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1 **Leaf litter morphological traits, invertebrate body mass and phylogenetic affiliation**  
2 **explain the feeding and feces properties of saprophagous macroarthropods.**

3 Pierre Ganault<sup>1\*</sup>, Sandra Barantal<sup>2,1</sup>, Sylvain Coq<sup>1</sup>, Stephan Hättenschwiler<sup>1</sup>, Shéhérazade  
4 Lucas<sup>1</sup>, Thibaud Decaëns<sup>1°</sup>, Johanne Nahmani<sup>1°</sup>

5 <sup>1</sup> CEFE, Univ. Montpellier, CNRS, EPHE, IRD, Univ. Paul-Valéry Montpellier, Montpellier,  
6 France

7 <sup>2</sup> Montpellier European Ecotron, Univ Montpellier, CNRS, Campus Baillarguet, 34980,  
8 Montferrier-sur-Lez, France

9 <sup>°</sup>*co-senior author*

10 <sup>\*</sup> *corresponding author*

11 **Abstract**

12 Saprophagous macroarthropods are important actors in litter decomposition as they process  
13 large amounts of litter and transform it into fecal pellets that differ in chemical and physical  
14 properties compared to ingested litter. When having a choice among several litter types,  
15 saprophagous macroarthropods exhibit feeding preferences depending on their nutritional  
16 requirements and body size. However, how these preferences affect feces properties is not  
17 well known. We compared the feeding preferences, production of fecal pellets and their  
18 properties for six widespread saprophagous macroarthropods species feeding on a litter mix  
19 of four common tree species from Mediterranean forests. The six animal species showed  
20 different feeding preferences that were not correlated to litter nutritional quality. Instead,  
21 we suggest that the use as microhabitat of the leaves of one litter species with tubular shape  
22 by macroarthropods induced its higher consumption despite having the lowest nutritional  
23 value. Larger species consumed less litter per unit of body mass and had a more diverse diet  
24 composition. Furthermore, feces properties could not be linked to the diet composition.  
25 However, fecal pellets always had higher nutritional and water holding capacity value  
26 compared to the leaf litter. The three woodlice species consistently produced feces with  
27 higher tannin concentration, higher specific area, and lower water holding capacity than that  
28 of the three millipede species. Our study calls for the consideration of other leaf litter  
29 properties than the generally studied physical and chemical ones, as well as quantifying the

30 difference between millipede and woodlice faeces properties that may have functional  
31 implication for nutrient cycling.

## 32 **Keywords**

33 feeding preferences, litter transformation, palatability, microhabitat, consumption rate,  
34 feces production

## 35 **Highlights**

- 36 • Six widespread saprophagous macroarthropod species differed in their feeding  
37 preferences.
- 38 • Litter morphology rather than nutritional quality determined feeding preferences.
- 39 • Larger animals had lower feeding and feces production rates and higher diet  
40 diversity.
- 41 • Feces properties were not predictable from the animal diet composition and differed  
42 among classes

43

## 44 **1. Introduction**

45 During the decomposition of dead organic matter, soil fauna feed on leaf litter and therefore  
46 interact with microbial communities involved in the enzymatic breakdown of organic  
47 molecules [1–4]. Saprophagous macroarthropods (e.g. millipedes, woodlice or some insect  
48 larvae) are important for litter decomposition where they are abundant as they can  
49 consume up to 50% of the total annual litter input [5] and produce large amounts of fecal  
50 pellets composed of poorly digested material due to their typically low assimilation rate [6].  
51 Litter conversion into fecal pellets is associated with a number of physical and chemical  
52 transformations of organic matter that alters considerably its further decomposition  
53 compared to the initial litter material [3,7]. Physical transformations include litter  
54 fragmentation into smaller pieces (litter comminution) of 2 to 40  $\mu\text{m}$  [8] that are assembled  
55 in fecal pellets of different size, shape, and compactness depending on the invertebrate  
56 species [3,4]. Chemical transformations following litter conversion into fecal pellets are the  
57 result of digestion through the activity of the enzymes produced by the animal itself or by its  
58 microbiota and ingested bacteria [9,10]. This may homogenize the initial differences in litter

59 properties and reduce variability in microbial abundance and activity among the feces  
60 compared to the original intact leaf litter [7,11]. Despite these transformations feces  
61 properties are still dependent on the properties of ingested litter, a mechanism described as  
62 the “litter identity effect” [3,12,13]. This means that the net change in feces compared to  
63 litter properties depends strongly on the diet composition of the animal.

