

1 **Running head:** Rainfall control on detritivore activity

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3 **Title:** Synergistic interactions between detritivores disappear under reduced rainfall

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10

11 **Abstract:** Understanding the consequences of altered rainfall patterns on litter decomposition

12 is critical to predicting the feedback effect of climate change on atmospheric CO<sub>2</sub>

13 concentrations. While their effect on microbial decomposition received considerable

14 attention, their effect on litter fragmentation by detritivores, the other dominant

15 decomposition pathway, remains largely unexplored. Particularly, it remains unclear how

16 different detritivore species and their interactions respond to changes in rainfall quantity and

17 frequency. To fill this knowledge gap, we determined the contribution to litter decomposition

18 of two detritivore species (millipede and isopod), separately and in combination, under

19 contrasting rainfall quantity and frequency in a temperate forest. Although halving rainfall

20 quantity and frequency decreased top-soil moisture by 7.8 and 13.1%, respectively, neither

21 millipede- nor isopod-driven decomposition were affected by these changes. In contrast,

22 decomposition driven by both detritivore species in combination was 65.5% higher than

23 expected based on monospecific treatments under high rainfall quantity, but unchanged or

24 even lower under low rainfall quantity. This indicates that while detritivore activity is

25 relatively insensitive to changes in rainfall patterns, large synergistic interactions between

26 detritivore species may disappear under future rainfall patterns. Incorporating interspecific  
27 interactions between decomposers thus seems critical to evaluate the sensitivity of  
28 decomposition to altered rainfall patterns.

29

30 **Keywords:** Carbon cycling – Climate change – Isopod – Litter decomposition – Millipede –  
31 Precipitation regime – Rainfall pattern – Soil moisture

32

### 33 **Introduction**

34 Understanding the consequences of climate change for processes underpinning the  
35 global carbon cycle is essential to predicting its feedback effect on atmospheric CO<sub>2</sub>  
36 concentrations. This critical challenge prompted major research efforts evaluating the  
37 response of plant litter decomposition – the largest flux of CO<sub>2</sub> to the atmosphere  
38 (Schlesinger 2005) – to expected changes in climate change. In particular, predictions of  
39 altered rainfall patterns with larger but less frequent rainfall events leading to enhanced  
40 probabilities of drought and heavy rains (IPCC 2013) led numerous studies to evaluate how  
41 decomposition responds to various rainfall manipulation. To date, the vast majority of these  
42 studies have focused on the response of microbial decomposition (Sanaullah et al. 2012,  
43 Walter et al. 2013, Joly et al. 2017), and reported strong negative responses of microbial  
44 decomposition to reduced rainfall quantity and frequency. In contrast, the response of  
45 detritivorous soil animals to altered rainfall patterns remains poorly documented.

46 Litter-feeding soil invertebrates (detritivores hereafter) play a major role in organic  
47 matter turnover by consuming large amounts of decomposing litter (García-Palacios et al.  
48 2013) and returning most of it to the soil as feces (David 2014). This conversion of litter into  
49 feces consisting of a myriad of fecal particles facilitates further leaching and microbial  
50 activity, thereby accelerating decomposition (Joly et al. 2020). Despite the importance of this

51 pathway, its response to expected changes in rainfall patterns is difficult to predict.  
52 Particularly, it remains poorly understood how detritivores respond to changes in rainfall  
53 quantity (cumulative rainfall) and frequency (infrequent large rainfall event vs frequent  
54 smaller events). Among the few studies that evaluated this response, Coulis et al. (2013)  
55 reported a limited decrease in the feeding activity of one millipede species (*Ommatoiulus*  
56 *sabulosus*) in response to reduced rainfall quantity and frequency. In turn, Joly et al. (2019)  
57 found that the feeding activity of one isopod species (*Armadillidium vulgare*) was not  
58 affected by large changes in rainfall quantity, but controlled by rainfall frequency with higher  
59 activity at low rainfall frequency. The relative insensitivity of detritivore activity to reduced  
60 rainfall quantity suggests a desiccation resistance, either morphological (e.g., exoskeleton;  
61 low surface/volume ratio) or behavioral (e.g., mobility allowing to shelter or find water in  
62 moist soil areas). In turn, the higher activity at lower rainfall frequency reported by Joly et al.  
63 (2019) suggests that, for a given rainfall quantity, large and infrequent rainfall events trigger  
64 detritivore activity more efficiently than more frequent but smaller events, as hypothesized by  
65 Nielsen and Ball (2015), or that alternation between dry and moist conditions induces  
66 compensatory feeding, with detritivores consuming higher quantities of moist litter following  
67 drought periods to satisfy their water requirements. The contrasting responses to rainfall  
68 frequency between the two studies indicate that the influence of rainfall pattern on  
69 detritivore-driven decomposition may depend on detritivore species, yet species-specific  
70 sensitivities to rainfall patterns are unclear. Also, both studies were performed under  
71 laboratory conditions with detritivores collected from populations commonly exposed to  
72 drought (Mediterranean shrubland and dryland, respectively) and there are so far no data on  
73 the importance of this rainfall pattern control under field conditions and in mesic ecosystems.  
74 In addition to interspecific differences in the response of feeding activity to rainfall  
75 pattern, the contribution of detritivores to decomposition also depends on the nature of

