. We found that isopod-driven decomposition responded
32 positively to an increase in the weekly range of soil moisture and not to mean soil or litter
33 moisture, suggesting that an alternation of dry and moist conditions enhances detritivore activity.
34 Collectively, our results suggest that *A. vulgare* morphological and behavioral characteristics
35 may reduce its sensitivity to varying moisture conditions relative to microbial decomposers. We
36 conclude that the activity of microorganisms and isopods are controlled by distinct aspects of
37 rainfall patterns. Consequently, altered rainfall patterns may change the relative contribution of
38 microbial decomposers and detritivores to litter decomposition.

39

40 **Keywords**

41 Carbon cycling – Detritivore – Macrofauna – Precipitation frequency – Precipitation regime –

42 Rainfall pattern

43

44 **Introduction**

45 Decomposition, the physical and chemical breakdown of organic matter, is one of the major

46 fluxes of CO₂ from terrestrial ecosystems to the atmosphere (Schlesinger, 2005). Given the

47 decomposition sensitivity to climatic conditions (Adair et al., 2008; Aerts, 1997; Swift et al.,
48 1979), understanding the consequences of ongoing climate changes on decomposition is
49 fundamental to predicting the feedback effect on atmospheric CO₂ concentrations. This critical
50 challenge has spurred the development of studies investigating the sensitivity of litter and soil
51 organic matter decomposition to altered temperature (e.g., Davidson and Janssens, 2006; Fierer
52 et al., 2005; Hobbie, 1996) and rainfall (e.g., Wieder et al., 2009; Yahdjian et al., 2006; Yuste et
53 al., 2011). Yet, such studies typically focus on changes in the mean state of climate (e.g.,
54 increased average temperature; decreased cumulative rainfall), thereby omitting climate
55 variability, one of the dominant components of climate change. Rainfall events in particular are
56 expected to become more variable, with larger but less frequent rainfall events leading to
57 enhanced probabilities of drought and heavy rains (IPCC, 2013). These predictions raise a
58 critical question: for a given cumulative rainfall quantity, are large and infrequent rainfall events
59 equivalent to smaller but more frequent ones at inducing and sustaining decomposition?
60 Furthermore, it is unknown whether responses differ among groups of organisms in the
61 decomposer food web (e.g., microbial decomposers that break down leaf litter through
62 saprotrophic processes versus detritivores that directly ingest leaf litter).

63 The limited understanding of rainfall variability effects on decomposition derives in part
64 from the difficulty of manipulating rainfall regimes in a manner sufficient to capture the
65 complexity of current and future rainfall regimes. Partial rainout shelters consisting of elevated
66 frames with gutters exclude a known proportion of each rainfall event, thus reducing cumulative
67 rainfall but keeping rainfall frequency unchanged (e.g. Shihan et al., 2017; Yahdjian & Sala,
68 2002). Alternatively, rainout shelters consisting in full roofs deployed during a subset of rainfall
69 events reduce both cumulative rainfall quantity and rainfall frequency simultaneously,

70 confounding the effect of each factor (e.g. Taylor et al., 2004; Vogel et al., 2013). While such
71 methods have improved our understanding of the consequences of reduced cumulative rainfall or
72 seasonal drought on litter decomposition, they provide little insight on the rainfall variability
73 effect on decomposition. To our knowledge, advances in understanding rainfall frequency effects
74 on decomposition have been limited to work in arid ecosystems, where a few studies have
75 applied artificial rainfall events by watering the soil with equivalent amounts of water delivered
76 as either large and infrequent pulses, or small and frequent ones. One study by Whitford et al.
77 (1986), reported that 25-mm cumulative precipitation in the Chihuahuan Desert accelerated litter
78 decomposition when added as small weekly pulses, but not when added as larger monthly pulses.
79 This suggests that smaller but more frequent pulses may sustain decomposition better than large
80 infrequent ones. In contrast, in the Patagonian steppe, Austin et al. (2009) reported that litter
81 decomposition was similar when litter received a 10-mm pulse once a week or 3.3-mm pulses
82 three times a week. These conflicting results indicate that reduced frequency does not always
83 lead to a decline in decomposition, but may depend on cumulative rainfall quantity. Recently,
84 Joly et al. (2017a) reported that large, infrequent pulses induced lower litter decomposition than
85 small, more frequent pulses, but only at high level of cumulative rainfall when the differences in
86 pulse size were highest. This suggests that decomposition may saturate at a certain threshold in
87 pulse size (Fig. 1a), leading to non-linear responses of decomposition to increasing cumulative
88 rainfall quantity when delivered at low frequencies. Yet, the mechanisms underlying such
89 saturation of decomposition remain unclear.

90 Another challenge in assessing decomposition responses to rainfall frequency is that
91 studies to date have largely focused on microorganisms, omitting soil fauna responses. Studies
92 have typically incubated litter over sieved and dried soil (e.g., Austin et al., 2009; Joly et al.,

93 2017a) or within fine-mesh litterbags (e.g., Whitford et al., 1986). These methods may
94 inadvertently affect research findings as soil fauna play an important role on litter
95 decomposition, increasing mass loss by 37% on average across biomes (García-Palacios et al.,
96 2013). Macrofauna are particularly important to litter decomposition, with detritivores such as
97 millipedes catalyzing litter decomposition by fragmenting and compacting litter into fecal pellets
98 (Joly et al., 2018, 2015). To date, the few studies assessing the response of detritivore feeding
99 activity to altered rainfall pattern focused on drought intensity and duration, i.e. a change in both
100 cumulative rainfall quantity and frequency. For instance, Coulis et al. (2013) found that
101 millipede feeding activity decreased less than microbial activity in response to simulated drought
102 (reduced watering amount and frequency). Similarly, in a four year field experiment simulating
103 droughts with rainout shelters that reduced summer rainfall by 40%, Thakur et al. (2018) found
104 that summer droughts did not reduce detritivore activity except when accompanied by increased
105 temperatures. These results suggest that detritivore activity might be more resistant to dry
106 conditions than the largely moisture-driven microbial activity (Schimel et al., 1999). Yet, in both
107 studies the effect of frequency and cumulative rainfall were confounded. On the other hand,
108 Nielsen & Ball (2015) hypothesized that greater soil moisture and hence large precipitation
109 events are needed to trigger the activity of soil fauna relative to microorganisms. Such different
110 responses are expected as small rainfall events that keep soil moist for short periods may be
111 sufficient to trigger the activity of organisms with fast growth and reproduction time, such as
112 microorganisms. However, larger rainfall events that keep the soil moist for longer time periods
113 may be required to trigger the activity of larger organisms with slower growth and reproduction
114 such as detritivores (Schwinning and Sala, 2004). In line with this reasoning, for a given
115 cumulative rainfall quantity, detritivores should be less active with small and frequent events

116 than with large, infrequent events, as a larger event would more likely trigger their activity (Fig.
117 1b). However, this hypothesis by Nielsen & Ball (2015) was put forward based on a synthesis of
118 micro- and mesofauna studies, and was not tested experimentally. A better quantification of the
119 sensitivity of distinct groups of organisms within the decomposer food web (e.g., microbial
120 decomposers versus detritivores) to changes in rainfall frequency thus appears to be an important
121 step toward improving predictive capability of the consequences of rainfall patterns on litter
122 decomposition.

