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RESEARCH ARTICLE

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Litter conversion into detritivore faeces reshuffles the quality control over C and N dynamics during decomposition

François-Xavier Joly[1,2] | Sylvain Coq[1] | Mathieu Coulis[3] | Johanne Nahmani[1] | Stephan Hättenschwiler[1]

[1]Centre of Evolutionary and Functional Ecology (CEFE), CNRS, Univ. Montpellier, Univ. Paul-Valéry Montpellier 3, EPHE, IRD, Montpellier, France

[2]Biological and Environmental Sciences, University of Stirling, Stirling, UK

[3]Persyst – UPR GECO, Campus Agro-Environnemental Caraïbe, BP 214, Le Lamentin Cedex 2, France

Correspondence
François-Xavier Joly, Biological and Environmental Sciences, University of Stirling, Stirling, UK.
Email: joly.fx@gmail.com

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Abstract

1. In many terrestrial ecosystems, detritivorous soil organisms ingest large amounts of leaf litter returning most of it to the soil as faeces. Such conversion of leaf litter into faeces may stimulate decomposition by increasing the surface area available for microbial colonisation. Yet, experimental support for either the outcome or the mechanism of these conversion effects is lacking.
2. Based on the hypothesis that the identity of plant species from which leaf litter is transformed into faeces has a critical role in how faeces decomposition proceeds, we collected faeces of the widely abundant millipede *Glomeris marginata* fed with leaf litter from seven distinct tree species. We compared the physical and chemical characteristics and the rates of carbon (C) and nitrogen (N) loss between litter and faeces.
3. We found that after 100 days of exposure under controlled conditions, C loss was on average higher in faeces (40.0%) than that in litter (26.6%), with a significant increase for six of the seven species. Concurrently, N dynamics switched from a net immobilisation (7.7%) in litter to a net release (14.6%) in faeces, with a significant increase for five of the seven species.
4. Litter conversion into faeces generally homogenised differences in physical and chemical characteristics among species. Despite such homogenisation, variability in rates of faeces C and N loss among species was similar compared to leaf litter, but correlated with a different set of traits. Specifically, faecal pellet C loss was positively related to compaction (decreased specific area and increased density of faecal pellets), and both C and N loss from faecal pellets were positively related to fragmentation (increased specific area and perimeter of particles within faecal pellets).
5. We conclude that litter fragmentation and compaction into detritivore faecal pellets lead to substantially enhanced decomposition, with a particularly strong impact on N dynamics that changed from immobilisation to net release depending on litter species. Moreover, litter quality control on decomposition is reshuffled by litter conversion into faeces. In ecosystems with high detritivore abundance, this so far largely overlooked pathway of organic matter turnover may strongly affect ecosystem C and N cycling.

KEYWORDS
faecal pellet, litter traits, litter transformer, macroarthropod, nitrogen immobilisation, saprophagous invertebrate, soil fauna

1 | INTRODUCTION

Assessing ecosystem carbon (C) and nutrient fluxes requires a detailed understanding of the process of litter decomposition, which involves a wide diversity of decomposer organisms (Wardle, 2002). The decomposer effect is difficult to assess quantitatively, and it is particularly challenging to partition the relative contribution of different groups of decomposer organisms such as microbial communities and detritivores that play different roles in the decomposition process (Berg & McClaugherty, 2014). Several large-scale studies and meta-analyses reported increased litter disappearance in the presence of soil fauna compared to when it was excluded (García-Palacios, Maestre, Kattge, & Wall, 2013; Handa et al., 2014), but it is currently unknown whether this increased disappearance translates into faster mineralisation of organic matter. Indeed, litter-feeding soil fauna can ingest a large part of the annual litterfall (Cárcamo, Abe, Prescott, Holl, & Chanway, 2000; David & Gillon, 2002), but only a small portion is assimilated with the majority of the consumed litter being returned to the soil as faeces. It is assumed that litter conversion into faeces increases the surface area available for microbial colonisation, thereby stimulating microbial activity and accelerating decomposition (e.g., Bardgett & Wardle, 2010; Lavelle & Spain, 2001; Wardle, 2002). However, there is currently little experimental evidence supporting either the outcome, that is the faster decomposition, or the mechanism, that is the increased surface area (David, 2014).

1.1 | The outcome

The majority of studies that investigated the consequences of litter conversion into detritivore faeces focused on the response of microorganisms and compared microbial activity in fresh faeces with that in intact leaf litter. However, these microbial changes on fresh faeces are only transitory (Frouz & Šimek, 2009) and their longer-term consequences on decomposition are currently unknown. To date, only four studies compared the mass loss of detritivore faeces with that of uneaten leaf litter yielding contrasting results. One study with fly larvae (*Penthetria holosericae*) found a lower mass loss rate in faeces compared to leaf litter (Frouz & Šimek, 2009). Two studies, each with a different millipede species (*Glomeris marginata* and *Narceus annularis*) found no differences between faeces and leaf litter mass loss rates (Nicholson, Bocock, Heal, & Webb, 1966; Webb, 1977). Only one study with a millipede species (*Ommatoiulus sabulosus*) reported higher mass loss in faeces compared to leaf litter (Coulis, Hättenschwiler, Coq, & David, 2016), but this increase was observed in only one of the 2 L species used in that study. These distinct results may be caused by several factors, including experimental conditions, detritivore species identity and litter species identity as was reported for microbial activity in faeces produced from litter of different plant species (Joly, Coulis, Gérard, Fromin, & Hättenschwiler, 2015). In addition to carbon (C) cycling, rates of nitrogen (N) loss may also change in faeces compared to litter. Indeed, numerous microcosm experiments found higher N mineralisation rates in the presence of detritivores (e.g., Hättenschwiler & Bretscher, 2001; Kaneko, 1999), but the underlying mechanisms remain unexplored. A better quantification of both C and N dynamics following litter conversion into detritivore faeces may eventually allow to specifically consider fauna in litter decomposition models.

