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► To cite this version:

Guille Peguero, Jordi Sardans, Dolores Asensio, Marcos Fernández-Martínez, Albert Gargallo-Garriga, et al.. Nutrient scarcity strengthens soil fauna control over leaf litter decomposition in tropical rainforests. *Proceedings of the Royal Society B: Biological Sciences*, 2019, 286 (1910), pp.20191300. 10.1098/rspb.2019.1300 . hal-02622626

HAL Id: hal-02622626

<https://hal.inrae.fr/hal-02622626v1>

Submitted on 16 Aug 2024

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This item is the archived peer-reviewed author-version of:

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Reference:

Peguero Guille, Sardans Jordi, Asensio Dolores, Fernandez-Martinez Marcos, Gargallo-Garriga Albert, Grau Oriol, Llusà Joan, Margalef Olga, Márquez Laura, Ogaya Romà,- Nutrient scarcity strengthens soil fauna control over leaf litter decomposition in tropical rainforests
Proceedings of the Royal Society B: Biological Sciences - ISSN 0962-8452 - 286:1910(2019), p. 1-9
Full text (Publisher's DOI): <https://doi.org/10.1098/RSPB.2019.1300>

1 Nutrient scarcity strengthens soil fauna control over leaf litter
2 decomposition in tropical rainforests
3

4 *Running head:* Fauna control over litter decomposition
5

6 Guille Peguero^{1,2,3*}, Jordi Sardans^{2,3}, Dolores Asensio^{2,3}, Marcos Fernández-Martínez^{1,2,3},
7 Albert Gargallo-Garriga^{2,3}, Oriol Grau^{2,3}, Joan Llusà^{2,3}, Olga Margalef^{2,3}, Laura Márquez^{2,3},
8 Romà Ogaya^{2,3}, Ifigenia Urbina^{2,3}, Elodie A. Courtois^{1,4}, Clément Stahl⁵, Leandro Van
9 Langenhove¹, Lore T. Verryckt¹, Andreas Richter⁶, Ivan A. Janssens¹, Josep Peñuelas^{2,3}
10

11 ¹ Centre of Excellence PLECO (Plants and Ecosystems), Department of Biology, University of
12 Antwerp, 2610 Wilrijk, Belgium.

13 ² CSIC, Global Ecology Unit CREAM-CSIC-UAB, 08913 Bellaterra, Spain.

14 ³ CREAM, 08913 Cerdanyola del Vallès, Spain.

15 ⁴ Laboratoire Ecologie, Evolution, Interactions des Systèmes Amazoniens (LEEISA),
16 Université de Guyane, CNRS, IFREMER, 97300 Cayenne, French Guiana.

17 ⁵ INRA, UMR EcoFoG, CNRS, Cirad, AgroParisTech, Université des Antilles, Université de
18 Guyane, 97310 Kourou, France

19 ⁶ Department of Microbiology and Ecosystem Science, University of Vienna, 1090 Vienna,
20 Austria.

21
22 * Corresponding author: guille.peguero@gmail.com

23 **Abstract**

24 Soil fauna is a key control of the decomposition rate of leaf litter, yet its interactions with litter
25 quality and the soil environment remain elusive. We conducted a litter decomposition
26 experiment across different topographic levels within the landscape replicated in two rainforest
27 sites providing natural gradients in soil fertility to test the hypothesis that low nutrient
28 availability in litter and soil increases the strength of fauna control over litter decomposition.
29 We crossed these data with a large dataset of 44 variables characterizing the biotic and abiotic
30 microenvironment of each sampling point and found that microbe-driven Carbon (C) and
31 Nitrogen (N) loss from leaf litter were 10.1 and 17.9 % lower in the nutrient-poorest site but
32 this among-site difference was equalized when meso- and macrofauna had access to the
33 litterbags. Further, on average soil fauna enhanced by 22.6 % the rate of litter decomposition,
34 and this contribution consistently increased as nutrient availability in the microenvironment
35 declined. Our results indicate that nutrient scarcity increases the importance of soil fauna on C
36 and N cycling in tropical rainforests and that is able to equalize differences in microbial
37 decomposition potential thus buffering to a significant extent nutrient shortages at an
38 ecosystem level.

39

40 **Keywords**

41 Biogeochemistry, extracellular enzyme activity, litter decomposition, nutrients, soil fauna.

42 **Introduction**

43 More than 90% of the net primary production of global terrestrial ecosystems is channeled into
44 the detrital food web [1], and soils store the majority of the Earth's organic carbon (C)
45 (Crowther et al., 2016). Identifying the drivers of organic-matter decomposition is therefore
46 crucial to understanding and predicting global ecosystem functioning. Abiotic factors like
47 climate and litter quality, have traditionally been recognized as the dominant controls on
48 decomposition at large spatial scales, while decomposer organisms would operate as
49 additional, but secondary, local agents [3,4]. Recent evidence, however, indicates that the effect
50 size of microbial biomass on decomposition rates can be equivalent to that of soil temperature
51 and litter moisture, suggesting that biotic factors may explain as much or even more variation
52 than climate in multi-site comparisons, thus questioning such a hierarchical model of litter
53 decomposition [5–7]. In addition, soil fauna has recently been reported to consistently increase
54 the rates of litter decomposition across biomes by 37% [8] and losses in their functional
55 diversity are expected to slow global cycling of C and nutrients [9]. Consequently, the role of
56 biota (i.e. microorganisms and soil fauna) should attain a more central position in the emerging
57 biogeochemical models, to emphasize their ability to modulate the effects of the environment
58 and a changing climate on organic-matter decomposition [10–14].