123 In this study, we aimed to determine the relative importance of cumulative rainfall
124 quantity and frequency on microbial and detritivore-driven litter decomposition. In line with the
125 aforementioned expected responses (see Fig. 1), we hypothesized that (H1) microbially-driven
126 decomposition would increase linearly with cumulative rainfall, but would reach a plateau for the
127 low rainfall frequency at high cumulative rainfall (Fig. 1a). Further, we hypothesized that (H2)
128 detritivore-driven decomposition would increase with decreasing rainfall frequency and would
129 be less sensitive to increasing cumulative rainfall than microbial decomposition (Fig. 1b). We
130 tested these hypotheses by measuring litter decomposition of velvet mesquite (*Prosopis velutina*)
131 in the absence or presence of detritivores, in addition to the presence of microbial decomposers,
132 after a six-week incubation under controlled conditions. As an operational definition for this
133 study, we defined decomposition as litter carbon (C) loss during the course of the experiment,
134 regardless of whether from saprotrophic processes or ingestion by detritivores. Litter C loss in
135 the absence of detritivores was used as an indicator of microbially-driven decomposition, while
136 the increase in C loss with the addition of detritivores was considered as detritivore-driven
137 decomposition. We used the isopod *Armadillidium vulgare* Latreille as a model detritivore
138 species. Rainfall was delivered as a factorial combination of four cumulative rainfall levels and

139 three rainfall frequencies (Fig. 2). To assess the effect of varying rainfall amounts and
140 frequencies on soil and litter moisture and to assess the control of these variables over microbial
141 and detritivore-driven decomposition, we monitored soil and litter water content throughout the
142 incubation.

143

144 **Methods**

145 *Detritivore, litter, and soil collection*

146 We chose the common pill woodlouse (Isopoda: Armadillidiidae) *Armadillidium vulgare*
147 (referred to as “isopods” hereafter) for our experiment, as it is a widespread detritivore species.
148 This species is native to Europe and introduced in North America. It is widely distributed,
149 existing in mesic temperate ecosystems as well as semi-arid ecosystems that undergo long
150 periods of drought. We collected around 400 individuals in April 2017 from the litter layer of a
151 tree-covered and drip-irrigated area landscaped with native Sonoran Desert species in Tempe,
152 Arizona, USA (33°25'8" N, 111°55'39" W). The isopods were kept until the start of the
153 experiment in containers containing soil and moist decomposing litter from the collection site.

154 We collected leaf litter of velvet mesquite (*Prosopis velutina* Woot.) in May 2017 from a
155 Sonoran Desert mesquite shrubland (33°32'13" N, 111°25'56" W), near Phoenix, Arizona, USA.
156 We used decomposing leaf litter rather than freshly senesced litter due to detritivore preference
157 for partially decomposed litter (David and Gillon, 2002; de Oliveira et al., 2010). Collected leaf
158 litter was air-dried, cleaned of debris (small rocks, twigs, non-targeted litter species, adhering
159 soil particles), and stored in paper bags until the start of the experiment. Leaf litter C and
160 nitrogen (N) concentrations were 0.392 g C g⁻¹ litter and 0.023 mg N g⁻¹ litter, C:N ratio was
161 17.0, and water-holding capacity was 1.64 g H₂O g⁻¹ litter.

162 Surface soil (top 5 cm) was collected in April 2017 at the Desert Botanical Garden
163 (33°27'51"N, 111°56'26"W) in Phoenix, Arizona, USA, from inter-canopy areas of a mesquite
164 shrubland. Soil was air-dried at 30°C and passed successively through 5 mm and 2 mm sieves.
165 We discarded the > 5 mm fraction and retained the 2-5 mm fraction (hereafter 'fine gravel') and
166 the < 2 mm fraction (hereafter 'soil'). The soil texture was loamy sand (71% sand, 25% silt, 4%
167 clay) with a water-holding capacity of 0.339 g H₂O g⁻¹ soil.

168

169 *Experimental setup*

170 In a full-factorial experiment, we manipulated cumulative rainfall, rainfall frequency, and isopod
171 presence. Cumulative rainfall treatments consisted of 30, 40, 50 and 60 mm month⁻¹ (for a total
172 of 42, 56, 70 and 84 mm throughout the six-week incubation). The corresponding weekly
173 amount for each cumulative rainfall treatment was delivered in three different frequency
174 treatments: rainfall was added in one large pulse each week, two intermediate-sized pulses each
175 week, or three small pulses each week (Fig. 2). Each cumulative rainfall and frequency treatment
176 combination was applied to two decomposer treatments: one treatment with microorganisms
177 only and one treatment with microorganisms plus four isopods. Each treatment combination was
178 replicated 4 times for a total of 96 microcosms (4 cumulative rainfall levels x 3 frequencies x 2
179 decomposer treatments x 4 replicates).

180 All microcosms consisted of 450 ml plastic containers that were perforated on the bottom
181 with 13 holes (1.5 mm diameter) to allow water drainage. Each microcosm was lined with an air-
182 and water-permeable polypropylene cloth to prevent soil loss. A layer of 70 ± 1 g of fine gravel
183 on top of the cloth facilitated drainage, and this was topped with 350 ± 1 g of soil. Because
184 terrestrial isopods including *A. vulgare* commonly seek shelter during dry conditions to avoid

185 desiccation (Dias et al., 2012), we constructed shelters (20 mm long and 5 mm high) made from
186 plastic irrigation pipe cut lengthwise. We placed one shelter in each microcosm and then added
187 2.0 ± 0.01 g of air-dried leaf litter. Initial air-dried litter mass was converted into oven-dried
188 mass by weighing air-dried litter subsamples, drying them at 60°C for 48 h, and reweighing them
189 to obtain dry mass. We ensured that no leaf litter was placed under the shelters to avoid
190 preferential litter decomposition in the shelter microclimate. Four isopods were added to each
191 isopod treatment microcosm, with individuals selected to have a total mass of 300 ± 50 mg
192 without gender distinction. To prevent isopod escape while allowing evaporation from soil and
193 litter surfaces, microcosms were covered with 2×2 mm nylon mesh secured with rubber bands.
194 For all microcosms, the microbial community present was derived from microorganisms present
195 in the air-dried soil and litter. Microcosms were incubated in a controlled environment chamber
196 (20°C , 50% relative humidity, 12 h day/night cycle) for six weeks. This duration was chosen as it
197 allows substantial microbial decomposition even under dry conditions (Joly et al., 2017a) and to
198 prevent litter from becoming limiting in the isopod treatment.