76 interspecific interactions between cooccurring detritivores (Gessner et al. 2010). Several  
77 studies reported that when different soil animal species co-occur, their contribution to  
78 decomposition can be larger than predicted based on monospecific treatments (Heemsbergen  
79 et al. 2004, Hedde et al. 2010, DeOliveira et al. 2010). These synergistic effects of detritivore  
80 diversity may contribute substantially to decomposition, but the response of these interactions  
81 to climatic change is largely unknown. Theory predicts that as environmental stress increases,  
82 interspecific interactions switch from competition to complementarity and facilitation  
83 (Bertness and Callaway 1994). This stress-gradient hypothesis implies that an increase in  
84 environmental stress could drive a switch from antagonistic or non-additive diversity effects  
85 on ecosystem functioning to synergistic effects. The hypothesis is relatively well supported  
86 for plant-plant interactions and associated primary productivity (He et al. 2013), but remains  
87 poorly considered for interactions between soil organisms and associated decomposition  
88 processes, with the rare studies focusing on interactions between detritivore diversity and  
89 rainfall pattern reporting contrasted results (Collison et al. 2013, Coulis et al. 2015).  
90 Examining the nature of interactions between detritivores and their response to altered  
91 rainfall patterns thus appears critical to predict decomposition under future climate scenarios.

92         We evaluated the consequences of halving rainfall quantity and frequency on the  
93 feeding activity of two common detritivore species from distant phylogenetic groups  
94 (millipedes and isopods), and on their interactions. We hypothesized that (H1) both  
95 detritivore species are more strongly affected by reductions in rainfall frequency than  
96 quantity, and that (H2) synergistic interactions between detritivore species increase with  
97 reduced rainfall quantity and frequency. We tested these hypotheses by measuring the  
98 contribution of millipedes (*Glomeris marginata*) and isopods (*Armadillidium vulgare*),  
99 separately and in combination, to leaf litter decomposition during a six-week field experiment  
100 in a Scottish temperate forest during which we fully manipulated rainfall patterns.

101 **Methods**

102 We conducted this experiment in a mixed woodland of the University of Stirling (56°08'34"  
103 N, 3°55'12" W; 40 m a.s.l), located within the Scottish Lowlands, UK. The climate is  
104 characterized by mean annual precipitation of 1019 mm and a mean annual temperature of  
105 8.5 °C (MetOffice, 1981-2010). The months of August and September, during which we ran  
106 this experiment, have mean monthly precipitation of 72.4 and 90.6 mm, respectively and  
107 have 11.4 and 11.9 days with rainfall > 1 mm, respectively. The vegetation at the site consists  
108 in a mixture of broadleaf and coniferous tree species, including *Acer pseudoplatanus* L.,  
109 *Fagus sylvatica* L., *Aesculus hippocastanum* L., *Picea sitchensis* (Bong.) Carr, and *Larix*  
110 *decidua* Mill. In May 2018, we collected two detritivore species from nearby woodlands,  
111 including the millipede *Glomeris marginata* (Villers, 1789) in a woodland near Peebles,  
112 Scotland, UK (55°38'46" N, 3°07'55" W), and the isopod *Armadillidium vulgare* (Latreille,  
113 1804) in a coastal woodland near Dunfermline, Scotland, UK (56°01'35"N, 3°23'14"W). We  
114 chose these species as they are widespread across Europe, occurring in diverse ecosystems  
115 from Mediterranean to temperate. Detritivores were kept in plastic boxes and fed with moist  
116 litter until use. In July 2018, we collected *Aesculus hippocastanum* leaf litter from the study  
117 site. This litter consisted in 0.465 g C g<sup>-1</sup> litter and 0.0089 g N g<sup>-1</sup> litter, for a C:N ratio of  
118 52.0. Litter of this tree species is characterized as relatively recalcitrant, with high C:N ratio  
119 and tannin concentrations, and low concentration of water-soluble compounds and capacity  
120 to retain water (Joly et al. 2020). We used decomposing leaf litter rather than freshly  
121 senesced litter because detritivores prefer feeding on partially decomposed litter (David and  
122 Gillon, 2002). We air-dried the litter, cleaned it of debris (twigs, non-targeted litter species),  
123 and stored it in paper bags until the start of the experiment.