1.2 | The mechanism(s)

Any differences in faeces versus leaf litter decomposition should be related to changes in physical and/or chemical characteristics and their consequences on microbial diversity, abundance and/or activity. Among these changes, the increase in surface area available for microbial colonisation appears as a key mechanism. However, there is uncertainty about the scale at which this increase occurs and how it matters for decomposition, that is either at the scale of the entire faecal pellet, or that of the particles constituting the faecal pellet. The total surface area of all the particles (litter fragments) constituting the faecal pellet is commonly referred to when discussing a positive effect of litter conversion into faeces on decomposition (fragmentation hypothesis; Bardgett & Wardle, 2010; Lavelle & Spain, 2001; Wardle, 2002). An increase in surface area at the scale of the whole pellet is also mentioned as a mechanism (repackaging hypothesis, Bardgett & Wardle, 2010). Strikingly, there is very limited evidence for either the fragmentation or the repackaging hypothesis as only two studies addressed these specifically. Kheirallah (1990) reported an increased total surface area of constituent particles within faecal pellets in support of the fragmentation hypothesis. In a second study, Webb (1977) found that the specific area at the scale of a pellet decreased compared to intact leaf litter, opposing the repackaging hypothesis. We do not know of any study that assessed the impact of changes in specific area at either the particle or the pellet scale on faeces decomposition. The conversion of litter into faeces was also found to modify other important traits for decomposition, with reports of increased water-holding capacity (WHC; Coulis et al., 2016), reduced tannin concentrations (Coulis, Hättenschwiler, Rapior, & Coq, 2009), and reduced or increased C:N ratios depending on studies and litter types (Bastow, 2011; Coulis et al., 2016). Given the strong control of litter quality on decomposition (Makkonen et al., 2012), understanding the direction and magnitude of changes in litter quality associated with the conversion into faeces, and how this may differ among different plant species,

is important to improve the understanding of decomposition and its consequences on C and nutrient cycling.

Here, we aimed at answering two questions: (a) do plant species differ in how the conversion of leaf litter into detritivore faeces affect subsequent decomposition? and (b) can this conversion effect be predicted from the changes in physical and chemical quality? To address these questions, we collected faeces of the macroarthropod species *G. marginata* (Villers, 1789; Figure 1), a common millipede species in European forests, fed with litter from each of seven tree species. In a 3-month incubation under controlled conditions, we evaluated carbon and nitrogen losses for leaf litter of each tree species, as well as for the faeces produced by *G. marginata* feeding on each individual litter species separately. In parallel, we evaluated the differences in physical and chemical characteristics between litter and faeces. We hypothesised that (H1) litter conversion into faeces homogenises, but overall improves organic matter quality for further decomposition, and (H2) consequently rates of C and N cycling in faeces would be more similar among species, and proceed overall more rapidly compared to leaf litter.

2 | MATERIALS AND METHODS

2.1 | Leaf litter collection and faeces production

Leaf litter from seven tree species was collected in three sites representing major European forest types including a Mediterranean forest in Spain, a thermophilous deciduous forest in Italy, and a mountainous beech forest in Romania. The selected tree species were *Quercus ilex rotundifolia* L. (Spain), *Castanea sativa* Mill., *Ostrya carpinifolia* Scop., *Quercus cerris* L. and *Quercus ilex ilex* L. (Italy), and *Acer pseudoplatanus* L. and *Picea abies* (L.) H. Karst (Romania). Leaf litter was collected at species-specific peak leaf litterfall using suspended litter traps, as described in Joly et al. (2015), air-dried and stored until use.

We produced macrodetritivore faeces from each of the litter species individually by feeding the seven leaf litter species to pill millipedes (*G. marginata*). We selected this species because it is widespread and abundant across different European forests, and because it feeds on leaf litter from a large range of tree species. Animals were collected from a *Q. ilex ilex*-dominated forest near Montpellier (43°39′N, 3°40′E). As detritivores usually prefer feeding on decomposing leaf litter that is well colonised by microorganisms rather than freshly fallen litter (David & Gillon, 2002), air-dried litter from each species were placed on a *Q. ilex ilex* forest floor in separate 25 × 25 cm litterbags that excluded macrofauna (mesh size: 0.5 mm) for 16 days in April 2016. Litterbags were watered regularly to maximise microbial colonisation. We then placed half of all species-specific litter (*c.* 60 g of moist leaf litter) in large plastic boxes (40 × 33 × 8.5 cm) each containing 50 individuals of *G. marginata*. The remaining litter material was placed in another set of the same type of plastic boxes without fauna, under the exact same conditions as those used for faeces production. The boxes were kept at room temperature (*c.* 20°C) for 6 weeks, and faeces were collected twice a week using a 2-mm sieve that let pass faecal pellets but not leaf litter. Leaf litter and animals were then placed back in their boxes and sprayed with water to maintain optimal humidity conditions. To ensure similar desiccation and perturbation dynamics for the leaf litter that did not contain millipedes, we opened the boxes without fauna and agitated leaf litter using the sieve in the same manner and at the same time like those containing millipedes. After each faeces collection, the species-specific pools of faeces were dried at 30°C. At the end of this faeces production period, decomposing leaves from the control boxes without fauna were dried at 30°C and randomly selected subsamples were cut in pieces of 4 × 4 mm. This cutting was carried out to obtain representative samples from different leaves, small enough to fit within the miniaturised decomposition containers (see below), which size was determined by the amount of faeces available for decomposition.