199 Another set of 48 microcosms without isopods (4 cumulative rainfall levels \times 3
200 frequencies \times 4 replicates) was set up to monitor soil and litter moisture three times a week
201 throughout the incubation (hereafter 'moisture control'). Litter water content was estimated by
202 selecting three leaflets from the litter layer, weighing these immediately, drying at 60°C for 48h,
203 and reweighing. This led to a sampling of ca. 54 leaflets per moisture control microcosm
204 throughout the incubation. We assumed that this decrease would have negligible impact on litter
205 and soil water content as each microcosm was filled with ca. 200 leaflets. Soil water content was
206 estimated by weighing microcosms, given the known initial soil dry mass for each microcosm.
207 The water contained in the litter was considered negligible compared to the soil water content.

208 From these estimates, we calculated the overall mean litter and soil moisture throughout the
209 incubation, mean weekly minimum, mean weekly maximum, and mean weekly range of litter
210 and soil moisture.

211 Water pulses were added to microcosms from all frequencies on Fridays, to twice and
212 three times a week frequencies on Mondays, and to three times a week frequencies on
213 Wednesdays (Fig. 2). Water additions took place after moisture content measurements. These
214 pulses were applied to microcosms by adding the designated volume of deionized water minus 3
215 ml to the litter surface with a bottletop dispenser. The remaining 3 ml were added with a hand
216 sprayer (volume controlled by weighing the microcosm), ensuring a consistent distribution of
217 water on the litter layer for all treatments. All isopod treatment microcosms were checked for
218 dead isopods three times a week. Occasional dead isopods were replaced with live isopods of
219 known mass.

220 At the end of the experiment, isopods were weighed for final mass and released at their
221 collection site. For each microcosm, the mean isopod mass throughout the incubation was
222 estimated as the mean of initial and final measurements. For microcosms in which we replaced
223 dead isopods with live ones, we estimated the mean isopod mass as the mean of initial,
224 intermediate, and final measurements weighted by the duration between measurements. All
225 microcosms except those from the moisture controls were dried in a glasshouse for 48 h at ca.
226 40°C. The remaining leaf litter in each microcosm was collected, cleaned of foreign material
227 (small rocks, soil particles, and feces), dried at 60°C for 48h, and reweighed. Decomposed litter
228 from each microcosm and five samples of initial litter were pulverized with a ball mill (8000D,
229 Spex CertiPrep, Metuchen, NJ, USA) and analyzed for C concentration using an elemental
230 analyzer (ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA, USA).

231

232 *Response variables*

233 Litter decomposition was expressed as the percentage of C lost from the litter during the
234 incubation: $\% \text{C loss} = (M_i \times C_i - M_f \times C_f) / (M_i \times C_i) \times 100$, where M_i and M_f are the initial and
235 final 60°C dry masses, respectively, and C_i and C_f are the initial and final litter C concentrations
236 (% of litter dry mass), respectively. We used litter C loss rather than total litter mass loss to
237 correct for inorganic contamination of leaflets retrieved from microcosms where they were in
238 direct contact with soil. Since the initial litter consisted of decomposing rather than freshly fallen
239 leaf litter, we assumed that most of the leaching, which dominates the early decomposition stage
240 (Berg and McClaugherty, 2014), had already occurred. We thus considered that C losses from
241 the treatment without isopods resulted from microbially-driven decomposition. In turn, we
242 considered that C losses from the treatment with isopods resulted from both microbially- and
243 isopod-driven decomposition. To isolate isopod from microorganism effects on total C loss, we
244 subtracted the C loss without isopods (mean value per treatment combination) to the C loss with
245 isopods (Bocock's formula; David, 1998). This isopod effect was then corrected for differences
246 in isopod mass among microcosms by dividing it by the isopod mass (average throughout the
247 incubation) for each microcosm, providing a percentage of isopod-driven C loss per mass of
248 isopod. We further multiplied this value by the mean isopod mass for all isopod microcosms
249 (0.33 g), to ensure that isopod- and microbially driven decomposition were expressed with the
250 same units, thus facilitating comparisons.

251

252 *Statistical analyses*

253 The hypothesized effects of cumulative rainfall quantity, rainfall frequency, and their interaction
254 on (H1) microbially- and (H2) isopod-driven decomposition were tested using two-way
255 ANOVAs. Additionally, the effects of cumulative rainfall quantity, rainfall frequency, and their
256 interaction on soil and litter moisture were tested using two-way ANOVAs. For all ANOVAs,
257 among-treatment differences were identified using Tukey HSD tests. We considered differences
258 significant when $p < 0.05$ and differences marginally significant when $0.05 < p < 0.10$.
259 Furthermore, we assumed that any effect of rainfall quantity and frequency over decomposition
260 would be mediated by their effect on litter and soil moisture. Thus, to disentangle the underlying
261 mechanisms, we used regressions to evaluate the control of litter and soil moisture (overall mean,
262 mean weekly minimum, mean weekly maximum and mean weekly range) over both microbially-
263 and isopod-driven decomposition. For each relationship, both linear and non-linear regressions
264 (including asymptotic exponential, exponential, and power) were fitted and the best-fit model
265 was chosen using the Akaike Information Criterion (AIC). All data were checked for
266 homoscedasticity and normal distribution of residuals and transformed when needed. All
267 analyses were performed using R version 3.4.4 (R Core Team, 2018).

268

269 **Results**

270 *Microbially- and isopod-driven decomposition*

271 Mean microbially-driven litter C loss after six weeks was $13 \pm 1.8\%$ (mean \pm SE) across all
272 rainfall treatments. Litter C loss increased linearly with cumulative rainfall quantity when
273 considered across all rainfall frequencies (Fig. 3a, Table 1). However, because rainfall frequency
274 had a marginally significant effect ($p = 0.085$, Table 1), patterns of litter C loss were distinct for
275 each frequency. While C loss linearly increased with cumulative rainfall quantity for the three

276 pulses per week frequency, it plateaued with increasing cumulative rainfall quantity for the one
277 and two pulses per week frequencies (Fig. 3a). Indeed, as indicated by the letters from the Tukey
278 HSD test, when pulses were added once or twice a week, there were no significant differences in
279 litter C loss between the 40, 50 and 60 mm month⁻¹ treatments (Fig. 3a).

280 Mean isopod-driven litter C loss was $39 \pm 1.8\%$ (mean \pm SE) across all rainfall
281 treatments. In contrast to microbially-driven C loss, isopod-driven litter C loss was unaffected by
282 cumulative rainfall quantity (Table 1), with no significant differences in C losses across
283 cumulative rainfall quantity levels for a given frequency (Fig. 3b). However, isopod-driven litter
284 C loss significantly decreased with increasing rainfall frequency (Table 1). This was particularly
285 important at low levels of cumulative rainfall quantity (30 and 40 mm month⁻¹) for which C loss
286 was significantly higher for the one pulse per week than for the three pulses per week treatment
287 (Fig. 3b).