124 We manipulated rainfall quantity (18 vs. 36 mm/month), rainfall frequency (one vs.  
125 two pulses a week) and detritivore community composition (control without detritivore;

126 millipedes only; isopods only; millipedes and isopods together) in a full-factorial design of  
127 field mesocosms during a six-week period in August and September 2018. Each treatment  
128 combination was replicated five times for a total of 80 mesocosms (2 rainfall quantities  $\times$  2  
129 rainfall frequencies  $\times$  4 detritivore treatments  $\times$  5 replicates). To do so, we set up five  
130 replicate full-rainout shelters (6.25 m<sup>2</sup> surface area), consisting of 2.5  $\times$  2.5 m wooden frames  
131 covered by a transparent polythene sheet (0.127 mm thick, 508 g/m<sup>2</sup>), elevated at 0.75 m  
132 above the soil surface with wooden legs in corners to allow air passage. To prevent rainwater  
133 from accumulating in the middle of the polythene sheet, we placed a 1 m stake in the center  
134 of each shelter to elevate the sheet and allow the rainwater to runoff. Under each shelter, we  
135 set up four subplots (0.5 m<sup>2</sup> surface area); one per rainfall treatment. These subplots consisted  
136 in 0.7  $\times$  0.7 m wooden frames placed on the soil surface and inserted 5 cm into the soil. We  
137 placed these frames such that they were 40 cm away from the shelter edges to avoid moisture  
138 from shelter run-off, and 20 cm from one another. Within subplots, we removed the existing  
139 litter layer and inserted four mesocosms (one per detritivore treatment) made of PVC pipe (9  
140 cm long; 16 cm diameter) 7 cm into the soil. Because detritivores shelter during dry  
141 conditions to avoid desiccation, we added small tunnels made of PVC pipe (35 mm long; 35  
142 mm diameter) buried halfway, lengthwise, in the middle of each mesocosm. We then added  
143  $6.0 \pm 0.01$  g of air-dried leaf litter to each mesocosm. We converted air-dried litter mass into  
144 60°C dry mass by weighing air-dried litter subsamples, drying them at 60 °C for 48 h, and  
145 reweighing them to obtain dry mass. In each subplot, we randomly attributed a detritivore  
146 treatment to mesocosms and added either (1) no detritivore for the control treatment without  
147 detritivore, or  $0.6 \pm 0.01$  g of (2) millipedes, (3) woodlice, or (4) millipedes and woodlice.  
148 Because of variation in body size, the number of detritivores per microcosm varied between 5  
149 and 6. To prevent detritivores from escaping while allowing evaporation, we covered  
150 mesocosms with a 2  $\times$  2 mm nylon mesh secured with rubber bands. Within each subplot, we