2.2 | Physical and chemical characteristics

A number of quality parameters were measured on three subsamples drawn from each species-specific pool of leaves (cut in 4 × 4 mm pieces) and faeces. Specific area (surface area per unit mass) for (a) litter, (b) faecal pellets and (c) faeces particles was measured with photographs using a stereo microscope. Leaf litter and faecal pellets were photographed directly. To visualise faeces particles, faeces were weighed and placed in a beaker with 60 ml of deionised

FIGURE 1 *Glomeris marginata* (left and centre) ingest large amounts of leaf litter and return most of it as faeces (centre and right) (Photograph credits: F.-X. Joly)

water, agitated with a magnetic agitator for 2 hr, allowing complete dissolution of the faeces, filtered and photographed under a stereo microscope. Surface area and dimensions of each litter pieces/faecal pellets/faeces particles were estimated using an image analysis software (ImageJ, version 1.46r). For leaf litter and faeces particles, the total surface area was estimated by multiplying the projected surface area by two. For faecal pellets, surface area was estimated using the formula for prolate spheroids. Specific area was then computed by dividing the estimated area by the sample weight. In order to identify whether the change in specific area in faecal pellet was due to a change in density (mass per unit of volume), or a change in surface-to-volume ratio (Supporting Information Figure S1), we also estimated the faecal pellet volume using the formula for prolate spheroids. Because the specific area of faeces particles available to microbial colonisation may also be influenced by the perimeter of particles, we calculated the specific perimeter of faeces particles by dividing the sum of particle margins length by faeces mass (Figure S1). Water-holding capacity was measured by placing *c*. 15 mg of leaf litter or faeces in an Eppendorf tube with 2 ml of deionised water for 1 hr, weighing it wet after gently removing excess water and re-weighing after drying at 60°C for 48 hr. Total carbon (C) and nitrogen (N) concentrations were measured with a flash CHN Elemental Analyser (Flash EA 1112 Series; ThermoFinnigan, Milan, Italy), on leaves and faeces samples ground with a ball grinder. Concentrations of condensed tannins were measured spectrophotometrically using the butanol HCl method (Coulis et al., 2009).

2.3 | Carbon and nitrogen dynamic during decomposition

To evaluate the effect of leaf litter conversion into millipede faeces on C and N cycling, leaf litter and faeces of each of the seven tree species were exposed in microcosms under controlled conditions for 100 days of decomposition. Microcosms consisted of 250-ml plastic containers filled with 100 mg of soil collected from a Mediterranean old field (see Joly et al. (2015) for soil characteristics). We chose this soil to avoid any effects of home-field advantages as none of the studied species were present. About 100 mg of leaves and faeces of each species were placed separately within a small PVC tube (20 mm in diameter × 15 mm in height) closed on the bottom with a 100-µm mesh and left open on the top. Each container was then placed on top of the soil within the microcosm. Five replicates per treatment were prepared, for a total of 70 microcosms (7 species × 2 substrate types × 5 replicates). Microcosms were watered so as to reach 80% of soil WHC and incubated at 20°C in incubation chambers. To ensure gas exchange while limiting desiccation, three small holes (2 mm in diameter) were drilled on each microcosm cap. To limit variability due to differential desiccation among microcosms, they were weighed weekly and watered to their initial weight at 80% of soil WHC. Replicates were placed on separate shelves of two incubation chambers, according to a randomised complete block design. Both block position among shelves and between the two incubation chambers, and microcosm position within a shelf were randomised weekly. After 100 days, remaining leaves and faeces in the microcosms were collected, dried at 30°C, weighed and ground with a ball grinder. We measured C and N concentrations in all samples with a flash CHN Elemental Analyser (Flash EA 1112 Series; ThermoFinnigan). The percentage of C and N lost from the leaves and faeces after the incubation was calculated as $[(M_i \times CN_i - M_f \times CN_f)/(M_i \times CN_i)] \times 100$, where M_i and M_f are the initial and final 30°C dry mass, respectively, and CN_i and CN_f are the initial and final litter C or N concentration (% of leaves or faeces dry mass), respectively. Negative litter N loss represents a net immobilisation of N, and positive litter N loss represents a net release of N.

2.4 | Statistical analyses

The effects of plant species identity (with all species included as individual levels) and substrate type (faeces vs. litter) on rates of C and N cycling, final C and N concentration and final C:N ratio, were tested using two-way ANOVAs, with block as a random-effect factor. The effects of plant species identity and substrate type on each quality parameter (C:N ratio, C, N and condensed tannins concentrations, WHC, specific area) were tested using two-way ANOVAs. Effects of plant species identity on each faeces-specific trait (density and surface-to-volume ratio of faecal pellets, fragment perimeter of faeces particles) were tested using one-way ANOVAs. Tukey's HSD tests were used to determine significant differences among treatment combinations. The distribution in variation among all litter and faeces traits was visualised through two separate principal component analyses (PCA).

To evaluate the control of litter quality on litter C and N loss and the legacy effect of litter quality and faeces C and N loss, correlations between litter and faeces C and N loss and the species coordinates on the two main axes of the PCA based on litter traits were represented on the PCAs. To evaluate the control of faeces quality on faeces C and N loss, correlations between faeces C and N loss and the species coordinates on the two main axes of the PCA based on faeces traits were represented on the PCAs. Additionally, species coordinates on the first four axes of each PCA were used in multiple linear regressions to explore how litter/faeces C and N loss related to the overall litter/faeces quality. To further detail the control of each quality parameter, simple linear regressions were run between litter/faeces C and N loss, and each litter/faeces quality parameter, with a significance threshold lowered according to Bonferroni correction to reduce chances of type I errors. All data were checked for normal distribution and homoscedasticity of residuals, and transformed to meet the requirements when needed. We used the R software, version 3.4.2.