288

289 *Changes in litter and soil moisture under altered rainfall pattern*

290 Litter moisture increased with increasing cumulative rainfall quantity (Fig. 4a, Table 1).
291 However, patterns of litter moisture differed among frequency treatments (Table 1) with litter
292 moisture less responsive to cumulative rainfall quantity for the one pulse per week frequency
293 compared to the two and three pulse per week frequencies (Fig. 4a), as indicated by the
294 significant interaction between cumulative rainfall quantity and frequency (Table 1).

295 Similar to litter moisture, mean soil moisture throughout the incubation significantly
296 increased with increasing cumulative rainfall quantity (Fig. 4b, Table 1). In contrast to litter
297 moisture, patterns of soil moisture were fairly similar among frequency treatments (Fig. 4b), but
298 with significantly higher soil moisture at lower rainfall frequency (Table 1).

299

300 *Moisture control over microbially- and isopod-driven decomposition*

301 Microbially-driven litter C loss responded positively to litter moisture, with the best-fit model
302 following an asymptotic exponential function (Fig. 5a). Soil moisture was also positively
303 correlated with microbially-driven litter C loss, explaining 52% of the variance in C loss (Fig.
304 5c). All other litter and soil moisture variables (mean weekly minima, maxima and range) also
305 positively correlated significantly with microbially-driven litter C loss (data not shown).

306 In contrast, isopod-driven litter C loss correlated neither with litter nor soil moisture (Fig.
307 5b, d). Of all litter and soil moisture variables (mean weekly minima, maxima, mean and range
308 of moisture), the range of soil moisture was the only variable significantly related to isopod-
309 driven litter C loss, explaining 11% of variation (Fig. 6).

310

311 **Discussion**

312 With this study, we provide some of the first elements to begin answering the question: are large
313 and infrequent rainfall events equivalent to smaller but more frequent ones at inducing and
314 sustaining decomposition? We found that the relative importance of cumulative rainfall quantity
315 and frequency on litter decomposition was different for microbially-driven than for isopod-
316 driven decomposition within the range of experimental treatments used for our study.
317 Specifically, we report that the contribution of microorganisms to litter decomposition is
318 primarily controlled by the overall cumulative rainfall quantity and only marginally affected by
319 its frequency. In contrast, the contribution of soil detritivores (*A. vulgare*) to litter decomposition
320 is unaffected by cumulative rainfall quantity, but strongly controlled by rainfall frequency, with
321 higher detritivore-driven decomposition at low rainfall frequency. These contrasting responses

322 suggest that changing rainfall patterns due to climate change may change the relative
323 contribution of microbial decomposers and detritivores to litter decomposition.

324

325 *Microbial response to changes in rainfall pattern*

326 In line with our first hypothesis, microbially-driven decomposition generally increased with
327 increasing cumulative rainfall. This control fits with the common view that macroclimatic
328 variables, such as annual precipitation, are dominant drivers of litter decomposition
329 (Meentemeyer, 1978). However, as expected based on recent findings (Joly et al., 2017a); Fig.
330 1a), microbially-driven decomposition increased linearly with increasing cumulative rainfall only
331 when simulated rainfall events were delivered as small and frequent pulses (Fig. 3a). In contrast,
332 when delivered as large and infrequent pulses, microbially-driven decomposition appeared to
333 saturate (Fig. 3a). The effect of rainfall frequency on microbially-driven decomposition was
334 however only marginally significant (Table 1), contrasting with the higher effect of rainfall
335 frequency observed in our previous experiment (Joly et al., 2017a). This may be due to the
336 narrower range of cumulative rainfall quantity used in this study (30-60 mm month⁻¹), compared
337 to the range (30-120 mm month⁻¹) used in Joly et al. (2017a), and to distinct environmental
338 conditions such as lower temperature and higher relative humidity in the present study that may
339 have reduced desiccation between rainfall events.

340 Saturation of microbial activity with increased cumulative rainfall quantity may result
341 from three mechanisms. First, above a given threshold of event size, litter or soil may reach its
342 maximum water-holding capacity with excess water lost to runoff or drainage. Second,
343 increasing event size may not linearly increase the duration during which litter or soil is within
344 the moisture range appropriate for microbial activity. Collectively, these mechanisms may limit

345 the efficiency of rainfall to increase and sustain litter/soil moisture when rainfall is delivered as
346 large and infrequent events. In line with this, we found that mean litter moisture was lower when
347 pulses were large and infrequent, at high level of cumulative rainfall (Fig. 4a). In parallel, soil
348 moisture tended to saturate with increasing cumulative rainfall quantity (Fig. 4b), which likely
349 results from the fact that soil often reached its maximum water-holding capacity, and excess
350 water was lost out of microcosms through drainage. As a third mechanism, microorganisms may
351 no longer be limited by moisture conditions above a given threshold of litter and/or soil moisture.
352 In line with this mechanism, we observed a saturation of microbially-driven decomposition with
353 increasing litter moisture (Fig. 5a). Such saturation was previously reported for microbial
354 respiration with increasing litter moisture (Schimel et al., 1999), with a decrease at very high
355 levels of litter moisture. Such decrease was not observed in our study, possibly because we did
356 not include a very high moisture treatment to prevent isopods from drowning. On the other hand,
357 microbially-driven decomposition did not saturate with increasing soil moisture (Fig. 5c).
358 However, because microbially-driven decomposition is likely to be more directly controlled by
359 litter moisture rather than soil moisture, and because soil moisture also saturates with increasing
360 cumulative rainfall quantity (Fig 4b), it may be that the linearity of the relationship is
361 coincidental rather than mechanistic. Nonetheless, soil microbial respiration may saturate with
362 increasing soil moisture, as was reported by Sponseller (2007). Regardless of the underlying
363 mechanisms, this saturation of microbial contribution to litter decomposition with decreasing
364 frequency could have substantial consequences on C cycling and CO₂ emissions from terrestrial
365 ecosystems.