59 Leaf litter fall is a dominant pathway for returning nutrients to the soil [15], and soil
60 fauna plays a fundamental and often undervalued role in the litter decomposition process
61 [9,16]. Assemblages of soil animals stimulate litter breakdown by a variety of interconnected
62 mechanisms that alter the composition and performance of the microbial community, which
63 ultimately transform complex plant-derived compounds into CO₂, mineral and organic
64 nutrients and humus [12,13,16]. Despite their identification as key agents of organic-matter
65 decomposition, the interaction between soil fauna with litter traits, and particularly, with the
66 soil microenvironment have remained elusive so far. A descriptive example is the hypothetical
67 link between litter quality and the contribution of soil fauna to decomposition. Through
68 selective feeding soil invertebrates could preferentially increase the decomposition of litter
69 with a low C to N or C to P ratio (C:N and C:P, respectively), i.e. litter with a high nutritional
70 value [17,18]. Other studies, however, have suggested that the primary effect of soil fauna is
71 precisely to promote the decomposition of low-quality litter [19–23]. Likewise, a landmark
72 study documented that increasing diversity of leaf-litter within a litterbag substantially
73 enhanced the rate of disappearance of the more recalcitrant litter types, but only in presence of

74 soil fauna, suggesting that animals could bolster the effects of litter diversity through a top-
75 down mechanism [24]. Notwithstanding, evidence supporting this hypothesis is still sparse and
76 comes from single-site or laboratory-based microcosmic experiments [25,26], which may
77 underestimate the large small-scale variability of decomposition rates in natural conditions
78 [5,27]. Moreover, the nutritional status of the soil and the litter microenvironment may affect
79 microbial communities and interact with soil fauna influencing its contribution to
80 decomposition [28]. For instance, the decomposition of low-quality litter may be bottom-up
81 controlled especially in nutrient-poor environments, thus being more dependent on the
82 fragmentation and the microbial stimulation driven by soil fauna [18,28–31]. Still, multi-site
83 litterbag decomposition studies often fail to incorporate high enough within-site replicates
84 along with data of environmental features like nutrient availability measured at the same spatial
85 and temporal grain, therefore masking underlying local variability and hampering our ability
86 to identify alternate regulatory factors [7].

87 We hypothesize that low nutrient concentrations in the litter substrate and in the
88 surrounding litter and soil microenvironment should increase the importance of soil fauna
89 promoting decomposition. To test this avoiding the limitations of lab microcosms or single-
90 site studies, we conducted a litterbag experiment at two rainforest sites in the Guiana shield
91 (Table 1), and additionally including a high within-site replication to take into account the
92 natural biogeochemical variability typically associated with the topography in these nutrient-
93 poor ecosystems [32,33]. To determine the contribution to the loss of litter mass by mesofauna
94 alone and by meso- plus macrofauna (i.e., invertebrates with body widths smaller and larger
95 than 2 mm, respectively [3]), we used litterbags with three mesh sizes (hereafter referred to as
96 microbes ($< 70 \mu\text{m}$), mesofauna ($< 2 \text{ mm}$) and macrofauna ($< 7 \text{ mm}$) for clarity) and filled
97 them with leaf litter substrates from two native tree species with contrasting C:P ratios and
98 their combination: 1561 ± 337 for *Goupia glabra* Auble. and 2773 ± 307 for *Platonia insignis*
99 Mart. [34] (hereafter referred as *Goupia* and *Platonia*). We focused on P because recent
100 findings have indicated that this element is the predominant limiting nutrient for microbial
101 decomposers in tropical forests [35,36]. Additionally, we also assessed the dependency of the
102 effect of soil fauna on decomposition on a wide range of biotic and abiotic environmental
103 factors, by compiling a unique data set of 44 variables characterizing the below- and
104 aboveground compartments (see Table S1). These variables included soil and litter elemental
105 compositions, activities of extracellular enzymes associated with CNP stoichiometry as
106 indirect measures of the nutritional status of microbial communities [36,37], community-level

107 metrics of functional foliar traits in tree canopies, and abundance and richness of the main
108 orders of litter-dwelling arthropods. Importantly, all these potential regulatory factors were
109 quantified -where appropriate- at the same spatial scale as our individual experimental
110 observation unit (i.e. each block of litterbags). Therefore, by explicitly including this high
111 heterogeneity at a landscape and at a within-plot scale as a set of continuous covariates, we
112 were able to test our hypothesis across the natural environmental gradient included in our study
113 sites, which ranged from low availability to extreme nutrient scarcity.

114 **Materials and Methods**

115 **Study sites and sampling design**

116 This study was conducted in two primary tropical forests in French Guiana near the research
117 stations of Nouragues (04°04'53"N, 52°41'13"W) and Paracou (05°16'38"N, 52°55'38"W).
118 Both sites have a mean annual temperature of 25.2 and 25.8 °C and a tropical climate, with a
119 wet season typically from December to June and a dry season from August to November.
120 Rainfall at the annual scale is similar (2849 vs 3280 mm y⁻¹) although Paracou has a more
121 pronounced dry season due to a higher evapotranspirational demand (mean precipitation and
122 temperature during the driest quarter are 22.3 mm mo⁻¹ and 26.3 °C at Paracou vs 29.9 mm mo⁻¹
123 and 25.7 °C at Nouragues, respectively; Fig. SM1 in Supporting Information). The bedrock
124 at Paracou and Nouragues is Precambrian schist and Caribbean granite, respectively. Soil
125 texture and biogeochemistry in tropical forests can fluctuate with topography due to variations
126 in drainage capacity and erosion, which are usually associated with topographic position. Soils
127 between hills are nutrient-poor sandy Podzols, with clay minerals (kaolinite) and oxides
128 contents increasing toward the tops where Acrisols dominate (Margalef et al. *unpublished*
129 results). We established 12 plots of 0.25 ha at each site stratified by three topographic positions
130 to account for this heterogeneity: at the top, at the middle and at the bottom between slopes
131 (henceforth referred to as top, slope and bottom plots). We delimited a central 20-m quadrat in
132 each plot where we marked five evenly spaced sampling points around which we focused all
133 our measurements (Fig. SM2). This design thus contained a total of 120 sampling points (2
134 sites × 3 topographic positions × 4 replicate plots per topography × 5 sampling points in each
135 plot).

136 **Litterbag experiment**

137 We assessed the contribution of invertebrate meso- and macrofauna (body widths smaller and
138 larger than 2 mm, respectively) to the rates of litter-mass loss using 10-cm square polyamide
139 litterbags differing in mesh size: 70 μm (PA-21-71 SEFAR NYTAL, Heiden, Switzerland)
140 excluding both faunal groups but allowing microbes (i.e. fungi and prokaryotes) to decompose
141 the litter substrates, and 2 mm (06-2000/53 SEFAR NYTEX, Heiden, Switzerland) and 7 mm
142 (PE-01903-013 FIBERCORD, Alicante, Spain) allowing the entry of mesofauna and meso-
143 plus macrofauna, respectively. The bottom layers of the litterbags with the largest opening size
144 was made of 0.5-mm mesh [26] (06-500/38 SEFAR NYTEX, Heiden, Switzerland) to prevent
145 the loss of litter fragments. Each litterbag was filled with 2 g of dried leaf litter in three
146 combinations: 1) only *Goupia*, 2) only *Platonia* and 3) equal proportions by weight of both
147 species. These native tree species were chosen due to their contrasting C:P and N:P ratios (1561
148 \pm 337 and 36.9 \pm 3.1 for *Goupia* vs 2773 \pm 307 and 80.7 \pm 1.3 for *Platonia*; mean \pm standard
149 error, data from [34]).