151 also added leaf litter between mesocosms, in a similar density as within mesocosms to ensure  
152 homogeneous surface conditions (including desiccation) throughout the subplot. We  
153 randomly attributed a rainfall treatment to each subplot for each rainout shelter. Rainfall  
154 quantity and frequency treatments consisted in 18 and 36 mm/month, with the equivalent  
155 weekly amounts added as large pulses once a week or smaller pulses twice a week. These  
156 quantities approximately reflected the actual throughfall (ca. 42 mm/month) during the  
157 incubation period and a 50% reduction (ca. 21 mm/month), respectively. This throughfall was  
158 estimated by correcting the mean monthly rainfall by an estimated 50% rainfall losses due to  
159 canopy interception and stemflow (Johnson 1990). Similarly, the frequencies approximately  
160 reflected the actual number of days with > 1 mm of throughfall and a 50% reduction,  
161 respectively. We added the water pulses for both frequency treatments on Monday mornings  
162 and those for the high frequency treatment additionally on Thursday afternoons. These pulses  
163 were applied to mesocosms by watering subplots with a Knapsack pressure sprayer (PS16,  
164 Kingfisher). We monitored the moisture of the topsoil (top 1 cm) throughout the incubation  
165 by collecting soil samples from all subplots on Mondays and Thursdays, before and after  
166 each watering events. Soil samples were weighed, dried at 60°C for 48 h and weighed again  
167 to determine their water content. After six weeks of incubation, detritivores were collected,  
168 counted and weighed, and remaining leaf litter was collected carefully, dried at 60°C for 48  
169 h, and weighed. All decomposed litter samples and five samples of initial litter were ground  
170 with a disc mill and analyzed for C concentration with a flash CHN Elemental Analyser  
171 (Flash Smart, ThermoScientific). The percentage of C lost after the incubation was calculated  
172 as  $[(M_i \times C_i - M_f \times C_f) / (M_i \times C_i)] \times 100$  where  $M_i$  and  $M_f$  are the initial and final 60°C dry  
173 masses, respectively, and  $C_i$  and  $C_f$  are the initial and final C concentrations, respectively. We  
174 used litter C loss rather than total litter mass loss to correct for inorganic contamination of  
175 leaf litter retrieved from mesocosms where they were in direct contact with soil. To isolate

176 detritivore from microorganism effects on total C loss, we subtracted the C loss without  
177 detritivore from the C loss with detritivores. This detritivore-driven litter C loss was then  
178 corrected for slight differences in detritivore mass among mesocosms by dividing it by the  
179 detritivore mass for each mesocosm (average throughout the incubation) and multiplying it  
180 by the mean detritivore mass across all mesocosms with detritivores (0.596 g). For  
181 mesocosms including both millipedes and isopods, the relative mixing effect was calculated  
182 as  $[(\text{observed value} - \text{expected value})/\text{expected value}] \times 100$  for each rainfall treatment  
183 separately, where the expected value is the mean of litter C loss driven by millipede and  
184 isopods separately, in monospecific treatments. Fourteen mesocosms for which we noted  
185 anomalies upon harvest (e.g., presence of snails or lower numbers of detritivores than  
186 initially added) were not used for response variable calculations and further data analyses.  
187 These removed mesocosms were relatively equally distributed among rainfall treatments (5  
188 for the low quantity and frequency treatment; 3 for all other treatments).

189 We used two-way ANOVAs to evaluate the effect of rainfall quantity and frequency  
190 and their interaction on (1) soil moisture, on the contribution of (2) millipedes, (3) isopods,  
191 (4) millipedes and isopods to litter C loss, and on (5) the relative effect of mixing millipedes  
192 and isopods. To determine differences in detritivore-driven decomposition among detritivore  
193 treatments across all rainfall treatments, we evaluated the effect of detritivore community  
194 composition on detritivore-driven decomposition with a one-way ANOVA. For all tests,  
195 Tukey HSD post hoc mean comparisons identified difference among treatments. Student's *t*  
196 tests were used to determine if the relative mixing effect for each rainfall treatment was  
197 significantly different from zero. All data were checked for normal distribution and  
198 homoscedasticity of residuals. All statistical analyses were performed using R version 3.6.1.

## 199 **Results**



200           The exclusion of natural rainfall and application of simulated rainfall according to  
201 four treatments (current rainfall vs. 50% reduction, each delivered at current frequency vs.  
202 50% reduction) led to variable mean soil moistures throughout the six-week incubation,  
203 ranging from 0.25 g H<sub>2</sub>O g soil<sup>-1</sup> for the low rainfall quantity treatment delivered at low  
204 frequency, to 0.31 g H<sub>2</sub>O g soil<sup>-1</sup> for the high rainfall quantity treatment delivered at high  
205 frequency (Fig. 1). Halving rainfall quantity and frequency led to significant relative  
206 decreases in mean soil moisture by 7.8% ( $P < 0.05$ ) and 13.1% ( $P < 0.001$ ; Fig. 1).