366

367 *Isopod responses to changes in rainfall pattern*

368 In contrast to microbially-driven decomposition, isopod-driven decomposition was not affected
369 by cumulative rainfall but was exclusively affected by rainfall frequency (Table 1). Isopod-
370 driven decomposition was higher at low frequency (one pulse per week), than at high frequency
371 (two or three pulses per week), particularly at low cumulative rainfall quantity (Fig. 3b). The
372 lack of response of isopod-driven litter decomposition to cumulative rainfall quantity indicates
373 that the activity of individuals from our studied population of *A. vulgare* was even more resistant
374 to decreasing cumulative rainfall quantity than we had predicted (Fig. 1b) based on reports that
375 soil fauna activity is relatively resistant to drought (Coulis et al., 2013; Thakur et al., 2018). This
376 drought resistance may be due to strategies that limit desiccation, including morphological
377 characteristics such as a lower surface:volume ratio compared to microorganisms, an
378 exoskeleton, and, in the case of *A. vulgare*, the capacity to coil into a sphere (known as
379 ‘volvation’). Additionally, mobility coupled with behavioral characteristics such as sheltering
380 (Dias et al., 2012) may allow macrofauna to temporarily relocate towards favorable conditions.
381 Although relocation away from dry areas reduces the time spent on leaf litter foraging, it may
382 allow satisfying water requirements by permitting water intake while minimizing water losses, as
383 soil protected under shelters (e.g., rocks or wood in natural environments, artificial shelters in
384 our study) may remain moist for longer than litter or exposed soil. Such spatial decoupling of
385 food and water intake may allow isopods to remain active after the litter has dried down and as
386 long as the soil in the shelter remains sufficiently moist. This behavior was reported for the
387 desert isopod *Hemilepistus reaumuri*, which under dry conditions alternates feeding periods at
388 the soil surface with resting periods in their moister burrows (Shachak et al., 1979). In the
389 burrows, *H. reaumuri* obtain water via cutaneous absorption of saturated air and by feeding on
390 wet sand (Coenen-Staß, 1981). Our microcosms contained artificial shelters only, which may

391 have offered some opportunity for mobility and behavioral responses to the moisture treatments.
392 However, these responses may be even greater under field conditions than in our experiment,
393 potentially leading to an even greater resistance to low moisture levels.

394 Greater isopod-driven decomposition at low rainfall frequency compared to high
395 frequency fits our prediction that isopod-driven decomposition increases with decreasing rainfall
396 frequency and associated increase in pulse size (Fig. 1b). This finding is in line with the
397 theoretical framework put forward by Nielsen & Ball (2015) which suggests that a larger rainfall
398 event that induces greater soil moisture is needed to trigger activity of invertebrates compared to
399 microorganisms. However, we observed lower isopod-driven decomposition for the 60 mm
400 month⁻¹/two pulses a week treatment than for the 30 mm month⁻¹/one pulse a week treatment
401 (Fig. 3b), despite identical pulse sizes (7.5 mm per pulse) and lower average soil and litter
402 gravimetric moisture content for the 30 mm month⁻¹/one pulse a week treatment (Fig. 4a and 4b).
403 Furthermore, mean litter and soil moisture did not affect isopod-driven decomposition (Fig. 5b
404 and 5d). Consequently, our results suggest that higher pulse sizes and average soil moisture alone
405 are not sufficient to increase invertebrate activity – at least within the range of environmental
406 conditions present for this experiment and for our studied species – in contrast with the
407 hypothesis of Nielsen & Ball (2015). Instead, we found that the average weekly range of soil
408 moisture (average difference between weekly maximum and minimum soil moisture) was the
409 only moisture parameter related with isopod-driven decomposition (Fig. 6). This suggests that an
410 alternation of dry and moist conditions is needed to maximize isopod activity. One possible
411 explanation for this is that isopods such as *A. vulgare* perform compensatory feeding, consuming
412 a higher quantity of moist leaf litter following periods of drought to satisfy their water
413 requirements. Compensatory feeding has been reported for isopods feeding on low quality litter,

414 i.e. consuming more low-quality than high-quality litter to compensate for its low nutritive value
415 (Hättenschwiler and Bretscher, 2001), while moisture-related compensatory feeding has been
416 reported for vertebrates (Nicolson and Fleming, 2003) but not isopods.

417 Collectively, our results based on the isopod *A. vulgare* suggest that rainfall frequency
418 may have important consequences to detritivore-driven litter decomposition, in contrast to the
419 important influence of cumulative rainfall for microbial litter decomposition. In ecosystems
420 subject to long periods of drought that are interrupted with infrequent large rainfall events, slight
421 changes in the size and frequency of these events may have important consequences on the
422 activity of detritivores. In the Sonoran Desert, for instance, the litter consumption and survival of
423 the desert millipede *Orthoporus ornatus* (Girard, 1853), which remains inactive for most of the
424 year and emerges out of the soil only after monsoon rains (Wooten et al., 1975), may be
425 jeopardized by a change towards more frequent but smaller rainfall events. On the other hand, a
426 reduction in rainfall frequency and increase in event size in temperate ecosystems may lead to an
427 increased contribution of soil macrofauna to litter decomposition.

428
429 *Limits and ways forward*

430 It is important to stress that we considered a single detritivore species in our experiment and our
431 results may be specific to *A. vulgare*. The wide distribution of this species, spanning arid and
432 mesic ecosystems, may explain its lack of sensitivity to cumulative rainfall quantity. Other
433 detritivore species with narrower distributions, and/or with different physiological and
434 behavioral reactions to desiccation may respond differently to changes in rainfall patterns.
435 Indeed, desiccation resistance varies among detritivore species, including among isopod species,
436 and was found to be higher in detritivore communities living in environments with low soil

437 moisture than those in high soil moisture environments (De Smedt et al., 2018; Dias et al., 2013).
438 Thus, detritivores less adapted to low soil moisture may still be affected by cumulative rainfall
439 quantity, unlike *A. vulgare* in our study. Additionally, by comparing the response of a macro-
440 detritivore to that of microorganisms, our study focused on the extreme ends of the decomposer
441 food web size range. Intermediate-sized soil organisms (micro- and meso-fauna) may exhibit
442 intermediate response to changes in rainfall patterns. In light of our results, assessing the
443 response of other detritivores and other groups of the decomposer food web (e.g. microbivores,
444 predators) to changes in rainfall patterns will be important for holistic prediction of litter
445 decomposition. In addition, our experiment focused on the short-term responses of microbial and
446 detritivore activities through their effect on litter decomposition. Over longer temporal scales,
447 microbial and detritivore community composition may change as a response of rainfall pattern
448 changes (David and Handa, 2010; Nielsen and Ball, 2015; Yuste et al., 2011). Notably, Zimmer
449 (2004) reported that populations of four abundant isopod species in a floodplain forest in
450 Germany were reduced by more intense precipitation during spring and dry summers.
451 Understanding the consequences of rainfall variability on both community composition and
452 feeding activity will thus be needed to predict the overall change in detritivore-driven
453 decomposition. Given these limitations, we recognize that it is difficult to generalize our findings
454 to field conditions where different detritivores species occur. Instead, we view our results as
455 being most useful for testing hypotheses between rainfall pattern and the activity of different
456 groups of the decomposer food web, and as a way to identify climatic controls over ecological
457 processes that warrant further exploration *in situ*. Additionally, assessing the consequences of
458 altered rainfall patterns in concert with changes in temperature is needed as these different

459 aspects of climate change may have interactive effects on detritivore activity (Thakur et al.,
460 2018).