64 Saprophagous macroarthropods feed on a wide variety of resources, but in most studies,  
65 they exhibit feeding preferences related to the chemical and physical characteristics of their  
66 food [10]. They prefer leaf litter with high nutrient contents (e.g. low C:N and C:P ratio, high  
67 calcium content), low contents in deterrent compounds like tannins, and low toughness  
68 related to low lignin concentration [10,14,15]. The intensity of microbial colonization of the  
69 leaves also increases leaf palatability [10,16,17]. The morphology of individual leaves, such  
70 as curliness (height of a leaf deposited on a flat surface), 3-dimensionality (volume occupied  
71 by a defined mass of leaves), or tubularity (the capacity of a leaf to roll into a tube), shapes  
72 microhabitats, and influence soil arthropod communities that live in a “house made of food”  
73 [18–22]. The use of a leaf as a microhabitat may promote its decomposition through either  
74 direct consumption or stimulated microbial activity by the deposition of arthropods feces on  
75 the leaf surface [23]. However, leaf litter morphology is not assessed in studies on  
76 saprophagous macroarthropods feeding preferences, despite being relevant in explaining  
77 litter decomposition rate [18,24].

78 Macroarthropod feeding (consumption rate, diet composition and diversity) is related to  
79 body size. Metabolic rate (linked to consumption and feces production rate) is known to  
80 decrease with body mass according to the metabolic scaling theory [25], with smaller  
81 saprophagous individuals consuming more food per unit of body mass, both within and  
82 across species [26–31]. Body size may also be linked to diet diversity, as was demonstrated  
83 for phytophagous insects (Lepidoptera, Orthoptera) where large individuals with larger  
84 mouthparts and higher digestive capacity are able to process a wider range of food [32].  
85 Secondly, phylogenetically distant taxa may exhibit anatomical and/or ecological niche  
86 differences that translate into different feeding specialization [33,34]. In the case of  
87 millipedes and woodlice, their digestive tracts differ in terms of relative length and function  
88 of the fore-, mid-, and hindgut, total length of the gut, type and form of the organs  
89 dedicated to produce and secrete enzyme into the gut, and possibly in terms of microbiota

90 [10,35,36]. Besides the distinction between millipede spheric and woodlice tile-shape feces  
91 [4], these differences and how they influence feeding behavior and feces properties remain  
92 poorly understood so far.

93 Feeding preferences, fecal pellets properties, animal size and phylogenetic affiliation are  
94 therefore important to explain the role of saprophagous macroarthropods in organic matter  
95 decomposition but were never studied together. Here, we experimentally assessed the  
96 feeding behavior of six different macroarthropod species (three woodlice and three  
97 millipedes) feeding on a mix of four litter species with contrasting chemical, physical, and  
98 morphological characteristics, and describe changes in these characteristics upon  
99 transformation into feces. We hypothesized that (H1) litter chemical and physical properties  
100 are a major predictor for macroarthropod consumption with preferential consumption of  
101 leaf litter with high nutrient concentrations and low tannin concentrations, and high water  
102 holding capacity and low thickness. Regarding litter transformation, we expected that (H2)  
103 feces properties are predictable from diet composition (plant identity effect). Additionally  
104 we hypothesized that (H3) larger species will exhibit lower consumption rate but higher diet  
105 diversity. Finally we expected that (H4) woodlice and millipede differences regarding their  
106 digestive track structure and enzymes will result in different feces properties, notably in  
107 millipede feces with lower specific area due to their spheric shape.

## 108 **2. Material and methods**

### 109 *2.1. Leaf litter and animal collection*

110 We selected six saprophagous macroarthropod species that often co-occur and are  
111 widespread in Western Europe, including the woodlice (Crustacea: Isopoda: Oniscidea)  
112 *Armadillidium vulgare* Latreille 1804 (Armadillidae), *Armadillo officinalis* Duaméril 1816  
113 (Armadillidae), *Porcellio laevis* Latreille 1804 (Porcellionidae), and the millipedes (Myriapoda:  
114 Diplopoda) *Glomeris marginata* Villiers 1978 (Glomeridae), *Cylindroiulus caerulocinctus*  
115 Wood 1864 (Julidae), and *Ommatoiulus sabulosus* L. 1758 (Julidae). Individuals were  
116 collected by litter hand sorting in different Mediterranean forests surrounding the city of  
117 Montpellier in Southern France (Table S1). Animals were kept in large plastic boxes with leaf  
118 litter and placed in climatic chambers (natural light fluctuations, constant temperature at  
119 12°C). Leaf litter from four common Mediterranean tree species were selected: *Acer*

