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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.**

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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 μm [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 ± 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⁻¹ day⁻¹) and to the
197 final fresh mass of fauna to obtain mass-specific consumption rate (C_m , g g_{fresh weight}⁻¹ day⁻¹)
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 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 Δ 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 ± 0.7 and 2942 ± 32 in the available litter mix to $32.6 \pm$
394 6.9 and 95.6 ± 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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