3 | RESULTS

3.1 | Changes in chemical and physical characteristics

All the chemical and physical characteristics we measured differed among plant species and changed considerably during the conversion from leaf litter into faeces, apart from the WHC, and

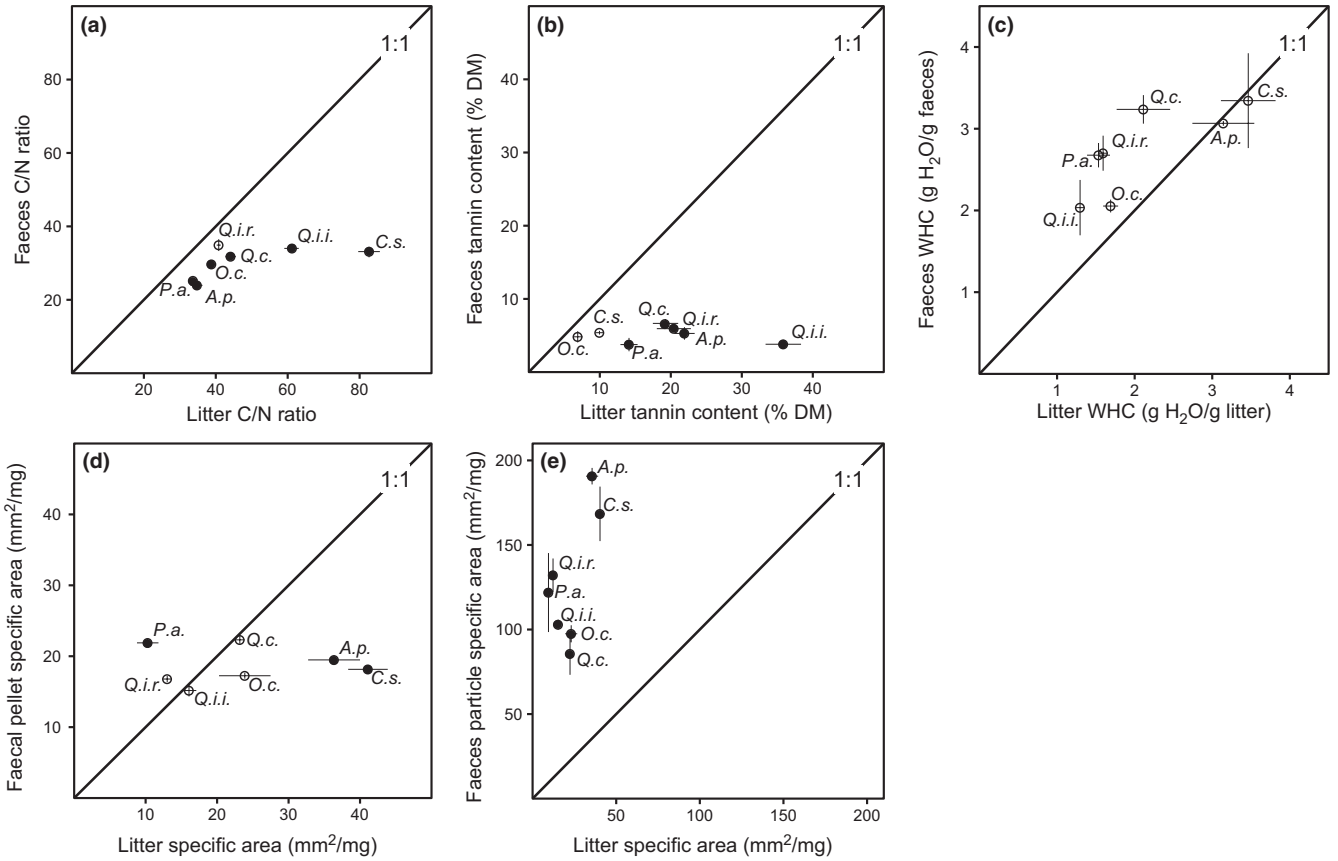

FIGURE 2 Comparison between faeces and litter of (a) C:N ratio, (b) condensed tannins concentrations, (c) water-holding capacity (WHC), (d) specific area (faecal pellet vs. litter), (e) specific area (faeces particle vs. litter) for each species (mean ± *SE*; $n = 5$). The 1:1 line defines identical value between litter and faeces. To keep *y* and *x* axes comparable for a given panel, on panel (e), litter specific area is presented on a different range than it is on panel (d). Each point represents a litter species. Points in black indicate that the difference between faeces and litter is significant ($p < 0.05$), while white points indicate no significant difference ($p > 0.05$). A.p.: *Acer pseudoplatanus*; C.s.: *Castanea sativa*; P.a.: *Picea abies*; O.c.: *Ostrya carpinifolia*; Q.c.: *Quercus cerris*; Q.i.i.: *Quercus ilex ilex*; Q.i.r.: *Quercus ilex rotundifolia*. Correction added after online publication on 25 July 2018: In Fig. 2(e), 'Faecal pellet' was corrected to 'Faeces particle'.

these conversion effects depended on the plant species identity (Supporting Information Table S1).