120 *monspessulanum* L. 1753 (Sapindaceae), *Arbutus unedo* L. 1753 (Ericaceae), *Quercus ilex* L.  
121 1753 (Fagaceae), and *Quercus pubescens* Willd. 1796 (Fagaceae). These species are  
122 widespread in the French Mediterranean basin, often found in mixed forests, and strongly  
123 differ in their leaf chemical, physical, and morphological traits, leaf lifespan, and litterfall  
124 phenology. Leaf litter was collected in different forests located nearby Montpellier (Table S1)  
125 with suspended litter traps for *A. monspessulanum* and both *Quercus* species, and from the  
126 ground for *A. unedo*, since for this species, field work was done a little bit after the peak of  
127 leaf litter fall. For this last species, the freshly fallen leaves were however clearly  
128 distinguishable on the forest floor and we selectively collected only these recently fallen  
129 leaves. This and the dry weather between leaf litter fall and litter collection makes it  
130 reasonable to assume that decomposition did not yet start. Litter material was dried at 30 °C  
131 for 48 hours in a drying oven.

## 132 2.2. Leaf litter properties

### 133 2.2.1. Chemical properties

134 Five subsamples per litter species were ground to a uniform particle size of 1 mm (Cyclotec  
135 Sample Mill, Tecator, Höganäs, Sweden). Total carbon (C) and nitrogen (N) concentrations  
136 were measured with a flash CHN Elemental Analyzer (Flash EA1112 Series, ThermoFinnigan,  
137 Milan, Italy). Phosphorus (P) concentration was measured colorimetrically after a  
138 mineralization step (Fanin et al, 2011) with an autoanalyzer (SmartChem 200, Alliance  
139 Instruments, Roma, Italy). Tannin concentrations were measured with the protein-  
140 precipitable phenolics microplate assay, a microplate protocol adapted from Hagerman and  
141 Butler [37], following [38]. Calcium (Ca) concentration was measured using an atom  
142 absorption spectrometer (AAS, ICE 3000 series, ThermoScientific, China).

### 143 2.2.2. Physical properties

144 To measure litter water holding capacity (WHC), six individual leaves per species were re-  
145 watered by dumping them in deionized water during one minute before removing adhering  
146 water drops. We then were weighing leaves before and after drying (48 hours at 105 °C).  
147 Immediately after WHC measurement (before drying), leaf thickness was measured on 8  
148 points per leaf avoiding leaf veins with a caliper to the nearest micrometer (Digimatic  
149 micrometer, Mitutoyo 0-25 mm). Specific Leaf Area (SLA) was measured on 20 leaves per

150 species as the ratio between leaf total surface area ( $A_{total}$ ) after re-moistening and flattening  
151 them in a scanner and their dry mass (after 48 hours at 105 °C).

### 152 *2.2.3. Morphological properties*

153 Litter curliness was measured on 20 leaves per litter species by measuring the height of a  
154 leaf when it is deposited on a flat surface [21]. On the same leaves, we developed a measure  
155 of litter tubularity by calculating the ratio of dry leaf projected surface area ( $A_{folded}$ ) over its  
156 total surface area ( $A_{total}$ ) after re-moistening the leaves and flattening it in a scanner.  
157 Tubularity was then calculated with the formula:

$$158 \text{ Tubularity} = 1 - \frac{A_{folded}}{A_{total}} \quad \text{eq. 1}$$

159 Tubularity is comprised between 0 and 1, with increasing values for highly folded leaves.  
160 Litter 3-dimensionality [22] was estimated by measuring the volume occupied in an  
161 Erlenmeyer flask with three different batches of leaves of known dry mass for each species.  
162 The size of glass flasks varied depending on the leaf size for accurate measurements and we  
163 used mean species SLA value to convert the mass of litter per unit of volume into surface of  
164 litter per unit of volume [22]. All litter characteristics of each litter species are summarized in  
165 Table 1.

### 166 *2.3. Microcosms and experimental conditions*

167 One day before the start of the experiment, we moistened one gram ( $1.04 \pm 0.03$  g) of each  
168 litter type again by dumping it in deionized water during one minute before removing  
169 adhering water drops. Fifty individuals of each saprophagous macroarthropod species were  
170 selected, taking care not to include gravid females and to have a representative sample of  
171 species body size range. The individuals were kept in plastic boxes with a moistened tissue  
172 for 24 hours to empty their guts. Litter of the four species were evenly mixed and placed  
173 with 10 randomly chosen animals per species in 115 x 85 x 43 mm transparent plastic boxes  
174 with a lid, with five replicate boxes per animal species. An additional 15 boxes without fauna  
175 were set up as controls. We used five climatic chambers (LMS, Sevenoaks, England) as the  
176 unit of replication, with one box of each animal species treatment and three boxes without  
177 animals in each climate chamber (i.e. nine boxes in each climate chamber). Every three days,  
178 the positions of the boxes within each climatic chamber were randomized and 0.8 mL of  
179 deionized water was added to all boxes to keep litter moisture visually constant without

180 resulting in water accumulation in the bottom of the boxes. The experiment lasted 15 days  
181 with a day/night duration of 12/12 h and a temperature of 17/12 °C.