150 Freshly fallen leaf litter was collected with litter traps placed under trees in monocultured
151 plantations established by the Center for the International Cooperation in Agronomic Research
152 for the Development (CIRAD) in 1983-84 near the Paracou research station. The traps were
153 harvested monthly, and the plant material was dried at 40 $^{\circ}\text{C}$ in a heater to a constant weight.
154 The leaf litter was placed inside the litterbags and visually inspected. Any material in an
155 advanced stage of degradation was discarded. All individually tagged litterbags were closed
156 and fixed to the soil surface with stainless-steel staples and wire. Each block of nine litterbags
157 (3 mesh sizes \times 3 litter combinations) was tied with polyamide thread at each sampling point
158 in November 2015 (end of the dry season) and retrieved in June 2016 (end of the wet season)
159 in the same order as they were initially placed. All harvested litterbags were dried at 40 $^{\circ}\text{C}$ in
160 a heater to constant weight, root and soil residues were gently removed, litter fragments were
161 identified to species for the *Goupia-Platonia* mixture and were then weighed. A subsample
162 representative of all site, topographic, mesh-size and litter-composition combinations, along
163 with five random samples of each litter type, were milled and analyzed to obtain initial and
164 final C and N contents. Losses of these two elements from the litter were calculated as $100 \times$
165 $[(M_i \times \text{CN}_i) - (M_f \times \text{CN}_f)] / (M_i \times \text{CN}_i)$, where M_i and M_f are the initial and final litter dry masses,
166 respectively, and CN_i and CN_f are the initial and final C or N concentrations (% of litter dry
167 mass), respectively [9]. Using C loss (%) in addition to total litter-mass loss allowed us to
168 assess the potential effects of any possible inorganic contamination of the litter retrieved from
169 the field [9].

170 **Environmental biotic and abiotic data**

171 We compiled data for 44 variables describing the below- and aboveground biophysical and
172 biological components surrounding each sampling point (i.e. block of litterbags) to identify the
173 potential microenvironmental and biotic drivers behind the effect of fauna on decomposition.
174 Briefly, we determined the concentrations of nutrients (C, N, P, K, Ca, Mg and Na) in the litter
175 (organic horizon) and soil (0-15 cm depth) pools at each sampling point by means of coupled
176 plasma/optical emission spectrometry. Additionally, the concentration of available P in the soil
177 was determined by both the Olsen and Bray methods. We also determined the activities of the
178 extracellular enzymes β -glucosidase, leucine and glycine aminopeptidases and acid and
179 alkaline phosphatases (henceforth referred to as β gluc, leu, gly, acidP and alkP, respectively)
180 in the litter and soil at each sampling point by means of colorimetric assays. We sampled the
181 communities of arthropods in the litter surrounding each sampling point by means of
182 Winkler/Moczarsky traps and then classifying each collected specimen into 33 Order or sub-
183 Order taxonomic categories covering all major lineages within Arthropoda. And finally, all
184 trees (diameter at breast height ≥ 10 cm) within the 0.25-ha plots were mapped, tagged and
185 identified to species or genus with herbarium vouchers for determining the tree species
186 richness, phylogenetic diversity and three complementary indexes of functional trait diversity
187 for each plot (please see Table S1 and supplementary methods for detailed procedural
188 descriptions).

189 **Data analyses**

190 All statistical analyses were carried out with R v3.4.3 [38]. The variation of litter mass lost
191 from the litterbags after the incubation was assessed using a linear mixed model as
192 implemented in the *lme4* package [39], including site, topography, mesh size, litter composition
193 and the interaction between site and mesh size as fixed-effects terms. Sampling point was
194 added as a random intercept term nested within plot, topography and site, thus representing the
195 spatial structure of our experimental design. Higher-order interactions were sequentially
196 removed when not significant ($P > 0.05$), additionally assessing the Akaike Information
197 Criterion (AIC) and retrieving the coefficients of determination (r^2). Parameter-specific P -
198 values for the mixed models were calculated by normal, Satterthwaite and Kenward-Rogers
199 approximations to the number of degrees of freedom, and all approaches yielded qualitatively
200 identical results. The same models were used for C and N losses, although the lower number
201 of samples precluded the inclusion of a random-effects structure.

202 We determined the distribution of all environmental biotic and abiotic variables using
203 a Principal Components Analysis (PCA). We confirmed the apparent differences between sites
204 and across topographic levels for the first and second PCA axes using a linear mixed model
205 with the PC1 and PC2 scores as response variables. Then, we analyzed the variation of the
206 most relevant environmental variables, i.e. those with larger loadings on these first two axes of
207 the PCA. The effects of soil fauna on leaf-litter decomposition were measured as the difference
208 in mass loss between the litterbags with and without fauna access [34]. To visualize these fauna
209 effects within the multivariate environmental space we repeated this PCA including the six
210 corresponding fauna-effect variables (two mesh sizes crossed with three litter combinations).

211 The relationship between the contribution of soil fauna to decomposition with the
212 microenvironment was assessed using a linear mixed model with fauna effect as a response
213 variable and replacing site and topographic categorical factors by the scores of each sampling
214 point over the PC1 and PC2 (obtained from the PCA without fauna-effect variables included),
215 as surrogates of variations in nutrient availability associated to the environment. This analytical
216 approach allowed us to synthesize a complex multidimensional scenario of regional and
217 topographically associated variation in the environment into a more tractable and interpretable
218 output [18,40]. Furthermore, by including this environmental heterogeneity as continuous
219 covariates, we were able to assess the effect of soil fauna on decomposition across the natural
220 gradient of nutrient availability encompassed in our study sites. Finally, we additionally
221 explored the potential contribution of the first six PCA axes (which together explained a
222 cumulative proportion of variance of 58%) over the effects of the fauna on decomposition using
223 automated model selection with the *dredge* function from the *MuMIn* package [41]. However,
224 the subset of models with the lowest AIC only included PC1, therefore discarding all other
225 axes.