The C:N ratio was strongly reduced by the litter conversion into faeces by up to −59.8% (*C. sativa*) in six of seven species (Figure 2a, Table S1). Lower faeces than litter C:N ratios resulted mostly from increased N concentrations in faeces compared to leaf litter, but C concentration also tended to be lower in faeces compared to leaf litter (Table S1). As a consequence, interspecific variability in litter C:N ratio ranging from 34.1 in *P. abies* to 83.2 in *C. sativa* (Figure 2a, 2.4-fold difference) decreased in faeces ranging from 24.3 in *A. pseudoplanatus* to 35.2 for *Q. ilex rotundifolia* (Figure 2a, 1.4-fold difference).

Similarly, the concentrations of condensed tannins were strongly reduced by the litter conversion into faeces by up to −89.0% (*Q. ilex ilex*), in six of seven species (Figure 2b, Table S1). Again, interspecific variability in condensed tannins was much lower in faeces (1.7-fold difference) compared to leaf litter (5.0-fold difference, Figure 2b, Table S1).

Litter conversion into faeces did not significantly affect the WHC for any of the litter species (Figure 2c, Table S1). Nevertheless, interspecific variability in WHC was reduced in faeces (1.7-fold difference) compared to leaf litter (2.6-fold difference, Figure 2c, Table S1), similar to C:N ratio and condensed tannins,.

When faeces-specific area was considered at the scale of faecal pellets, the direction and magnitude of the change following litter conversion into faeces depended on the litter species. It increased for one species (*P. abies*), decreased for two species (*C. sativa*, *A. pseudoplatanus*), and was unchanged for the remaining four species (Figure 2d, Table S1) compared to intact leaf litter. The variability in specific area among litter species was again reduced by the litter conversion into faeces, with a 1.5-fold difference in faecal pellets compared to a 3.9-fold difference in leaf litter (Figure 2d, Table S1).

In contrast, when the specific area was measured at the scale of the particles constituting the faeces, it was strongly increased by litter conversion into faeces for all litter species (Figure 2e). Similar to all other quality characteristics, interspecific variability was reduced in faeces (2.2-fold difference between the species with the lowest and the highest values, respectively, Figure 2e, Table S1).

3.2 | Changes in C and N cycling

After 100 days of incubation under controlled conditions, we found important differences in C and N loss between substrate types (litter vs. faeces) and among litter species (Table 1). Additionally, the

TABLE 1 Results of two-way ANOVAs testing the main effects of (i) plant species and (ii) substrate type (litter vs. faeces) and their interaction on carbon and nitrogen loss

	Carbon loss				Nitrogen loss			
Source of variance	***df***	**Mean sq.**	***F*-value**	***p*-Value**	***df***	**Mean sq.**	***F*-value**	***p*-Value**
Block	4	21	–	–	4	101	–	–
Plant species (PS)	6	498	53.62	<0.001	6	416	20.0	<0.001
Substrate type (ST)	1	3,127	336.48	<0.001	1	8,643	414.5	<0.001
PS × ST	6	158	16.97	<0.001	6	754	36.2	<0.001
Residuals	52	9	–	–	52	21	–	–

significant interaction between substrate type and litter species (Table 1) indicated that the effect of litter conversion into faeces on subsequent C and N loss depended on the species identity of the ingested litter.

On average across species, litter C loss was 26.6% of initial C, while it was considerably higher for faeces with 40.0% of initial C lost during the 100-day decomposition. This is 50.4% more C lost from faeces than from leaf litter, but depending on species this difference varied between +8.2% for *Q. cerris* (not significantly different) and +100.6% for *Q. ilex ilex* and was significant for six of the seven studied species (Figure 3a). Interspecific variability in C loss was similar between the two substrates with a 1.7-fold and 2.0-fold difference between the species with the lowest and the highest C loss from leaf litter and faeces, respectively (Figure 3a). Faeces C loss correlated positively with litter C loss ($r = 0.51$, $p < 0.01$).

The substrate identity profoundly influenced N loss dynamics. Leaf litter mostly immobilised N during the 100-day exposure, with an average 7.7% increase in absolute N content in leaf litter across all species. Net release of N was only observed for one species (*Q. ilex rotundifolia*, Supporting Information Table S2) of the seven studied species (Figure 3b). In contrast, faeces lost 14.6% of total initial N content on average, with a net N release for six of the seven studied species (all but *Q. cerris*, Table S2) and significantly increased N release for five of the seven studied species (Figure 3b). Interspecific variability in N loss was similar between the two substrates, with differences between the species with the highest and lowest N loss of 31.3% for leaf litter and 27.1% for faeces. Faeces N loss did not correlate with litter N loss ($r = -0.26$, $p = 0.13$).

As a result of the species- and substrate type-specific C and N loss dynamics, ratios of C:N in the 14 different materials narrowed towards an average of 26.7 during the 100-day incubation. Mean initial values were 48.5 and 30.7 in litter and faeces, respectively, while mean final values were 32.1 and 21.2 in litter and faeces, respectively. This was mostly driven by changes in N concentrations