## 182 2.4. Saprophagous macroarthropod characteristics

### 183 2.4.1. Physiological traits and feeding properties

184 At the end of the experiment, fecal pellets and remaining litter of each species were sorted  
185 and placed in the oven at 30 °C for 48 h and then weighed to the nearest 0.01 mg. Animals  
186 were sorted out, their gut emptied by keeping them 24 hours in a plastic box lined with a  
187 moistened tissue, and weighed before being released. The final animal fresh mass was used  
188 for later calculations. To quantify animal consumption of each litter species we used the  
189 formula [39]:

$$190 \quad C = \frac{M_0 - M_0 D - M_f}{\sqrt{1-D}} \text{ with } D = \frac{M'_0 - M'_f}{M'_0} \quad \text{eq.2}$$

191 with  $M_0$  the initial litter dry mass,  $M_f$  the final litter dry mass,  $D$  the contribution of  
192 microbial-driven decomposition to each litter species mass loss, i.e. the mean proportion of  
193 litter mass loss in the absence of saprophagous macroarthropods for each species,  $M'_0$  and  
194  $M'_f$  the initial and final litter dry mass in control boxes, respectively. The calculated  
195 consumption  $C$  was then referred to the duration of the experiment (15 days) and to the  
196 number of individuals (10) to obtain individual consumption rate ( $C_i$ , g ind<sup>-1</sup> day<sup>-1</sup>) and to the  
197 final fresh mass of fauna to obtain mass-specific consumption rate ( $C_m$ , g g<sub>fresh weight</sub><sup>-1</sup> day<sup>-1</sup>)  
198 [5]. Consumption values were calculated for each litter species separately and summed up to  
199 obtain total litter consumption by saprophagous macroarthropods. Individual ( $F_i$ ) and mass-  
200 specific ( $F_m$ ) fecal pellet production rates were calculated by dividing total feces mass by the  
201 experiment duration and the number of macroarthropod individuals or their total fresh  
202 weight, respectively. Assimilation rates ( $A$ ) were estimated by calculating the difference  
203 between mass-specific consumption and feces production rate. To quantify animal diet  
204 diversity, we calculated the Shannon diversity [40] of the saprophagous macroarthropod  
205 mass-specific feeding rates of each litter species, with the following formula:

$$206 \quad H_i = - \sum_{j=1}^S C_{m_{i,j}} \log C_{m_{i,j}} \quad \text{eq. 3}$$

207 with  $H_j$  the diet diversity of animal species  $i$ ,  $Cm_{i,j}$  the mass-specific consumption rate of litter  
208 species  $j$  by animal species  $i$ . This index informs on the diversity of the litter species  
209 constituting the animals' diet.

#### 210 2.4.2. Diet and feces characteristics

211 To estimate the quality of the available litter and diet (ingested litter), we calculated the  
212 community weighted mean [41] of litter trait using the following formula:

$$213 \text{CWM}(X)_m = \sum_{i=1}^4 p_i * \text{trait}_i \quad \text{eq. 4}$$

214 Where  $p_i$  is the relative proportion of litter available in the mixture, or saprophagous  
215 macroarthropod mass-specific consumption rate of litter species ( $\text{g g}_{\text{fresh weight}}^{-1} \text{day}^{-1}$ ) and  
216  $\text{trait}_i$  is the mean value of trait  $X$  for litter species  $i$ . Feces C, N, P, and tannin contents were  
217 measured following the same protocol as for leaf litter. Feces WHC capacity was measured  
218 by placing c. 2 mg of feces in an Eppendorf tube with 2 ml of deionised water for 1 hr,  
219 weighing it wet after gently removing excess water and reweighing after drying at 60°C for  
220 48 hr [7]. Feces specific area ( $\text{mm}^2 \text{mg}^{-1}$ ) can be linked to C and N cycling, water holding  
221 capacity, and is influenced by litter species identity [7]. It was measured by calculating the  
222 projected surface area of 10 fecal pellets from photographs using a stereo-microscope and  
223 reporting it to their total dry mass.