461

462 *Conclusions*

463 Our study provides clear evidence that the contributions of different groups of the decomposer
464 food web (i.e., microorganisms and a detritivore species) to litter decomposition are controlled
465 by distinct aspects of rainfall patterns. While cumulative rainfall quantity was the dominant
466 driver of microbially-driven decomposition, it did not affect isopod-driven decomposition within
467 the range of treatments applied. In turn, rainfall frequency had contrasting effects on
468 microorganisms and detritivores. At low rainfall frequency, microbially-driven decomposition
469 saturated with increasing rainfall quantity, while isopod-driven decomposition peaked,
470 particularly at low cumulative rainfall quantity. Change in rainfall frequency thus appear to be a
471 largely overlooked aspect of climate change of importance to C and nutrient cycling of surface
472 litter. In light of the recent reappraisal of the regulatory role of macroclimate over litter
473 decomposition (Bradford et al., 2017, 2016; Joly et al., 2017b), our results highlight the need to
474 consider climatic variables such as rainfall at smaller temporal scale and to consider the response
475 of different groups of the decomposer food web that may have markedly distinct response to
476 changes in rainfall patterns.

477

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484

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- 603

604 **Figures**

605 **Figure 1.** Hypothesized relationships between cumulative rainfall quantity and decomposition
606 driven by (a) microbial decomposers and (b) detritivores when rainfall is delivered as large and
607 infrequent events (yellow dashed line) or small but frequent events (blue dotted line). (a) For
608 microbial decomposer, we hypothesized that increasing cumulative rainfall quantity leads to a
609 linear increase in microbial decomposition when delivered as small frequent events. When
610 delivered as large but infrequent events, we hypothesized that microbially-driven decomposition
611 saturates because litter moisture saturates and microbial activity is no longer limited by moisture.
612 (b) For detritivores, we hypothesized an increase in detritivore-driven decomposition with
613 increasing cumulative rainfall quantity, but with a shallower slope than for microbially-driven
614 decomposition, as detritivores may be more resistant to drought than microbes. We also
615 hypothesized that large infrequent events lead to higher detritivore-driven decomposition than
616 small and frequent events, as detritivores may require greater soil moisture to trigger activity.

617
618 **Figure 2.** Simulated rainfall patterns throughout the incubation for the different cumulative
619 rainfall quantity (30, 40, 50 and 60 mm month⁻¹) delivered at three different rainfall frequencies
620 (once a week, yellow dashed line; twice a week, green dashed line; three times a week, black
621 dashed line). For a given cumulative rainfall quantity, less frequent pulses were also larger than
622 the more frequent ones.

623
624 **Figure 3.** Percentage of litter carbon (C) loss driven by (a) microorganisms and (b) isopods after
625 six weeks of incubation (mean \pm SE, n=4) under four different cumulative rainfall quantities (30,
626 40, 50 and 60 mm month⁻¹) and three different rainfall frequencies (1, 2 and 3 pulses per week).

627 Microbially-driven litter C loss was the C loss in microcosms without isopods. Isopod-driven
628 litter C loss was calculated for each microcosm as the difference in C loss between the litter loss
629 with isopods and the mean C loss without isopods per treatment combination. Points on the
630 cumulative rainfall quantity axis are jiggered for clarity. Letters indicate significant differences
631 in C loss among cumulative rainfall quantity and frequency treatment combinations (Tukey HSD
632 tests).

633

634 **Figure 4.** Mean (a) litter and (b) soil moisture for the six-week incubation (mean \pm SE, n=4),
635 under four different rainfall quantities (30, 40, 50 and 60 mm month⁻¹) and three different rainfall
636 frequencies (1, 2 and 3 pulses per week). Points on the cumulative rainfall quantity axis are
637 jiggered for clarity. Letters indicate significant difference in C loss among cumulative rainfall
638 quantity and frequency treatment combinations (Tukey HSD tests).

639

640 **Figure 5.** Microbially-driven litter C loss as a function of (a) mean litter moisture and (c) mean
641 soil moisture, and isopod-driven litter C loss as a function of (b) mean litter moisture and (d)
642 mean soil moisture. Mean moisture variables were computed from all measurements during the
643 six-week incubation. A black line represents the regression line if the slope is significantly
644 different from zero, and grey areas represent 95% confidence intervals of regression lines. The
645 regression line on panel (a) correspond to an asymptotic exponential non-linear model, while the
646 regression line on panel (c) correspond to a linear model. The r^2 and p-values are not reported for
647 Fig. 5a as they cannot be computed for nonlinear regression. ns, nonsignificant.

648

649 **Figure 6.** Isopod-driven litter C loss as a function of the mean weekly range of soil moisture.

650 This range of soil moisture was computed as the mean difference between the weekly maximum

651 and weekly minimum soil moisture. The black line represents the linear regression line and the
652 grey area represents the 95% confidence interval of the regression line.

ACCEPTED MANUSCRIPT

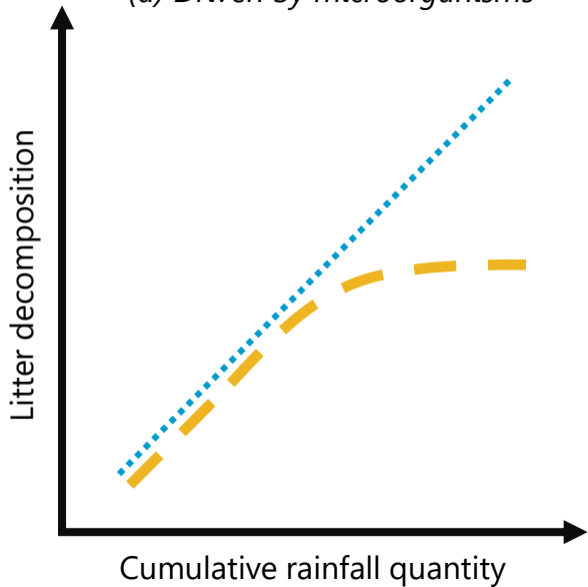
653 **Table 1.** Results of two-way ANOVAs testing the main effects of cumulative rainfall quantity, rainfall frequency, and their interaction
 654 on (i) microbially-driven litter C loss (n = 46) and (ii) isopod-driven litter C loss (n=46) after six weeks of incubation, and on (iii) litter
 655 moisture (n=48) and (iv) soil moisture (n=48). Soil and litter moisture variables were computed as the overall mean for all
 656 measurements taken per microcosm during the six-week incubation.