207           After six weeks of incubation in the field, millipedes contributed significantly more to  
208 decomposition than isopods ( $P < 0.001$ ), with an average detritivore-driven litter C loss of  
209 26.2% for millipedes compared to 10.0% for isopods (Fig. 2), across rainfall treatments. In  
210 monospecific treatments, detritivore-driven litter C loss was not significantly affected by  
211 rainfall frequency ( $P = 0.79$  and  $P = 0.76$  for millipede- and isopod-driven litter C loss,  
212 respectively). They were also not affected by rainfall quantity, although we observed a  
213 marginally significant reduction in millipede-driven litter C loss under low rainfall quantity  
214 treatments ( $P = 0.08$  and  $P = 0.62$  for millipede- and isopod-driven litter C loss, respectively).  
215 When millipedes and isopods cooccurred, their combined contribution to litter C loss reached  
216 22.1%, i.e., a level similar to the contribution of millipedes to litter C loss, but significantly  
217 higher than that of isopods ( $P < 0.001$ ). In contrast to monospecific treatments, detritivore-  
218 driven litter C loss was negatively affected by halving rainfall quantity ( $P < 0.05$ ) but not  
219 frequency ( $P = 0.57$ ) and ranged from 15.3% for the low rainfall quantity treatment delivered  
220 at low frequency to 27.4% for the high rainfall quantity treatment delivered at low frequency.

221           The relative effect of mixing isopods and millipedes, i.e., the relative difference  
222 between observed values of detritivore-driven litter C loss when millipedes and isopods  
223 cooccurred and predicted values based on the respective monospecific detritivore treatments,  
224 ranged from -15.4% for the low rainfall quantity treatment delivered at low frequency to

225 +70.1% for the high rainfall quantity treatment delivered at high frequency (Fig. 3). The  
226 mixing effect was negatively affected by halving rainfall quantity ( $P < 0.001$ ) but not  
227 significantly affected by halving rainfall frequency ( $P = 0.16$ ). Except for the low quantity  
228 and high frequency treatment, relative mixing effects significantly differed from zero (Fig. 3).  
229

## 230 **Discussion**

231 The lack of response of either millipede- or isopod-driven decomposition to halving  
232 rainfall quantity supports the view that detritivore feeding activities are largely insensitive to  
233 changes in rainfall quantity. This concurs with previous studies that reported no response of  
234 detritivore-driven decomposition for the isopod species studied therein (Joly et al. 2019) and  
235 for another millipede species (Coulis et al. 2013) to altered rainfall patterns and suggests the  
236 existence of morphological and/or behavioral desiccation resistance in these detritivore  
237 species. Our results indicate that the pattern observed in these studies performed under  
238 controlled laboratory conditions, also applies under field conditions. Furthermore, while these  
239 previous studies used detritivores collected from drought-prone ecosystems (dryland and  
240 Mediterranean shrubland, respectively), the use of detritivores from temperate ecosystems  
241 which are not commonly exposed to drought (Scottish Lowlands) in our study suggests that  
242 this lack of sensitivity to altered rainfall patterns reflects species rather than population  
243 adaptations. It is important to note, though, that despite halving rainfall quantity, we only  
244 reported a limited yet significant reduction of topsoil moisture (-7.8%), which may explain  
245 the lack of detritivore response to reduced rainfall. Such limited changes in soil moisture  
246 suggests that mechanisms other than rainfall quantity/frequency control soil moisture, with  
247 water run-off, infiltration and evaporation potentially limiting topsoil moisture under high  
248 rainfall quantity, and with air humidity, dew and capillarity potentially limiting topsoil  
249 desiccation under low rainfall quantity. On the other hand, halving rainfall frequency induced