#### 224 2.5. Statistical analysis

225 Differences in feeding properties (consumption, feces production, assimilation, diet  
226 diversity) and feces characteristics between macroarthropod species and orders, and  
227 differences between litter species physico-chemical and morphological properties were  
228 tested using one-way ANOVA (using *lm* function from *stats* package [42]) followed by post-  
229 hoc Tukey test (*HSD test* function, package *agricolae* [43]) on the R software v.4.0.5 [42].  
230 Normality and homoscedasticity of variance were assessed visually and with Shapiro and  
231 Breusch-Pagan test (*bptest* function, *lmtest* package [44]), and data were log-transformed if  
232 necessary. Differences in diet composition among species and orders were assessed  
233 separately with two permutational analysis of variance (PERMANOVA, [45]) with the  
234 *metaMDS* function (*vegan* package [46]) on the Bray-Curtis dissimilarity matrix of animal  
235 mass-specific consumption rate of the four litter species, after homogeneity of variance was  
236 checked with the *betadisper* function [46]. Results were visualized with NMDS ordination.

237 The relationships between feeding properties and body mass were tested with linear-mixed  
238 models with body mass as fixed effect and species identity as random factor since nesting  
239 species within order led to models with higher AIC [47,48]. Differences between available  
240 litter and diet quality, and available litter and feces quality were separately tested by one-  
241 way ANOVA. The relationships between diet and feces properties were tested by linear  
242 regressions with the properties that were measurable on both material i.e. C:N, C:P, tannins  
243 content and WHC. Further, we tested the effect of saprophagous macroarthropod mass-  
244 specific consumption and feces production rate, assimilation rate, and diet diversity on feces  
245 properties (C:N, C:P, tannins content and WHC). The best models were selected with the  
246 *dredge* function (*MuMIn* package [49]) by keeping the best models within a  $\Delta$ AIC of 2, or  
247 rejecting all models if the null model was included [47]. To assess which litter properties  
248 influenced animal feeding preferences, we constructed individual regression between each  
249 litter species relative consumption and the different litter properties [50]. This approach was  
250 used because the limited number of litter species and the high collinearity between litter  
251 properties (Fig. S1A) made impossible to include all litter properties as independent  
252 variables in the same model.

253

## 254 **3. Results**

### 255 *3.1. Litter properties*

256 Litter species differed strongly in their chemical, physical and morphological traits (Table 1).  
257 *A. monspessulanum* had the lowest C:N and C:P and the highest WHC and SLA. It also  
258 showed high curliness value and three-dimensionality but low tubularity. *A. unedo* was of  
259 poor nutritional quality with the highest C:N ratio and tannins concentration and lowest  
260 WHC, but had the highest tubularity value due to its cylindrical shape. *Quercus ilex* was N-  
261 rich but P-poor with low tannins concentration and was the thickest litter species. It was the  
262 only species with simultaneously low values of curliness, tubularity, and 3-dimensionality.  
263 Finally, *Q. pubescens* had the lowest tannin concentration, intermediate value of P, and  
264 physical traits, and similar morphological characteristics as *A. monspessulanum*.

### 265 *3.2. Saprophagous macroarthropod feeding preferences*

266 All saprophagous macroarthropod species fed on all litter species. Across all animal species  
267 *A. unedo* litter was consumed the most, constituting on average 42 % of the diet, followed  
268 by *A. monspessulanum* (32 %), *Q. ilex* (9%), and *Q. pubescens* (7 %). However, the  
269 PERMANOVA test identified different diet composition among species ( $F_{5,24}=3.69$ ,  $pval$   
270  $<0.001$ ) and between the two classes ( $F_{5,24}=2.99$ ,  $pval=0.03$ ; Fig. S2). In line with the overall  
271 average, the two millipede species *G. marginata* and *C. caerulocinctus* showed the highest  
272 consumption rates on *A. unedo* litter (Fig. 1). In contrast, the isopod *P. laevis* consumed *A.*  
273 *monspessulanum* at the highest rate (though not significantly different from *A. unedo* and *Q.*  
274 *ilex*), and isopods in general consumed *A. monspessulanum* litter at comparatively high rates  
275 similar to *A. unedo*. The only species without significant feeding preferences was *O.*  
276 *sabulosus*. Among the ten litter properties, only tannin concentration and tubularity  
277 explained litter preferences by saprophagous macroarthropods (Table 3).