226 **Results**

227 **Loss of litter mass and nutrients.** After seven months of incubation, between 68 and 70% of
228 the initial leaf-litter mass was lost when meso- and macrofauna had access to the litterbags.
229 However, in litterbags with the smallest mesh size (microbial decomposition only), litter mass
230 loss dropped to 48% on average in Nouragues, and to only 40% in the relatively nutrient-poorer
231 site at Paracou (Fig. 1 and Table 2, site \times size interaction). Models assessing C and N losses
232 yielded qualitatively similar results, although this between-site difference in microbial
233 decomposition potential was even larger for N, being 18% lower at Paracou than at Nouragues

234 (Table 2, site \times size interaction). The soil fauna in Paracou was nevertheless able to compensate
235 this lower baseline of microbial decomposition, so that the loss rates of litter mass and nutrients
236 were equalized between sites when both meso- and macrofauna had access to the litterbags
237 (Fig. 1 and Table 2).

238 Additionally, the decomposition rates of the comparatively P-richer litter of *Goupia* and
239 the P-poorer *Platonia* were unexpectedly similar, although the mass losses for the combination
240 of the two species was larger (+3.4%), indicating that when mixed both species decomposed
241 faster (Table 2, species).

242 **Environmental variation between and within study sites.** A principal component analysis
243 (PCA) combining 44 potential regulatory controls with the effect of soil fauna on litter
244 decomposition, measured as the difference in the loss of litter mass between the litterbags with
245 and without faunal access [34], showed that the first two axes comprised 29.7% of the total
246 variation between and within sites, underlining the high environmental heterogeneity at large
247 and small spatial scales (Fig. 2, see Table S1 for descriptions of the variables). Despite this
248 variability, the clear separation of the sampling points at both sites indicated that PC1 captured
249 regional-scale disparities mostly associated to nutrient-related variables in the litter layer.
250 Conversely, PC2 mainly identified within-site soil-related variation linked with topographic
251 position of sampling plots (Fig. S1). All fauna effects appeared to consistently correlate with
252 lower scores on the PC1 (Fig. 2, red vectors). Repeating this PCA excluding the fauna effect
253 variables resulted in very subtle changes but a slight increase in the amount of total variance
254 explained by PC1 and PC2 (32.6%, Fig. S2). Total N concentration in all compartments, foliar
255 C:nutrient ratios in the canopy and litter and phosphatase and aminopeptidase activities in the
256 litter were the most important variables in PC1 (Fig. S3). Overall, the Nouragues site was richer
257 in N in all compartments, from the canopy to the soil (Table 1 and Fig. S4), whereas the higher
258 litter C:nutrient ratios at Paracou suggested that the activity of microbial decomposers could
259 be constrained to some degree.

260 Indeed, we also found that the activities of the extracellular aminopeptidases and
261 phosphatases in the litter were lower at Paracou, indicating either a lower microbial biomass,
262 restricted microbial performance [37], or lower substrate availability [42]. The stoichiometry
263 of extracellular enzymes is a good indicator of the relative nutrient demands of microbial
264 communities [36,37]. The relative allocation between N- and P-acquiring enzymes was similar
265 at both sites, despite the lower activity of all extracellular enzymes at Paracou, suggesting that

266 the microbial communities there were generally nutrient-limited instead of stoichiometrically
267 unbalanced (Fig. S5). In contrast to the organic horizon, enzymatic activity in the topsoil
268 mostly varied across topographic levels, generally increasing toward the top as total nutrient
269 concentrations did in that compartment (Fig. S1).

270 **Environmental dependency of the effect of fauna on decomposition.** We assessed the
271 relationship between the contribution of soil fauna to decomposition and the microenvironment
272 using a linear mixed model with fauna effect as a response variable and replacing site and
273 topographic categorical factors by the scores of each sampling point on PC1 and PC2 (obtained
274 from the PCA without fauna effect variables included), as surrogates of regional (between-
275 sites) and locally (across topographies) associated variations in the microenvironment. This
276 analytical approach synthesized complex multivariate environmental scenarios into more
277 tractable and interpretable outputs [18,40], but most importantly, it allowed to assess the effect
278 of soil fauna on decomposition across the natural gradient of nutrient availability encompassed
279 within our study sites that ranged from low availability to extreme nutrient scarcity. The effect
280 of soil fauna on decomposition was strongly and negatively correlated with the PC1, but not
281 with the PC2 scores, indicating that the main drivers of the variation in the fauna effect on
282 decomposition were the microenvironmental variables associated with differences in nutrient
283 availability in the litter layer such as total N concentration, C:nutrient ratios and enzymatic
284 activities (Fig. 3 and Table 2).

285 The effect of the soil fauna was also larger in the mixed litter treatment (+3.8%) and
286 was marginally larger (+2.9%) in the relatively P-poor litter species (*Platonia*, Fig. 4a and
287 Table 2, species). The relationship between this fauna impact on decomposition and the
288 variation of the microenvironment (PC1 scores), however, had a smoother, less negative slope
289 for the mixed litter treatment, indicating that the combination of different litter substrates may
290 have weakened the context-dependency of fauna effects on decomposition (Table 2, PC1 ×
291 species, and Fig. S6). Finally, as anticipated in the analysis of litter mass loss, the net effect on
292 decomposition was larger (+4.1%) for the complete community of soil fauna (i.e. meso- plus
293 macrofauna) than for the mesofaunal component only, irrespective of the microenvironment
294 and in all litter combinations (Fig. 4b and Table 2).

295 **Discussion**

296 We here demonstrate that the strength of soil fauna control on litter decomposition is linked
297 with its biotic and abiotic environment. The net contribution of soil fauna to litter mass loss
298 increased as the conditions for microbial decomposition were more adverse, specifically when
299 nutrient concentrations, and N in particular, were lower, not only in the litter substrate within
300 each litterbag but also in the surrounding litter pool. This was consistent with the reduction of
301 the activity of N- and P-acquiring extracellular enzymes in the litter layer, which were
302 associated to stronger fauna effects on decomposition, thus providing additional support to the
303 view that when the microbial communities inhabiting the organic horizon are relatively nutrient
304 limited the facilitating role of soil fauna acquires a greater importance. Therefore, we found
305 that soil fauna was able to minimize differences in litter decomposition buffering ecosystem-
306 level nutrient shortages at regional scales. This supports recent findings challenging the long-
307 standing view that biotic controls on decomposition would be subordinate to regional and
308 global-scale features such as climate [6,7], and support propositions of local-scale variables
309 regulating microbial activity as predominant drivers of decomposition [5].

