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Research article

Soil fauna precipitate the convergence of organic matter quality during decomposition

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Plant litter constitutes the dominant resource to soil food webs, which gradually decompose litter and transform it into soil organic matter. A central paradigm of this transformation posits that differences in quality between distinct litter types disappear during decomposition, as litter types converge towards similar physicochemical characteristics. Yet, this paradigm is debated and not based on clear metrics. It is also largely derived from microbial decomposition studies, while the effect of litter-feeding soil animals, by transforming large quantities of litter into faeces, remains poorly documented. We addressed this knowledge gap by quantifying the variability in physicochemical characteristics amongst leaf litter of six tree species of contrasting quality, before and after conversion into faeces by six soil animal species. We found that litter conversion into faeces by diverse soil animals largely reduced the variability in physical and chemical characteristics between contrasting litter types. We also evaluated the consequences of this animal-driven convergence on further microbial-driven convergence during decomposition, by decomposing intact litter and soil animal faeces and comparing the chemical characteristics of decomposed materials. Chemical variability amongst uningested litter and amongst soil animal faeces converged at similar rates. This indicates that animal- and microbial-driven convergence are additive, and that soil animals precipitate organic matter quality convergence during decomposition. We propose here a new framework and an associated metric to study changes in organic matter quality variability during decomposition, which we argue are essential for an improved understanding and modelling of litter decomposition and soil organic matter formation.

Keywords: carbon cycling, litter-feeding macrofauna, litter complexity, nitrogen cycling, plant–soil interactions, soil biodiversity

Introduction

In terrestrial ecosystems, the majority of net primary production is not consumed by herbivores and fuels the soil food web as dead organic matter (Wardle et al. 2004). The consequent passage of this resource through complex networks of soil organisms gradually decomposes this litter and shapes the formation of litter-derived soil

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organic matter (Cotrufo et al. 2015), underpinning important ecosystem services such as carbon sequestration and climate regulation (Dangi 2014). The rate at which this organic matter decomposes tightly aligns with its physicochemical characteristics ('quality' hereafter) (Cornwell et al. 2008, Makkonen et al. 2012), which determine the capacity of microorganisms and soil fauna to use it as a primary resource (Hendriksen 1990, Cotrufo et al. 2013). While there has been a strong focus on the control of initial quality (i.e. before the onset of decomposition) on litter mass loss (Swift et al. 1979, Coûteaux et al. 1995, Aerts 1997, Cornwell et al. 2008, Zhang et al. 2008), the direction and drivers of changes in organic matter quality throughout the decomposition process and their consequence for further decomposition remain unresolved (Wickings et al. 2012). Moreover, the role played by soil fauna on these changes in organic matter quality is poorly documented. This limited understanding hampers our ability to predict the fate of this organic matter and the quality of litter-derived soil organic matter.