278

### 279 3.3. Saprophagous macroarthropod feeding properties

280 Consumption rates per unit fresh mass across all litter species were highest in *A. vulgare*  
281 (Table 2, Fig. 2), intermediate in *P. laevis* and *C. caerulocinctus*, and lowest in *A. officinalis*, *G.*  
282 *marginata*, and *O. sabulosus*. No differences between species were observed when  
283 consumption rates were expressed per individual (Table 2, Fig. S3). The rate of feces  
284 production (per capita and per unit animal fresh mass) mirrored largely that of consumption  
285 with *A. vulgare* producing more than three times the amount of feces compared to *A.*  
286 *officinalis* that had the lowest feces production rate (Table 2). The per capita consumption  
287 and feces production rates did not appear to depend on total animal fresh body mass, while  
288 both, consumption and feces production rates decreased with increasing total animal body  
289 mass (Fig. 2, Table S2). Diet diversity (Shannon) did not differ between saprophagous  
290 macroarthropod species but increased with total animal body mass. The assimilation rate did  
291 not differ significantly among species and was not influenced by animal body mass, but there  
292 was considerable variability within species.

### 293 3.4. Links between litter, diet, and feces traits

294 When all saprophagous macroarthropod species were pooled, diet properties differed  
295 significantly from the available litter properties with lower C:N ratios and tannin

296 concentrations in the available litter (Fig. 3). When evaluated at the species level, only *C.*  
297 *caerulocinctus* diet showed significant differences compared to the available litter with a  
298 higher C:P ratio and lower WHC in their diet. Across all species, feces showed lower C:N and  
299 C:P ratios, lower tannin concentrations, and higher WHC compared to the initial litter,  
300 except for tannin concentration of *A. vulgare* feces that did not differ from that of the litter.  
301 There were no significant correlations between feces and diet traits (Fig. S4). Some feces  
302 traits differed among saprophagous macroarthropod species (Fig. 3A, Table S3). Across all  
303 macroarthropod species, the feces of *G. marginata* had the lowest C:N and C:P ratios and  
304 the lowest tannin concentrations. On the opposite side of the gradient, *A. officinalis* feces  
305 showed the highest C:N and C:P ratios and *A. vulgare* feces showed the highest tannin  
306 concentrations. *Cylindroiulus caerulocinctus* produced feces with the highest WHC value  
307 while *A. officinalis* produced low-WHC feces, and overall, feces from woodlice had lower  
308 WHC than those from millipedes. Saprophagous macroarthropod feces differed in their  
309 specific area with the highest values measured in *A. officinalis* feces, and low values  
310 measured for all three millipede species. The difference between the two classes were  
311 significant (Table S3). Tannin concentrations of feces correlated positively with consumption  
312 and feces production rate (Fig. S1B), but no other correlations among feeding properties  
313 were observed.

#### 314 **4. Discussion**

315 Our study shows for the first time how leaf litter properties affects feeding preferences and  
316 consequently feces characteristics among six widespread saprophagous macroarthropods of  
317 to two distinct class, allowing to test the differences between phylogenetically distant taxa  
318 commonly considered functionally similar. If we confirm the existence of feeding  
319 preferences among four contrasted litter type, we show that they can be species-specific,  
320 and strongly influenced by litter morphology rather than its nutritional value. Additionally,  
321 feeding behavior and diet composition could be linked to species identity, and interestingly  
322 to animal body mass, supporting the use of this trait as a pertinent proxy of saprophagous  
323 macroarthropods role in litter transformation. We further confirmed the strong changes in  
324 physical and chemical properties of organic matter during gut passage as frequently  
325 reported in the literature. However, we identify key feces properties that differ between

326 millipedes and woodlice, stressing the importance to question the traditional functional  
327 group used to classify soil organisms.4.1. *Feeding preferences explained by litter properties*

328 In our study, *A. unedo* was the most consumed litter species, which is surprising given its  
329 high C:N ratio, tannin concentrations, and thickness, and low WHC and opposite to our first  
330 hypothesis. These trait values are usually indicative of rather poor food quality, and hence  
331 low preference by saprophagous macroarthropods. On the other hand, the tubular-shaped  
332 leaves of *A. unedo* may have allowed favorable microclimatic conditions such as higher  
333 moisture and lower light exposure. Microclimatic conditions such as small scale variation in  
334 moisture and light exposure are in fact important for the abundance and diversity of  
335 macroarthropods [51] that likely consumed the litter they inhabited according to the “house  
336 made of food” concept [19,52]. While study does not allow to clearly disentangle nutritional  
337 and microhabitat properties of leaf litter, we observed throughout the experiment  
338 macroarthropods inside the leaves of the lowest physico-chemical quality litter species, the  
339 latter being the most consumed. The use of leaf litter as microhabitat strongly suggests that  
340 other litter characteristics linked to their morphology such as tubularity can be as important  
341 or more important than nutritional traits in determining macroarthropod feeding.