Source of variance	Microbially-driven litter carbon loss				Isopod-driven litter carbon loss			
	df	Mean sq.	F-value	p-value	df	Mean sq.	F-value	p-value
Cumulative rainfall quantity (CRQ)	3	471.7	24	<0.001	3	26	0.8	0.478
Rainfall frequency (RF)	2	52.1	2.6	0.085	2	771.6	25.1	<0.001
CRQ x RF	6	33.2	1.7	0.155	6	17	0.6	0.765
Residuals	34	19.7	-	-	34	30.8	-	-

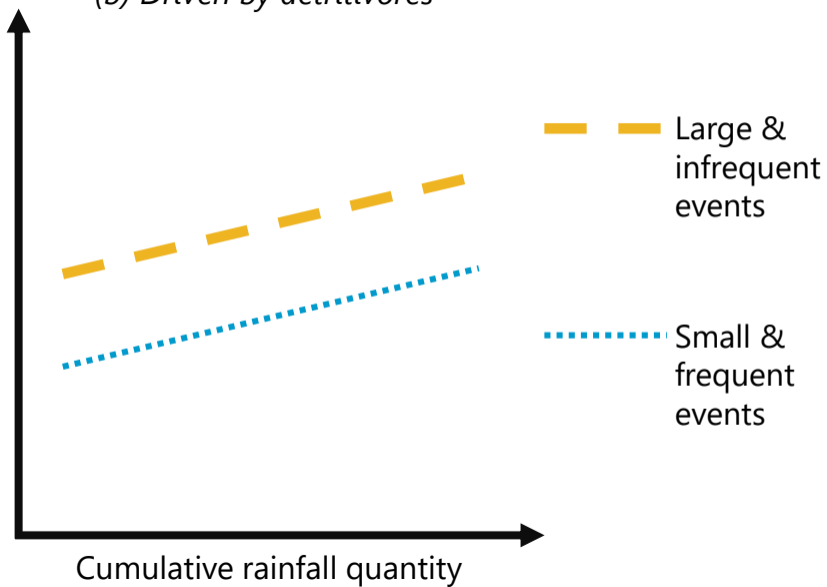
Source of variance	Litter moisture				Soil moisture			
	df	Mean sq.	F-value	p-value	df	Mean sq.	F-value	p-value
Cumulative rainfall quantity (CRQ)	3	15.7	79.6	<0.001	3	395.2	153.867	<0.001
Rainfall frequency (RF)	2	2	10	<0.001	2	16.8	6.529	<0.01
CRQ x RF	6	0.9	4.5	<0.01	6	0.5	0.183	0.979
Residuals	36	0.2	-	-	36	2.6	-	-

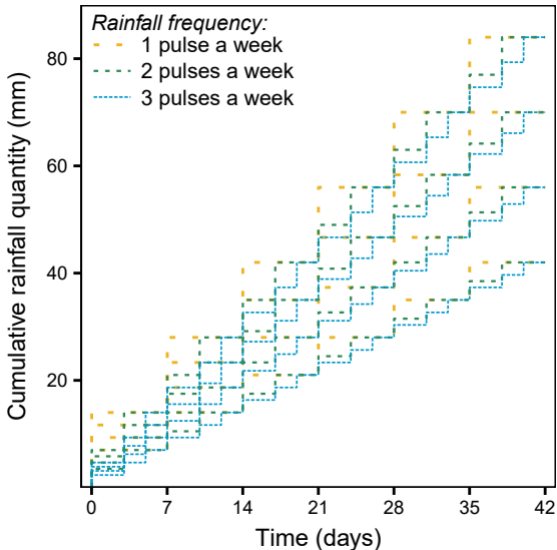
657

(a) Driven by microorganisms

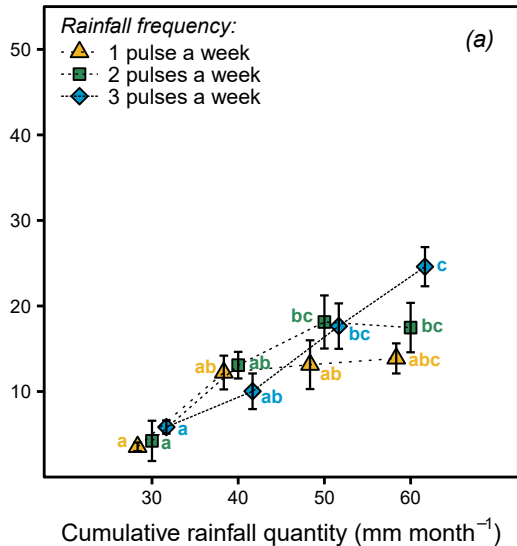


(b) Driven by detritivores

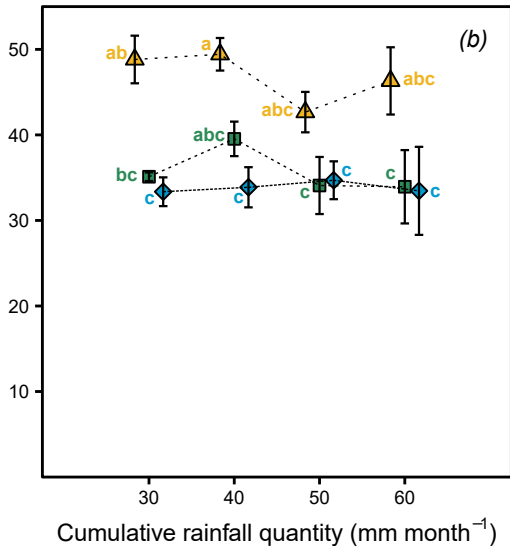


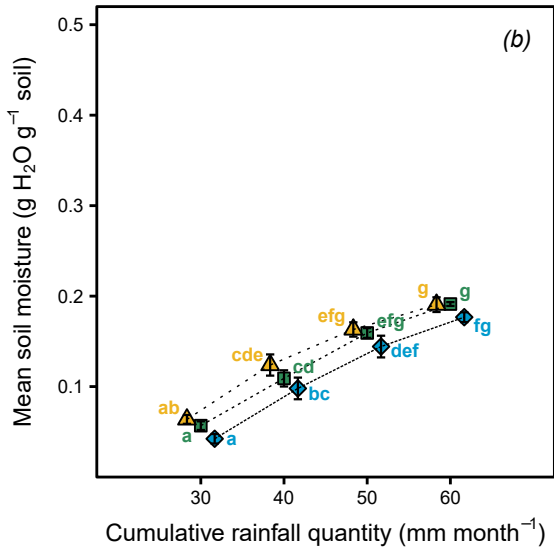
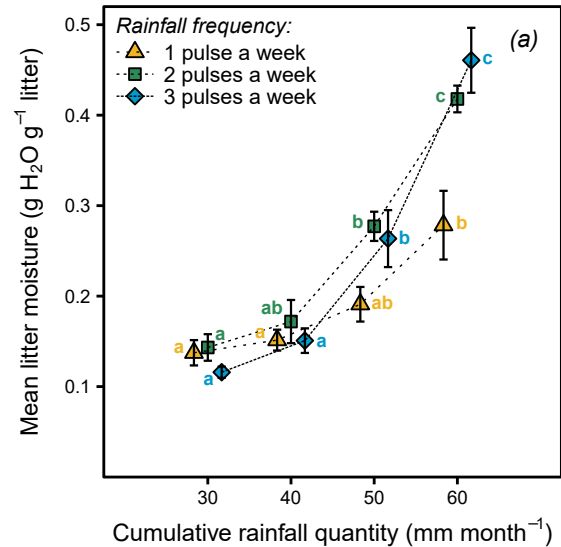