310 Microbes are the ultimate agents responsible for the transformation of dead organic
311 matter, mineralization to CO₂ and inorganic nutrients, and humus formation [12,13,16].
312 Nutrient availability rather than abundance of detritus per se is a main limitation to microbial
313 growth and so of litter decomposition [35,36]. Microbial communities inhabiting environments
314 differing in nutrient availability may face contrasting stoichiometric imbalances that can
315 restrict their ability to decompose organic matter [35,43]. In low-nutrient environments (e.g.
316 with high C:N ratios) microbes can adjust their metabolism to reduce their C-use efficiency
317 while increasing their nutrient-use efficiency (i.e. the ratios of growth over organic C or
318 nutrient uptake) to cope with the physiological challenges of resource imbalance [44,45]. Many
319 direct and indirect animal-mediated processes may enhance nutrient supply, potentially
320 stimulating microbial activity [12,13]. For example, the fragmentation and comminution of
321 litter increases its surface area to mass ratio, making it more readily attacked by microbes
322 (Chapin, Matson, & Mooney, 2002; Joly, Coq, Coulis, Nahmani, & Hättenschwiler, 2018). The
323 translocation and redistribution of freshly fallen litter across soil surfaces and depths together
324 with modifications of aggregation properties and pore structure may likewise accelerate
325 nutrient release [12,13]. Microbial inoculation and the preconditioning of litter during transit
326 through animal guts may also facilitate decomposition [12,13], and importantly, this effect can
327 be directly associated with initial litter quality (Joly, Coulis, Gérard, Fromin, & Hättenschwiler,
328 2015; Joly et al., 2018). In fact, Joly and collaborators found that the lower the initial litter

329 quality the greater the magnitude of microbial stimulation after invertebrate gut passage (Joly
330 et al., 2015), and that the positive effect of soil fauna was mainly related with greater N release
331 from faeces than from litter where this nutrient is more rapidly immobilized (Joly et al., 2018).
332 Direct grazing by soil fauna on living fungal hyphae, bacterial mat and microbial necromass
333 may also alter density-dependent community functions such as substrate, enzyme and nutrient
334 diffusion and exploitative and interfering competitive interactions affecting species
335 coexistence and thus the composition and performance of microbial communities
336 (Buchkowski, Bradford, Grandy, Schmitz, & Wieder, 2017; Crowther, Boddy, & Jones, 2011).

337 The nutrients acquired by soil animals generally exceed their demands, and the surplus
338 is excreted in easily available forms such as urea, ammonia, phosphate and other derivative
339 forms (Chapin et al., 2002). At a macroscopic scale, it is well-known that, through their dung
340 and flesh, megafauna increases nutrient diffusion across the landscape with strong impacts on
341 ecosystem functioning [51]. Likewise, soil fauna could improve the movement of nutrients
342 across the litter-soil interface. Indeed, nutrient transfer between litter types, from the N pool in
343 the soil or from microbial fixation, has been suggested as a widespread mechanism behind the
344 diversity-function effects on decomposition [9,29,52]. We argue that soil fauna may play a role
345 in these phenomena because they could locally enrich low-quality litter substrates by increasing
346 nutrient diffusivity, thereby relaxing the stoichiometric constraints that may hinder their
347 breakdown. If so, a low nutrient concentration in a particular litter substrate and in the
348 associated microenvironment should increase the importance of the facilitation of nutrient
349 mobility by soil fauna.

350 Previous studies have reported that soil fauna can strengthen the diversity-function
351 effects on litter decomposition, increasing the rates of loss of litter mixtures with higher
352 diversity [24,26]. Our results also indicated that soil fauna had a larger effect in the litter
353 mixture treatment. The stoichiometric heterogeneity of complex litter mixtures could better
354 match the nutritional demands of litter-feeding animals, thereby stimulating its activity [25].
355 The variation of their contribution to the decomposition of the richest mixture, however, was
356 less dependent on the microenvironment than for the single-species litterbags. From our point
357 of view, this finding implies that more complementary litter mixtures would be less reliant on
358 a potential animal-mediated mechanism of nutrient transfer, which delivers nutrients from the
359 pool in the microenvironment. Additional support to this hypothesis may come from an
360 experimental fertilization experiment, where synergistic diversity effects on decomposition

361 correlated with the stoichiometric dissimilarity of the litter mixture only in the presence of soil
362 fauna, while this relationship disappeared when the nutrient pool available in the
363 microenvironment was experimentally increased [26]. The same authors concluded that
364 microbial activity was subsidized by nutrient uptake coming from other sources than the litter
365 present in the litterbags. In light of our findings, we also suggest that soil fauna may be a key
366 facilitator of this external flow of resources, which could be increasingly important as nutrient
367 content in the microenvironment decreases or the litter mixtures become poorer or more
368 unbalanced.

369 **Acknowledgements**

370 This research was supported by the European Research Council Synergy grant ERC-2013-SyG
371 610028-IMBALANCE-P, the Spanish Government grant CGL2016-79835-P and the Catalan
372 Government grant SGR 2017-1005. G.P was supported by a postdoctoral fellowship from the
373 Ramon Areces Foundation. We thank the staff of the Nouragues station, managed by USR
374 mixte LEEISA (CNRS; Cayenne), and the Paracou station, managed by UMR Ecofog (CIRAD,
375 INRA; Kourou). Both research stations received support from “Investissement d’Avenir”
376 grants managed by Agence Nationale de la Recherche (CEBA: ANR-10-LABX- 25-01,
377 ANAEE-France: ANR-11-INBS-0001). We thank Vincent Freycon for the identification and
378 characterization of each topographical position and Pascal Petronelli for the botanical
379 determination.

380 **Authors’ contributions**

381 G.P, I.A.J and J.P designed the study. G.P, D.A, A.G-G, O.G, J.L, L.M, O.M, R.O, I.U, E.L.A,
382 C.S, L.V, L.T.V performed field and/or lab work. G.P compiled and analyzed the data with
383 advice of J.S, M.F-M and J.P. G.P wrote the manuscript with substantial inputs of J.S, A.R,
384 I.A.J and J.P, and revisions of all co-authors.