250 a larger reduction in topsoil moisture (-13.1%) but also had no effect on either millipede- or  
251 isopod-driven decomposition, unlike the expectation in our first hypothesis. This absence of  
252 response to even lower topsoil moisture echoes the general insensitivity of these detritivores  
253 to drought, but contrasts with the previous findings that isopod-driven decomposition  
254 increases with decreasing rainfall frequency (Joly et al. 2019). This finding from a dryland  
255 study reflected higher detritivore activities with increasing alternation of dry and moist  
256 conditions, suggesting a compensatory feeding in moist periods to satisfy water requirement.  
257 In our present study in mesic conditions, the range of litter and soil moisture may not have  
258 been sufficient to induce such a response. In turn, strong differences in detritivore-driven  
259 decomposition between millipede and isopod treatments suggest that detritivore community  
260 composition rather than rainfall patterns controls detritivore-driven decomposition. Such  
261 differences may be due to distinct consumption rates between detritivore species, and the  
262 higher detritivore-driven decomposition for the millipede compared to the isopod species is  
263 in line with previously reported differences in consumption rate for these two species (Coulis  
264 et al. 2015). While altered rainfall patterns may have limited effects on detritivore-driven  
265 decomposition, effects on detritivore community composition (Zimmer 2004) may have  
266 important consequences for decomposition. Furthermore, there is a strong need to consider  
267 multiple global change factors such as combined changes in temperature and rainfall that may  
268 have interactive effects on the detritivore-driven decomposition (Thakur et al. 2018).

269 A key result of our study is that interactions between detritivore species markedly  
270 varied depending on rainfall pattern with the effect of mixing millipedes and isopods on  
271 decomposition ranging from antagonistic (-15.4%) at low levels of rainfall quantity and  
272 frequency to synergistic (+70.1%) at high levels of rainfall quantity and frequency (Fig. 3),  
273 contrary to our second hypothesis. Such detritivore diversity effects were previously reported  
274 (Heemsbergen et al. 2004, DeOliveira et al. 2010), but this aspect of diversity on

275 decomposition remains poorly investigated compared with litter diversity (Gessner et al.  
276 2010, Handa et al. 2014). Although the contribution of isopods and millipedes together to  
277 decomposition did not exceed that of millipedes only, our results still suggest that important  
278 interactions between detritivores may be at play. Antagonistic effects could be explained by  
279 interspecific competition while synergistic effects could result from resource partitioning (use  
280 of different litter parts by different detritivore species) or facilitation if litter consumption by  
281 one species facilitates litter consumption for the other (Gessner et al. 2010). Importantly, our  
282 study suggests that the nature and magnitude of such interactions are strongly dependent on  
283 environmental conditions, as evidenced by the change from large positive interactions to non-  
284 additive or even negative interactions associated with the reduction in rainfall quantity and  
285 frequency. This could be driven by soil or litter moisture (not monitored in this study), with  
286 negative interactions decreasing and positive interactions increasing with greater moisture  
287 availability. This finding from our field experiment contrasts with laboratory studies that  
288 reported no response of detritivore interactions to changes in moisture treatments (Collison et  
289 al. 2013, Coulis et al. 2015). Such discrepancies may be due to the consideration of a  
290 reduction in rainfall frequency only in Coulis et al. (2015), or due to a lower study duration  
291 (two weeks) in Collison et al. (2013). More generally, our results do not support the stress-  
292 gradient hypothesis (Bertness and Callaway 1994, He et al. 2013) and suggest that rather than  
293 mitigating predicted changes in climate change (“insurance hypothesis”, Yachi and Loreau  
294 1999) positive interspecific interactions on ecosystem functioning may be vulnerable to  
295 predicted changes in climate change. Understanding the mechanisms underpinning these  
296 detritivore interactions and their sensitivity to rainfall, at larger temporal, spatial and  
297 phylogenetic scales thus represents an urgent research avenue.