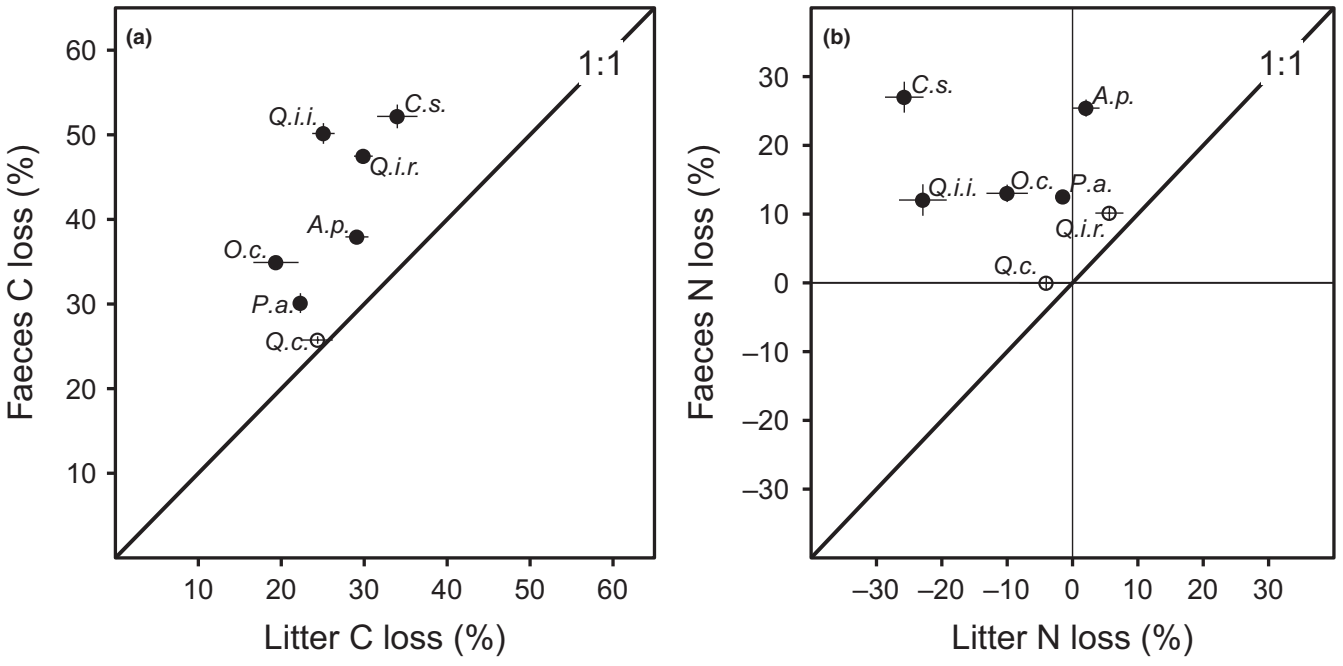

FIGURE 3 Comparison of (a) carbon (C) and (b) nitrogen (N) losses between faeces and litter, for each species (mean ± *SE*; $n = 5$). For further details, see Figure 2

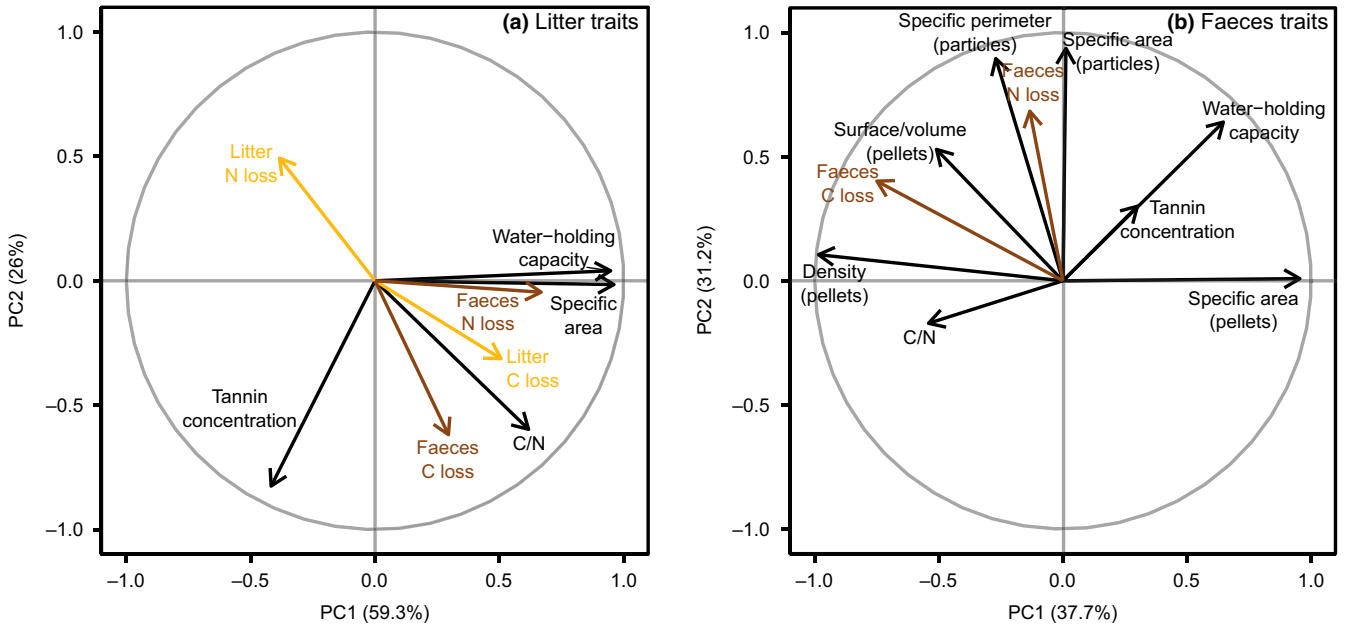

FIGURE 4 Principal component analyses of (a) litter and (b) faeces traits (represented as black arrows), of the seven plant species. Coloured arrows depict the correlations between C and N loss of litter (yellow) and faeces (brown), with the PCA axes. All traits were centred and standardised prior to ordination

while C concentrations remained largely stable during decomposition (Table S2).