385 **Data accessibility**

386 All data supporting the results presented in this contribution will be archived in an appropriate
387 public repository and the data DOI will be included at the end of the article upon acceptance
388 of the manuscript.

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530
531

TABLE 1 Characteristics of the study sites

	Nouragues	Paracou
Coordinates	04°04'53"N	05°16'38"N
	52°41'13"W	52°55'38"W
Soil type (FAO)	Sandy Podzols and Acrisols	Sandy Podzols and Acrisols
MAT (°C)	25.2	25.8
MAP (mm)	3280	2849
Aboveground biomass (t/ha)	423 ± 44	371 ± 20
Litter pool (g m ⁻²)	1259 ± 40	1265 ± 54
Foliar N (%)	2.05 ± 0.01	1.93 ± 0.01***
Litter N (%)	1.49 ± 0.03	1.32 ± 0.18**
Foliar C:N	25.21 ± 0.09	26.28 ± 0.12***
Litter C:N	33.53 ± 0.80	37.14 ± 0.70**
Litter AlkP activity	73.73 ± 4.75	33.58 ± 2.29***
Arthropod density (id m ⁻²)	477 ± 28	536 ± 32
Tree species richness	38 ± 2	32 ± 1**
Tree functional richness	-0.09 ± 0.12	-0.11 ± 0.08

Values are means ± standard errors (n=120, except n=24 for tree-community data). Elemental ratios are mass-based. AlkP refers to maximum potential activity of alkaline phosphatase in litter (μmol pNP g⁻¹ h⁻¹). Tree species richness refers to mean number of species per plot while functional richness is a unitless standardized effect size of the convex hull volume defined by six foliar traits. Between-site differences are based on linear mixed-effect models, with site and topography as fixed factors and sampling point within each plot as a random effect. *, ** and *** denote P<0.05, 0.01 and 0.001, respectively. See text and supplementary materials for further details.

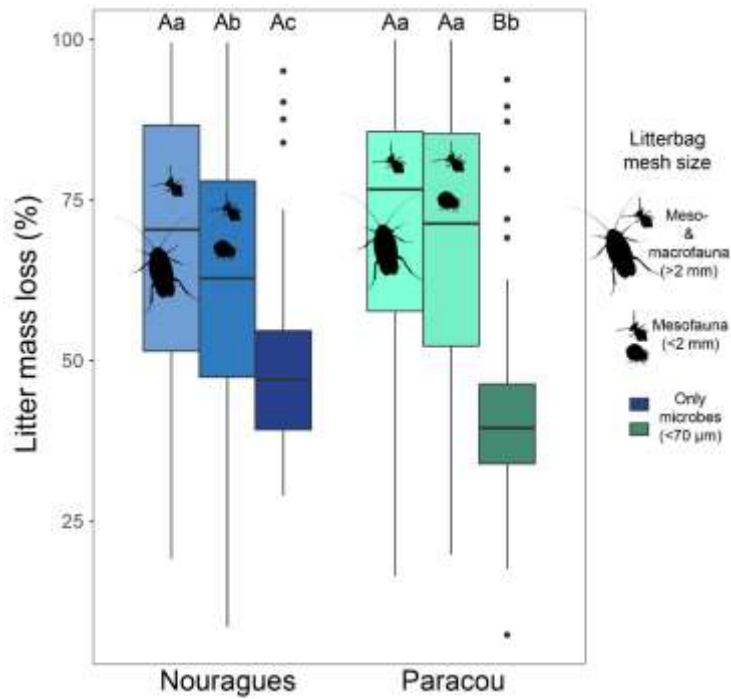
TABLE 2 Coefficients, significance and r^2 for the linear mixed models used to evaluate the controls on losses of litter mass and nutrients and faunal effects on decomposition

Variables		Model			
		Litter-mass loss	C loss	N loss	Fauna effect
Intercept		65.0 ± 2.3	71.8 ± 3.3	57.8 ± 3.9	22.6 ± 1.7
Site	Paracou	2.9 ± 2.4	-1.9 ± 3.5	3.4 ± 4.2	
Topography	Slope	0.6 ± 2.4	-0.5 ± 2.5	3.1 ± 2.9	
	Top	<i>4.1 ± 2.4</i>	<i>4.3 ± 2.4</i>	5.9 ± 2.9	
Size	Mesofauna	-5.3 ± 1.6	-6.1 ± 3.5	-4.4 ± 4.1	-4.1 ± 1.2
	Microbes	-19.8 ± 1.6	-19.9 ± 3.5	-20.6 ± 4.2	
Species	<i>Platonia</i>	0.8 ± 1.1	-2.9 ± 2.4	0.9 ± 3.3	2.9 ± 1.5
	<i>Platonia + Goupia</i>	3.4 ± 1.1	5.2 ± 2.4	9.1 ± 2.9	3.8 ± 1.5
PC1 (<i>nutrient availability</i>)					-3.1 ± 0.5
PC2 (<i>topography</i>)					-0.7 ± 0.5
Site × Size	Paracou-Mesofauna	2.4 ± 2.2	6.1 ± 4.9	3.7 ± 5.8	
	Paracou-Microbes	-10.3 ± 2.2	-10.1 ± 4.9	-17.9 ± 5.9	
PC1 × Species	<i>Platonia</i>				0.8 ± 0.5
	<i>Platonia + Goupia</i>				1.3 ± 0.5
Model r^2_m/r^2_c		29.5/50.2	44.1	45.0	12.6/43.3

Losses of litter mass, carbon (C) and nitrogen (N) are percentages from initial dry mass and C and N contents, respectively. The fauna effect on decomposition is the difference between the loss of litter mass from the litterbags with meso- and macrofauna relative to the losses from the corresponding microbial-only litterbag (mesh sizes of 2 and 7 mm vs 70 µm, respectively; see Methods). Intercept group-level is Nouragues-Bottom-Macrofauna-*Goupia* for the models of litter-mass loss (n=1080) and C and N losses (n=206), and the intercept for the fauna effect model (n=720) is Macrofauna-*Goupia*. The factor species denotes three litter combinations based on two species with contrasting C to phosphorus ratios. PC1 and PC2 are the scores of each sampling point for the first and second PCA axes, which encompass gradients of nutrient availability and topographic microenvironmental variation (see Figs. 3, S1 and S2). Models are linear mixed models, with sampling point as a random intercept nested within plot, topography and site, except for models of C and N loss, for which the lower number of samples precluded the inclusion of a random term. When applicable, marginal r^2 (r^2_m) values are associated to fixed factors while the conditional r^2 (r^2_c) additionally retain the random effects structure. Significant ($P<0.05$) and marginally significant ($P<0.1$) parameter coefficients are highlighted in bold and italics, respectively.