342 The deposition of fecal pellets on *A. unedo* litter might have been an additional non-  
343 exclusive reason for high feeding rates on this litter. Feces deposition may promote  
344 microbial communities along with the assumed more favorable microclimatic conditions,  
345 which is known to increase litter palatability to saprophagous macroarthropods [16,53,54]. It  
346 is important to note that *A. unedo* litter was the only one collected on the ground. Even if we  
347 took great care to select leaves with no sign of early decomposition (supported by the very  
348 low microbial decomposition in control microcosms, Table 1), it is not possible to rule out  
349 microbial colonization of the litter before collection, and that microbial necromass may have  
350 further attracted saprophagous macroarthropods in the experiment.

351 Finally the consumption of *A. unedo* may have been facilitated by the parallel consumption  
352 of *A. monspessulanum* that was the second most consumed litter species. This litter species  
353 was of high physico-chemical quality and showed the highest microbial decomposition rate.  
354 The mixed diet of all saprophagous macroarthropod species likely permitted them to reach  
355 their nutritional demands, allowing them to feed on poor-quality litter [10,55].

356 4.2. Feeding behavior and diet diversity are linked to saprophagous macroarthropod species  
357 identity and body mass

358 Based on physiological and morphological traits, *A. vulgare*, *P. laevis*, and *C. caerulocinctus*  
359 formed a distinct group of smaller bodied taxa with high rates of consumption and feces  
360 production per unit animal biomass and low diet diversity (Table 2, Fig. S5, Table S5). The  
361 negative relationship between body mass and mass-specific consumption and excretion rate  
362 is in line with the metabolic theory [25,27] and with several studies done on the same or  
363 closely related species, namely *G. marginata*, *C. caerulocinctus*, and *Ommatoiulus rutilans*  
364 (C.L. Koch, 1847) feeding on grass litter [30,56] and *G. marginata*, *G. hexasticha*, *C.*  
365 *caerulocinctus*, and *Porcellio scaber* feeding on *Alnus glutinosa* litter [28]. Interestingly, diet  
366 diversity was positively related to organism body mass. Higher food specialization of smaller  
367 taxa have been reported for phytophagous insects [57–60] but are less studied for soil  
368 saprophagous invertebrates. Larger organisms may have a more diverse diet because their  
369 higher mandibular gape and chewing strength offset the consumption limits set by leaf  
370 thickness and toughness [61,62]. If litter thickness partially explained feeding preferences  
371 (high consumption of *A. monspessulanum* that was the thinnest), additional measurement of  
372 litter toughness and mandibular strength would be required to support this hypothesis. Our  
373 data suggest that fresh body mass may be a good and easy to measure proxy to predict  
374 saprophagous macroarthropod consumption and diet diversity without complex  
375 measurement of consumption or metabolic rate [31]. Further studies including taxa with a  
376 wider spectrum of body size than that in our study and body size variation within species,  
377 would be interesting to explore how body size and diet diversity and consumption rates are  
378 related [63,64]. This also could improve our understanding of species coexistence through  
379 niche partitioning which is a mechanism of great importance for the positive role of  
380 macroarthropod diversity and community composition for litter decomposition through  
381 complementarity effects [55,64–69].

382 4.3. Chemical and physical transformation of organic matter during gut passage

383 Saprophagous macroarthropod species differed in their feces properties, but these  
384 differences are not easily explained by the differences in their diet. This highlights that, in  
385 our study, feces characteristics are poorly predictable from litter and diet characteristics. It  
386 must be noted that litter traits were measured using the whole leaf, including veins that are

387 of lesser quality and usually avoided by macroarthropods that prefer leaf lamina [4]. This  
388 may induce difference between the quality of what the animals actually ingested and how  
389 we measured it, limiting the detection of correlation between litter and feces properties.  
390 Nevertheless, on average, feces were of higher chemical quality (lower C:nutrient ratio, and  
391 tannin concentration) than the initial litter, which may have important consequences on  
392 microbial activity and the further decomposition of feces [3,35]. Indeed, by changing organic  
393 matter C:N and C:P ratio from  $95.6 \pm 0.7$  and  $2942 \pm 32$  in the available litter mix to  $32.6 \pm$   
394  $6.9$  and  $95.6 \pm 29$  in their feces, saprophagous macroarthropods likely promote microbial  
395 activity that usually is limited by substrate C:N and C:P ratios above 30 and 92 [7,70,71].  
396 Additionally, preferential consumption of the lowest-quality litter led to a higher proportion  
397 of high-quality litter in the remaining litter layer. All these effects combined result in  
398 improved organic matter quality (both in litter layer and feces) that may favor microbial  
399 activity in the remaining litter [72]. In addition to chemical changes, feces exhibited a 2.2  
400 fold increase in WHC compared to the litter mix. Therefore, conversion of litter into feces  
401 may therefore improve humidity conditions in the organic layer, which may significantly  
402 promote microbial activity.