3.3 | Initial quality control over C and N loss

Litter C loss was associated with the litter PCA axis related to the physical litter traits (PC1, Figure 4a, Supporting Information Table S3), particularly with litter WHC (Supporting Information Table S4). In contrast, faeces C loss was associated with the PCA axis related to the chemical traits of the litter from which it was produced (PC2, Figure 4a, Table S3) and particularly with litter C:N ratio (Table S4). Faeces-specific traits predicted faeces C loss better than litter traits, with all first four faeces PCA axes accounting for 95% of overall variance (Table S3). C loss was mostly associated with the faeces PCA axis related to repackaging (PC1, Figure 4b, Table S3), and less with the axis related to fragmentation (PC2, Figure 4b, Table S3). Particularly, faeces C loss was positively related to the faecal pellet density, particles specific area and perimeter (Table S4).

Litter N loss was moderately related to both main axes of the litter PCA (PC1 and PC2, Figure 4a, Table S3), and particularly negatively related to litter C:N ratio (Table S4, Supporting Information Figure S2). In turn, faeces N loss was related to the litter PCA axis representing physical traits of the litter from which it was produced (PC2, Figure 4a, Table S3). Faeces-specific traits predicted faeces N loss better than litter traits, with all first four faeces PCA axes accounting for 80% of overall variance (Table S3). N loss was mostly related to the fragmentation PCA axis (PC2, Figure 4b, Table S3) and particularly with the specific area and perimeter of faeces particles (Figure 4b, Table S4), but not with traits representing repackaging.

4 | DISCUSSION

4.1 | The outcome of litter transformation into faecal pellets: increased C and N cycling in faeces

With an average 50.4% higher C loss from faeces compared to the intact leaf litter (Figure 3a), accompanied by a switch from net N immobilisation to net N release (Figure 3b), our study provides strong support for higher decomposition rates of litter material that was transformed into faeces by detritivores. We may even have underestimated this increase, because with our experimental set-up, millipedes were not in contact with soil and hence did not incorporate soil particles into the faeces as it commonly occurs under more natural conditions (Kaneko & Salamanca, 1999). Moreover, litter and faeces both decomposed on the soil surface to allow direct comparison under exactly the same environmental conditions. Under natural conditions faeces may be transferred deeper into the soil due to passive sedimentation or active burial by soil animals (David, 2014). These experimental constraints limited the mixing of organic matter (faecal material) with mineral soil, which has previously been shown to favour decomposition of detritivore faeces (Coulis et al., 2016). On the other hand, our choice to cut leaf litter into smaller pieces obviously increased its surface area, which correlated positively with decomposition in our study (Figure 4a, Table S4). Therefore, leaf litter decomposition might have been higher in our study compared to a natural situation with whole leaves.

Our findings do not match those from the four previous studies that compared litter and faeces decomposition, reporting decreased (Frouz & Šimek, 2009), unchanged (Nicholson et al., 1966; Webb, 1977), or depending on the litter species, unchanged or

accelerated faeces decomposition (Coulis et al., 2016). Admittedly, our incubation was shorter (3.3 months) than these previous studies (*c*. 11 months). However, the use of controlled laboratory conditions close to the optimum for microbial activity permitted to reach levels of decomposition (33.3% of initial C lost on average among treatments) equivalent to that reported in the previous field studies (between *c*. 25% and 45% of initial mass lost on average within studies). More importantly, the previous studies and ours differed in two other aspects, that is the animal species that produced the faeces, and the litter species on which they were feeding. The use of detritivore species from different phylogenetic groups may partly explain these contrasting results, and it is interesting that the only study reporting slower decomposition rates for faeces (Frouz & Šimek, 2009) used fly larvae (*Bibio marci*) while the other studies and ours used millipedes. Notably, different responses (neutral and positive) were observed for faeces produced by the same detritivore species (*O. sabulosus*) but feeding on two different litter species (Coulis et al., 2016). In view of our results demonstrating clear differences in how faeces decomposition differed from that of leaf litter depending on litter species identity, it seems likely that distinct results among studies were, at least partly, related to the identity of litter species. Indeed, Joly et al. (2015) reported distinct stimulation of microbial activity in faeces depending on litter species from which faeces were produced. While this latter study reported a homogenisation of microbial activity in faeces compared to leaf litter, we observed similar variation in C and N loss in faeces compared to that in leaf litter. There were no obvious homogenisation effects on decomposition following transformation into faeces (Figure 2a), in contrast to our second hypothesis. Any initial homogenisation of microbial activity in freshly produced faeces (e.g., Joly et al., 2015) may be only transient and does not preclude strong species-specific differences in longer-term decomposition as indicated in our study. Moreover, while C loss from faeces showed a relatively weak correlation with that from leaf litter ($r = 0.50$, $p < 0.01$), the interspecific differences in N loss from faeces did not correlate at all with that from leaf litter. This suggests that conversion effects are difficult to predict from initial characteristics or decomposition rates of leaf litter. Hence, litter conversion into faeces reshuffles differences among litter of different plant species rather than accentuating initial differences. This seems particularly important for N dynamics with a switch from N immobilisation to net N release upon litter conversion into faeces. By resetting the C:N ratio of litter material during gut passage close to or below the threshold of 30 (Figure S2), above which microorganisms are thought to be N limited (Kaye & Hart, 1997), detritivores may have a particular strong influence on the N cycle and therefore on N availability and potentially ecosystem productivity.