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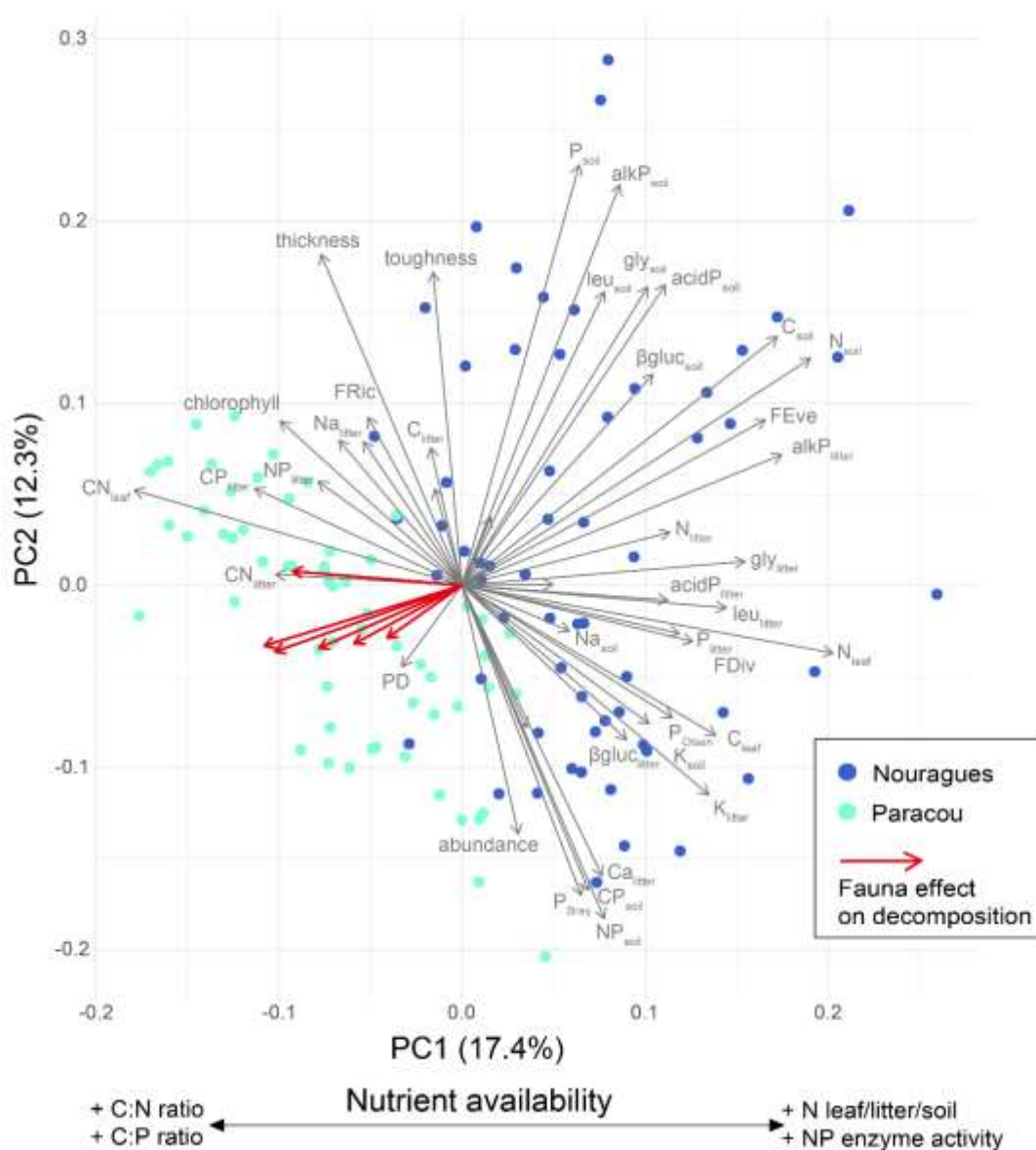
537 FIGURE 1. Variation in the loss of litter (as a percentage of initial dry mass) by site and
538 litterbag mesh size. Different uppercase letters denote significant differences between sites for
539 the same mesh size, and lowercase letters denote significant differences among mesh sizes
540 within the same site and points indicate outliers. Among-group comparisons are Tukey post-
541 hoc tests based on marginal means estimated from a linear mixed model. See Table 2 for model
542 output.