#### 403 *4.4. Differences between woodlice and millipede in OM transformation*

404 An interesting result of our study was that tannin concentrations remained higher in  
405 woodlice feces than in millipedes' feces, especially in *A. vulgare* feces where tannin  
406 concentrations in feces were similar to those in leaf litter. Our study is the first to our  
407 knowledge to show such differences that may be explained by the different digestive track  
408 structure between woodlice and millipede. Similar to woodlice, the digestive track of  
409 millipedes consists in a straight tube, but likely is longer as it occupies the major part of the  
410 longer body of julid-form millipede compared to woodlice. This may result in longer food  
411 retention time in the digestive system in millipedes, resulting in a prolonged digestion of  
412 complex molecules and reduction of tannins concentration in feces [73]. The body length of  
413 the pill millipede *G. marginata* is similar to that of woodlice, but its digestive track (hindgut)  
414 is composed of two limbs that increase its volume that can lead to longer retention time  
415 food as well. Low if not undetectable tannin concentrations in *G. marginata* feces have  
416 already been reported when feeding on different litter types varying in tannin  
417 concentrations and in decay stage [12,74]. Additionally, species and phylum-specific

418 microbiota composition in the digestive tube may also explain these differences since  
419 microbial communities largely contribute to saprophagous macroarthropod food digestion  
420 and assimilation [14], but complete description of microbial communities in these animals  
421 digestive tube and detailed comparison between distant phylogenetic groups are lacking  
422 [35,36]. Finally, highest tannin concentrations in feces were negatively correlated to mass-  
423 specific consumption rate (and therefore feces production rate) but not to assimilation. *A.*  
424 *vulgare* showed the highest consumption rate and feces production and therefore processed  
425 litter faster than other species, likely resulting in less time for tannins and protein to  
426 complex in the animal digestive track, making tannins more detectable by the method  
427 employed. If not complexed to proteins, tannins would also be more impacting for microbial  
428 activity and feces and litter decomposition [75].

429 In addition to tannins transformation, physical differences in feces were observed with  
430 higher WHC in millipede than in woodlice feces. This difference was notably due to the  
431 highest feces WHC of *C. caerulocinctus* whilst its diet, dominated by low WHC-leaves of *A.*  
432 *unedo* and *Q. ilex* particles, was of lower WHC compared to the litter mix. This means that  
433 feces WHC is not linked to the physical properties of the particles that constitute them, but  
434 rather to feces specific area. Millipede produce thicker and rounded fecal pellets compared  
435 to the thin, flat and squared woodlice feces, with lower specific area [14]. This is important  
436 as it may imply that those two phylogenetic groups, generally grouped in the same  
437 “functional group”, actually have quite a different impact on organic matter transformation  
438 and therefore on the carbon and nutrient cycle [4,7].

## 439 **5. Conclusion**

440 Our study provides support for the important chemical and physical transformation of  
441 organic matter due to the feeding activity of woodlice and millipedes, notably with improved  
442 nutritional quality and water holding capacity in feces compared to leaf litter. In addition, we  
443 show clear differences in the feeding preferences of six widespread species that, contrarily  
444 to current knowledge, cannot be predicted only by the nutritive value of the litter but is  
445 rather linked to morphological attributes of the leaves which were previously largely  
446 overlooked [19]. Our study showed a clear distinction between woodlice and millipedes that  
447 usually are considered functionally similar. The differences in tannins digestion as well as  
448 feces shape and water holding capacity deserve more interest as polyphenols and water

449 availability are major drivers of microbial activity [1,75]. If further confirmed, differences  
450 observable at the class level (Malacostraca vs Diplopoda) would suggest that traditional  
451 functional groups [76], that nowadays are confounded with taxonomic groups (“all woodlice  
452 and millipedes species are equivalent litter transformers”), hides important differences  
453 among saprophagous arthropods class, families or genera. Functionally meaningful  
454 differences at high taxonomic ranks would allow a more detailed and accurate description of  
455 soil food-web which would improve our understanding of C and nutrient cycles [3,77]. Since  
456 obtaining species-specific information can be tedious, the links between body mass and  
457 consumption rate and diet diversity that we observed (Fig. S5), are valuable as they could be  
458 more easily incorporated in C and N cycling models [78] and improve the integration of  
459 biological control on these processes [79].

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