298 Collectively, our results indicate that the feeding activities of the detritivore species  
299 *Armadillidium vulgare* and *Glomeris marginata* are relatively insensitive to changes in

300 rainfall patterns, but that their interspecific interactions may switch from synergistic to  
301 antagonist under reduced rainfall quantity and frequency. Such a reduction in the contribution  
302 of diverse detritivore communities to decomposition under future rainfall patterns could slow  
303 carbon release from litter. This could have important consequences for soil carbon storage,  
304 but an improved understanding of detritivore contribution to soil organic matter formation  
305 has yet to emerge (Joly et al. 2020) to predict the consequences on global carbon cycling.  
306 However, our focus on a single and rather recalcitrant litter prevents generalizing our  
307 findings to litter of different quality. Furthermore, although these species are common across  
308 Europe and cooccur in a wide range of ecosystems, our findings may not extend to other  
309 detritivore species and their interactions. Evaluating the response of diverse detritivore  
310 species with different phylogenetic origins and distribution, and their interactions will be  
311 necessary to identify general patterns in the climatic sensitivity of detritivores, thereby better  
312 predicting the consequences of climate change on decomposition. To this end, research  
313 efforts aiming to identify morphological traits underpinning such sensitivities appear  
314 particularly promising (e.g. Dias et al. (2013) for isopods).

315

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320

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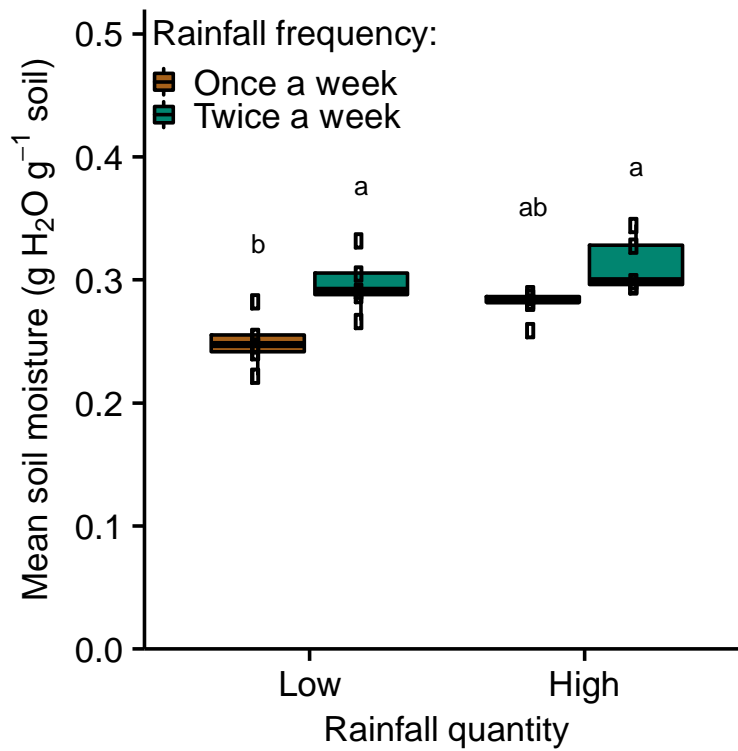
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- 393



394 **Figure legends**

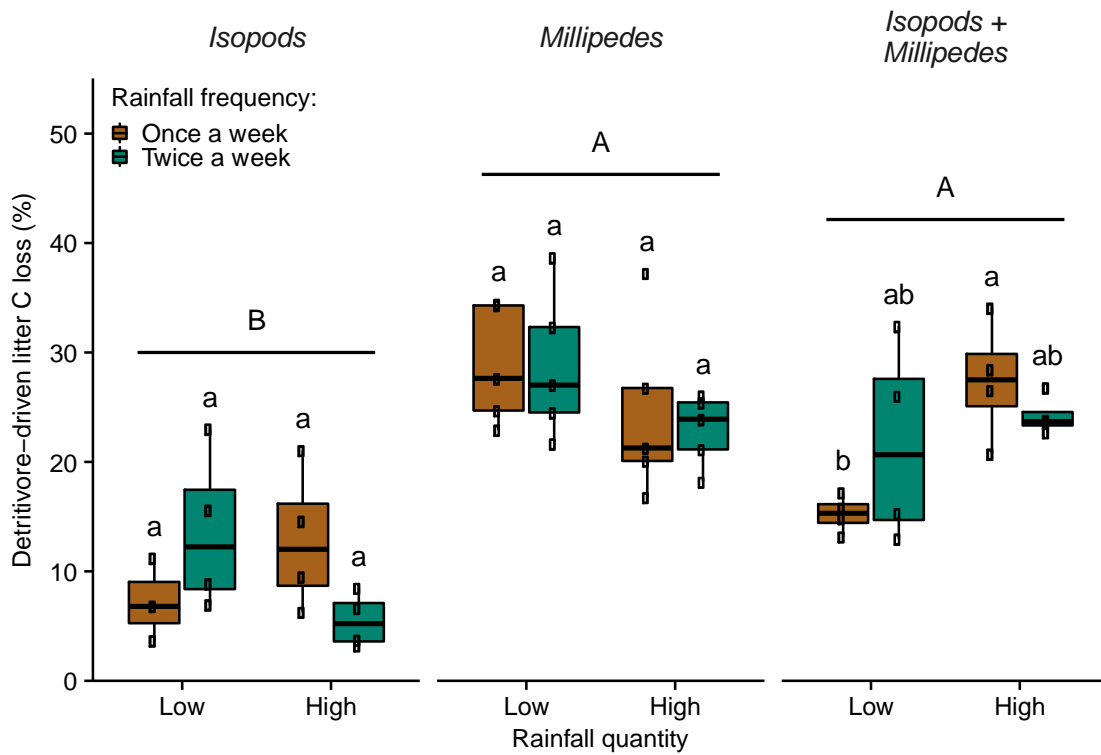
395 Figure 1: Mean moisture of the topsoil (top 1 cm) throughout the six-week incubation, under  
396 two different rainfall quantities (18 and 36 mm/month) and two different rainfall frequencies  
397 (one or two pulses per week). Lowercase letters indicate significant differences among  
398 rainfall treatments (Tukey HSD tests).