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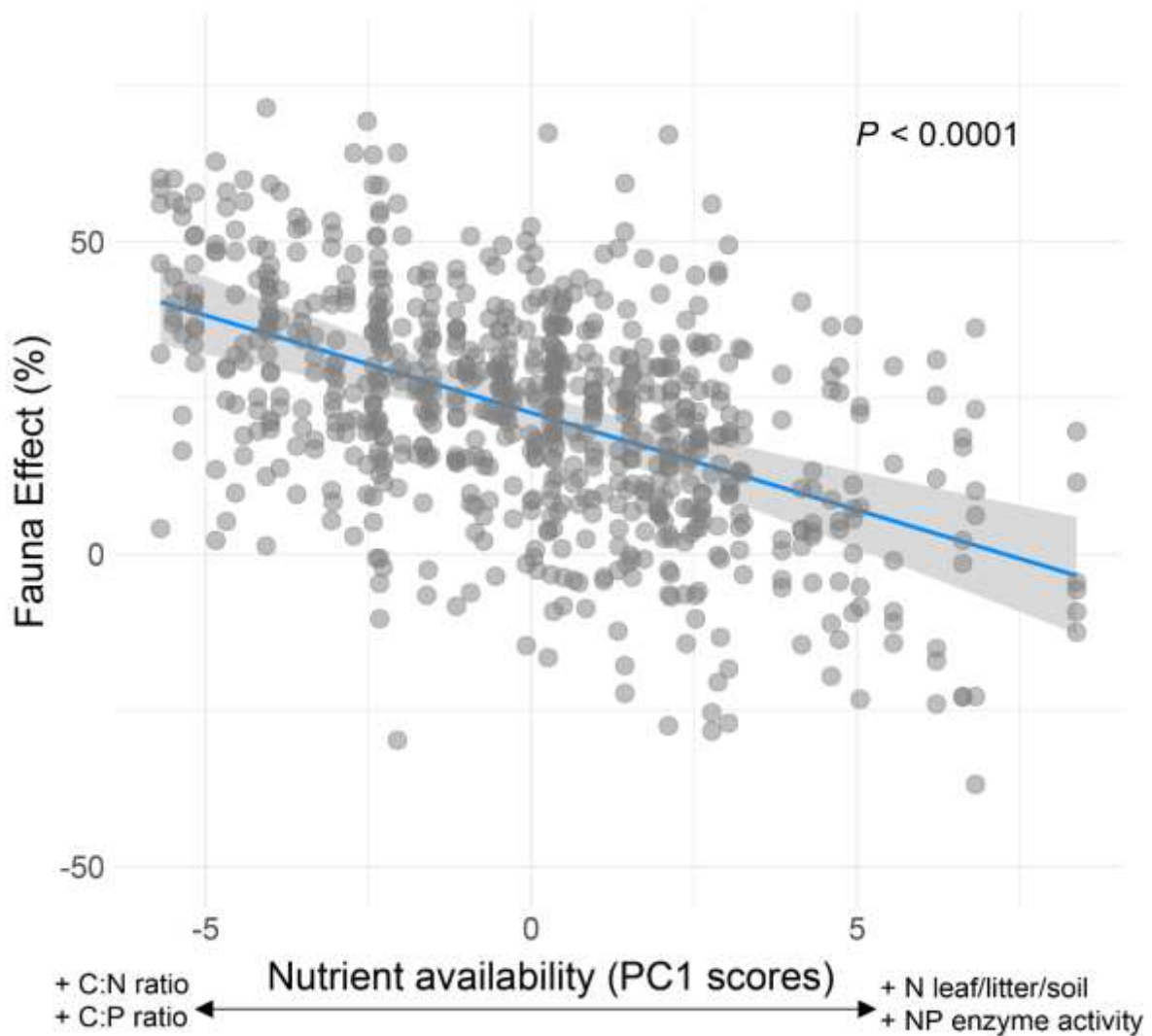
545 FIGURE 2. Principal component analysis (PCA) showing the distribution of all sampling
546 points at Nouragues (blue) and Paracou (green) and the loadings of the 44 biotic and abiotic
547 environmental variables (gray vectors). The contribution of soil fauna (mesofauna and meso-
548 plus macrofauna) on the decomposition of three litter combinations are included in this analysis
549 and highlighted in red for visualization. PC1 axis was mainly defined by nutrient-related
550 variables in the litter layer. Labels for the environmental vectors with the lowest loadings have
551 been removed for clarity. See Methods and Table S1 for variable descriptions and
552 abbreviations.



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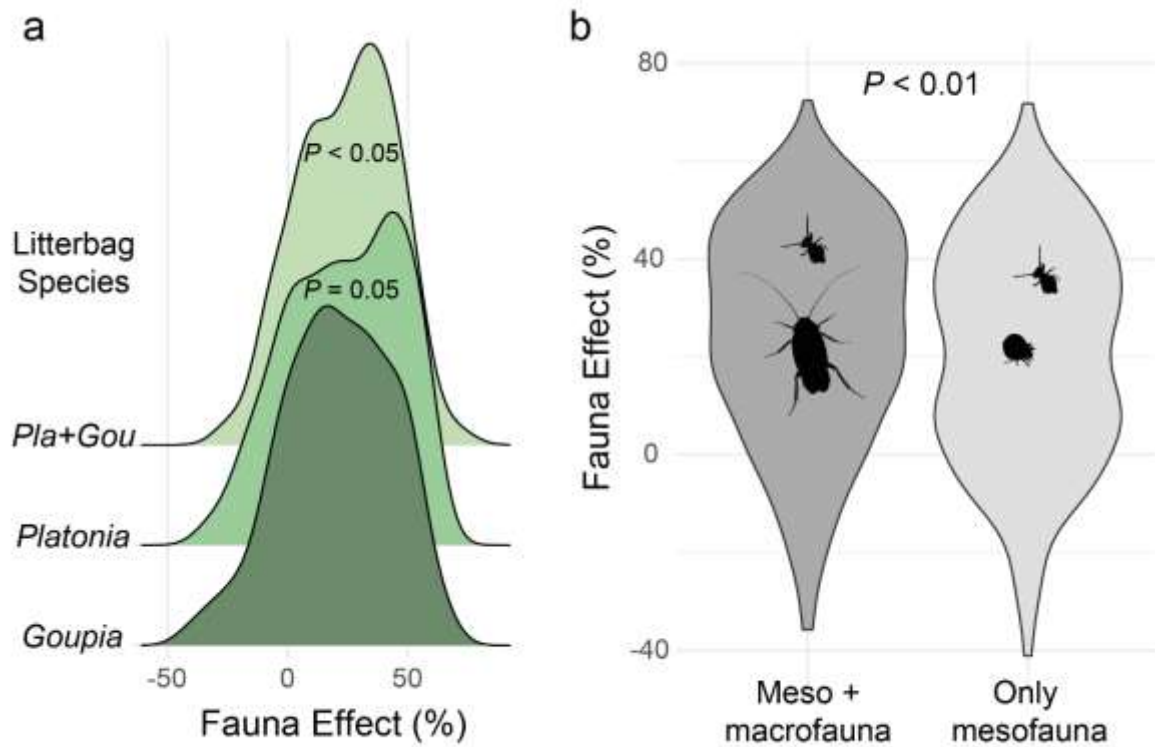
555 FIGURE 3. Relationship between the effect of soil fauna on decomposition (as the difference
556 between the litter mass loss in the litterbags with meso- and macrofauna relative to the
557 corresponding loss in the litterbags with only microbial access) with the PC1 scores of each
558 sampling point as a proxy of the relative nutrient availability in the litter microenvironment.
559 See Table 2 for model outputs.



560

561

562 FIGURE 4 (a) Differential effect of soil fauna on the decomposition of three litter combinations
563 differing in their C:P ratio. (b) Differential effect of soil mesofauna alone (<2 mm body width)
564 *versus* the combined effect of the meso- plus macrofauna. In both panels, the distribution of
565 fauna effects is modeled as a density function with highest or widest points having greater
566 probabilities within each categorical group. See Table 2 for model outputs.



567