4.2 | The mechanism of conversion effects: fragmentation for N loss, repackaging for C loss

Using a wide variety of leaf litter obtained from seven tree species, we found that litter conversion into faeces was generally accompanied by the homogenisation of initial litter quality differences into a quality more favourable for further decomposition (e.g., lower C:N ratio, less condensed tannins, Figures 1b,2a) in line with our first hypothesis. These findings are in accord with previous studies that showed lower C:N (Bastow, 2011) and tannin concentrations (Coulis et al., 2009) in faeces compared to leaf litter. With regard to physical characteristics, the specific area was strongly affected, but the changes depended on the scale considered. At the scale of the faeces particles, specific area increased greatly compared to leaf litter (Figure 2e), in line with expectations and previous results (Kheirallah, 1990). However, at the scale of the faecal pellet, the specific area either increased or decreased, depending on the litter species (Figure 2d). This suggests that a decrease in specific area at the faecal pellet scale as reported by Webb (1977) or an increase due to litter repackaging (Bardgett & Wardle, 2010) may both occur in some but not all litter species.

The observed changes in chemical and physical characteristics were also followed by changing quality control over C and N cycling. Indeed, the legacy effect of litter quality on faeces C and N loss (Figure 4a) showed that different sets of initial litter traits drive litter and faeces decomposition rates. This confirms that litter conversion into faeces reshuffles the control of litter quality on decomposition. In fact, faeces-specific traits were better predictors of faeces decomposition rates, with faeces C loss mostly driven by an increase in specific perimeter of faeces particles, an increase in density and decrease in specific area of faecal pellets (Figure 4b, Table S4). Similarly, faeces N loss was driven by an increase in specific area and perimeter of faeces particles (Figure 4b, Table S4). Such positive relationship between C and N loss and specific area and perimeter of faeces particles (both increasing the overall surface area available for microbial colonisation) supports the fragmentation hypothesis (Bardgett & Wardle, 2010; Lavelle & Spain, 2001; Wardle, 2002). In contrast, the negative relationship between faeces C loss and pellet specific area indicates that the repackaging participates in the accelerated decomposition of faeces, but through the opposite mechanism than commonly assumed (Bardgett & Wardle, 2010). This indicates that contrary to litter, denser faeces with low specific area decompose faster. Collectively, our data suggest that the mechanism of higher surface area available for microbial colonisation plays out only at the scale of the particles composing the faeces, while the mechanism of litter compaction seems to play at the whole faecal pellet scale. As these faeces-specific traits measured at the scale of faeces particles and faecal pellets vary independently from plant species-specific quality characteristics of leaf litter, the consequences for C and N dynamics during faeces decomposition appear difficult to predict from existing plant trait data. Because in this study, we aimed at understanding the conversion effect on C and N cycling rather than on microbial activity or biomass, we can only suppose but not prove that the higher rates of faeces C and N loss were associated to increased microbial colonisation compared to leaf litter. Fragmentation may also facilitate leaching, a process that can lead to higher C and N loss without any changes in microbial biomass or activity (Coulis et al., 2016). Future studies should

thus consider the evaluation of the relative impact of microbial metabolism and physical leaching losses of organic C and N during faeces decomposition, two pathways of distinct consequences for ecosystem C and N cycling.

4.3 | Ways forward

It is important to stress that our study focused on a single detritivore species. Although *G. marginata* is widespread and abundant across Europe and feeds on various litter species in distinct ecosystems, our findings may not extend to other detritivore species. Differences in their diet, consumption and assimilation rates, and particularly on the size, form and content of their faeces may modify the consequences on organic matter decomposition (David, 2014). Evaluating these interspecific differences that are also linked to relative abundance and activity data thus appears as a next important step in the assessment of ecosystem consequences of detritivore activity. Faeces-derived C may constitute a major contribution to soil C formation and stabilisation during either the leaching phase and/or the physical transfer phase of faecal pellets (Cotrufo et al., 2015). Moreover, the strongly accelerated N release from decomposing faeces compared to leaf litter suggests that detritivores may have a disproportionate influence on the dynamics and availability of N and potentially other nutrients. Future research may focus more specifically on the fate of carbon and nutrients during faeces decomposition, and the consequences on soil organic matter formation and nutrient availability.

5 | CONCLUSIONS

Our study provides clear experimental evidence supporting the postulated increase in decomposition of plant-derived organic matter following litter transformation into detritivore faeces. In addition to altered C dynamics, N was released much more rapidly from decomposing faeces compared to leaf litter. These changes in N dynamics could play a major role in the ecosystem N cycle, but remain largely neglected. Our results further contributed to clarify the underlying mechanisms by showing that an increase in faeces particles perimeter (i.e., fragmentation), and a decrease in faecal pellet specific area (i.e., repackaging) drove the variation in faeces decomposition. Litter conversion into faeces by saprophagous macroarthropods thus appears as a largely overlooked pathway, which may reshuffle the control of litter quality on further microbial decomposition and C and N cycling. Given the importance currently attributed to initial litter quality in decomposition models, and the documented strong contribution of fauna to decomposition world-wide (García-Palacios et al., 2013), exploring this pathway for other detritivore species appears as an important venue for future research. Improved quantification of how litter transformation into faeces influences elemental cycling may enable the incorporation of soil fauna effects into decomposition models and enhance their accuracy of prediction.

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AUTHORS' CONTRIBUTIONS

F.X.J., M.C. and S.H. designed the experiment. F.X.J., S.C. and J.N. collected the data. F.X.J. analysed the data and led the writing of the manuscript. S.C. and S.H. participated in the writing and all authors contributed to revisions.

DATA ACCESSIBILITY

The data associated with this article are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.m528023 (Joly, Coq, Coulis, Nahmani, & Hättenschwiler, 2018).

ORCID

François-Xavier Joly http://orcid.org/0000-0002-4453-865X

Sylvain Coq http://orcid.org/0000-0002-7887-0247

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