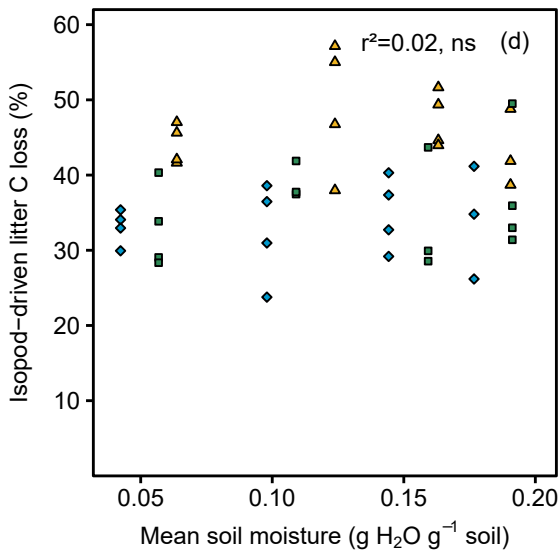
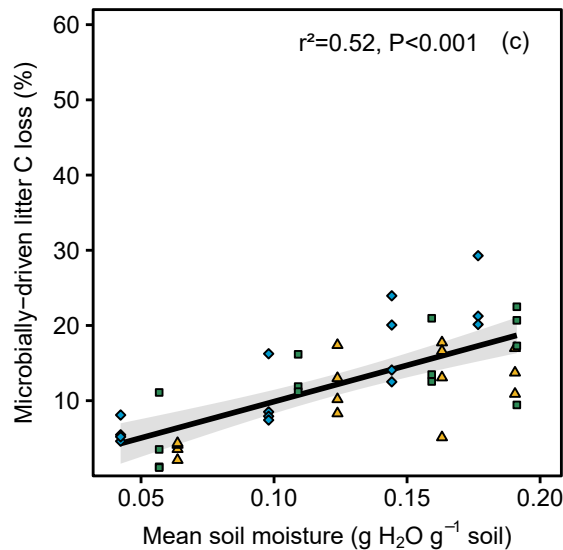
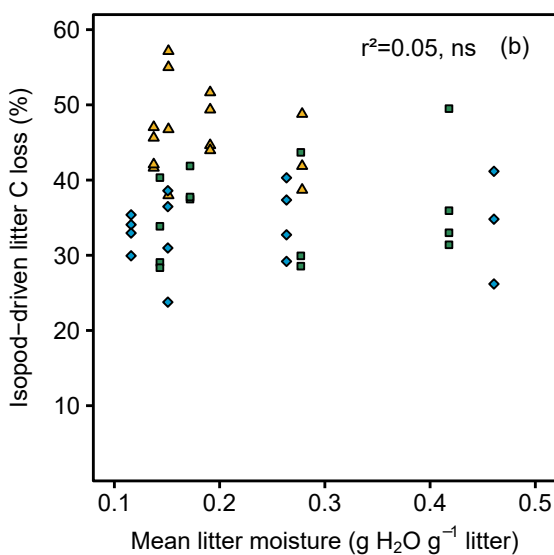
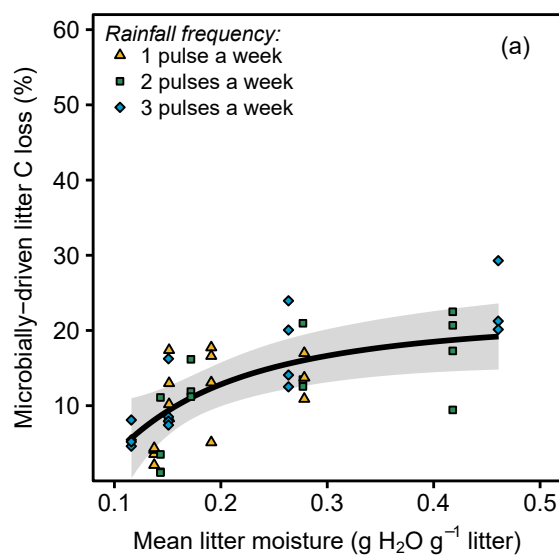
Microbially-driven litter C loss (%)

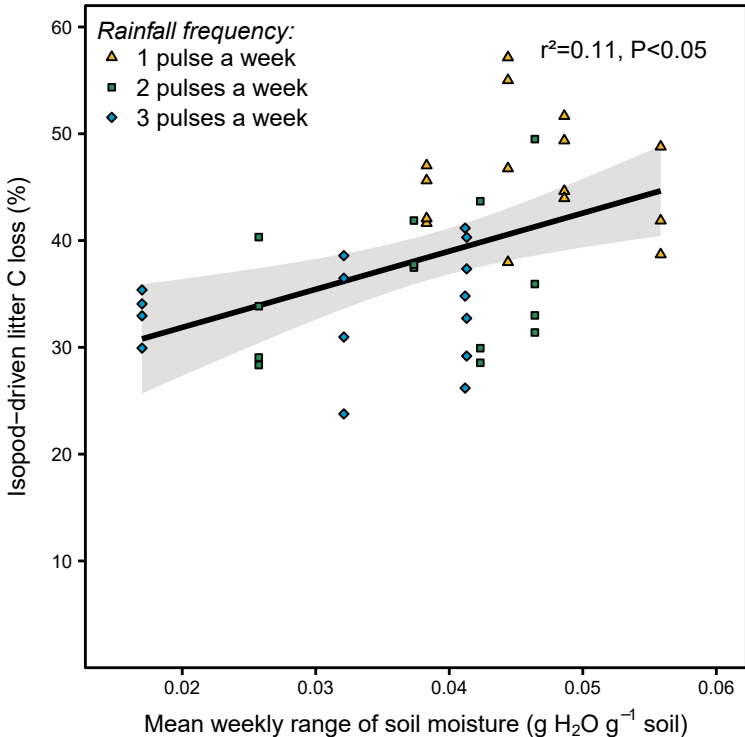


Isopod-driven litter C loss (%)









Highlights

- We disentangled the effect of rainfall quantity from frequency on decomposition
- We compared the responses of microbially- and isopod-driven litter decomposition
- Microbially-driven decomposition increased with increasing rainfall quantity
- Isopod-driven decomposition increased with decreasing rainfall frequency