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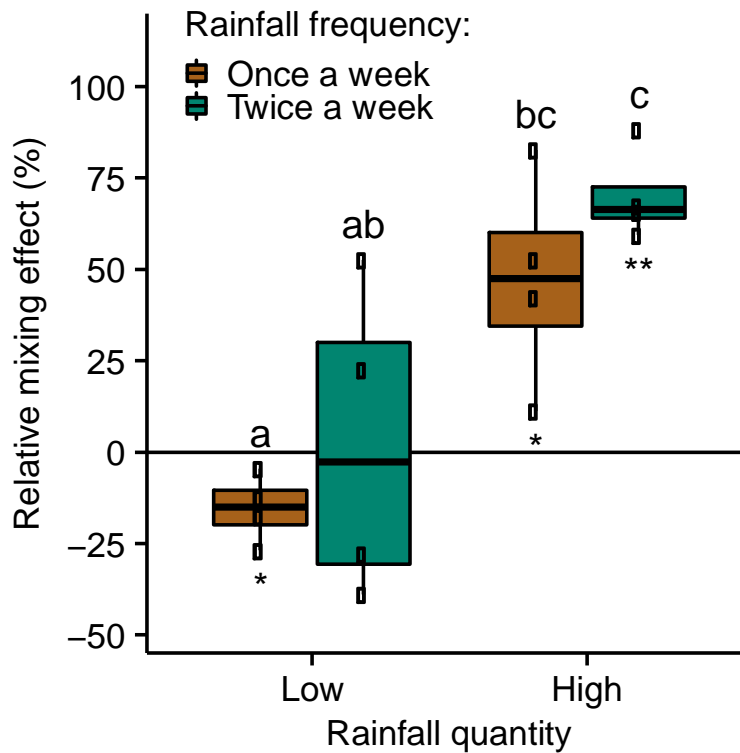
401 Figure 2: Percentage of litter carbon (C) loss driven by isopods, millipedes, as well as isopods  
402 and millipedes, after a six-week incubation under two different rainfall quantities (18 and 36  
403 mm/month) and two different rainfall frequencies (one or two pulses per week). Uppercase  
404 letters indicate significant differences among detritivore treatments, while lowercase letters  
405 indicate, for each detritivore treatment, significant differences among rainfall treatments  
406 (Tukey HSD tests).



407

408

409 Figure 3: Relative difference between the observed detritivore-driven litter C loss for the  
410 millipede-isopod mixture and the expected value based on monospecific treatments after a  
411 six-week incubation under two different rainfall quantities (18 and 36 mm/month) and two  
412 different rainfall frequencies (one or two pulses per week). Letters indicate differences  
413 among rainfall treatments (Tukey HSD tests). Asterisks indicate a relative mixing effect  
414 significantly different from 0 (\*:  $P < 0.05$ ; \*\*:  $P < 0.01$ ).



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