1) *Convergence versus divergence.* A key paradigm posits that quality of different litter types converge throughout decomposition (Fierer et al. 2009). This paradigm arose from multiple litter decomposition studies that found that litter types with distinct initial organic matter quality were consistently more similar at late decomposition stages (Melillo et al. 1989, Preston et al. 2009, Moore et al. 2011). The assumed mechanism underlying this convergence is that decomposer organisms share a similar set of stoichiometric constraints or metabolic abilities (McGill 2007, Fierer et al. 2009) that constrain the organic matter quality trajectory during decomposition towards a common quality. Contrasting with this paradigm, an analysis of organic matter quality during the decomposition of two contrasting litter types (grass and corn) by Wickings et al. (2012) revealed a divergence rather than convergence in organic matter quality after ca 80–95% mass loss. This overall divergence was driven by the convergence of some initially distinct characteristics (but still retaining differences) and other initially similar characteristics diverging. This finding challenges the widely accepted convergence paradigm and suggests that initial organic matter quality has a persistent effect on organic matter quality throughout decomposition. This central feature of decomposition ecology thus appears unresolved, making organic matter quality throughout decomposition difficult to predict. A major obstacle towards understanding the drivers of variability in organic matter quality lies in the absence of clearly defined metrics to quantify this change. It appears that the convergence or divergence were so far defined as a decrease or increase, respectively, in the absolute range of values. Yet, the range is a poor variability indicator for two reasons. First, it considers the minimum and maximum values only, thus losing information from values in-between. Comparing standard deviations as a metric of absolute variability could overcome this point. Second, the range (or standard deviation) is dependent on the mean value. Values of 1, 2 and 3 have a much smaller absolute variability than values of 10, 20 and 30 (range of 2 versus 20, standard deviation of 1 versus 10), despite being the same from a relative point of view. This relative variability could be calculated by measuring the coefficient of variation (standard deviation divided by the mean value). However, it is undefined if the convergence-/-divergence reflects a change in absolute variability only (e.g. standard deviation) or relative variability (e.g. coefficient of variation). Here, we propose quantifying changes in organic matter variability using both metrics.
2) *Litter identity versus decomposer identity.* Organic matter quality is assumed to be driven by the identity of the litter (due to persisting differences in initial organic matter quality), and by the identity of the decomposer organisms (due to differences in stoichiometric/metabolic constraints). Wickings et al. (2012) reported that both the litter identity (in the form of different litter types) and the decomposer identity (in the form of different soils with contrasted management) imposed a control on the organic matter quality after 80–95% mass loss. This indicates that the initial litter and the decomposer identity hypotheses are not mutually exclusive, and may both determine organic matter quality. Yet, the relative contribution of litter versus decomposer identity have not been studied, to our knowledge. Here, we propose quantifying the relative importance of these drivers through variance partitioning to clarify this aspect.
3) *Microbial versus faunal control.* The consequences of microbial activity on organic matter quality changes have received substantial attention (Moore et al. 2011, Wickings et al. 2012, Ball et al. 2022), but consequences of faunal activity, and detritivore activity in particular, remain mostly unexplored. Large quantities of litter transit through detritivores that feed on plant litter and return the majority to the soil in the form of faeces, which are then further decomposed by microorganisms. A recent study suggests that detritivore conversion of litter into faeces generally homogenises organic matter quality (Joly et al. 2020). However, the change in variability (see point 1 above) and the relative importance of litter identity versus detritivore identity (see point 2 above) on organic matter quality following detritivore conversion of litter into faeces remains unquantified. Moreover, it is unknown if this faunal-driven convergence is followed by a lesser, similar or higher microbial-driven convergence, when microorganisms decompose animal faeces, compared to when they decompose intact litter. It is thus unclear if convergence is dependent on the number of trophic levels using the organic matter as a resource.

To fill these knowledge gaps, we used the data from the aforementioned study (Joly et al. 2020), which investigated the consequences of litter conversion into detritivore faeces on organic matter quality and decomposition for litter of six tree species, following passage through guts of six distinct detritivore species, including millipedes, isopods and snails.

We reanalysed the data to quantify the changes in absolute and relative variability, to evaluate the relative importance of litter identity versus detritivore identity on faeces quality, and to examine how faunal-induced changes in organic matter quality affected the further microbial-induced changes (see point 3 above) with a focus on C:N ratio as a litter quality parameter (Fig. 1). We hypothesize that 1) detritivore conversion of litter into faeces leads to an overall convergence of organic matter quality variability, that 2) the remaining variability is driven both by litter identity and detritivore identity, and that 3) the microbial convergence is lower when decomposing detritivore faeces that have already undergone convergence, than when decomposing intact leaf litter.

Methods

Experimental design

The data that we analyse here was collected as part a soil fauna faeces experiment (Joly et al. 2020) which consisted in the collection of 36 types of faecal pellets, resulting from six temperate detritivore species feeding on leaf litter from six temperate tree species, separately. All faeces and intact leaf litter as control were analysed for physicochemical characteristics and decomposed microbially for six months on top of soil in microcosms to determine carbon and nitrogen cycling rates. The initial paper analysed the changes in absolute values of physicochemical characteristics and carbon and nitrogen cycling rates following litter conversion into detritivores faeces (Joly et al. 2020), with no evaluation of the changes in variability. Here, we analyse the changes in the variability of organic matter quality following litter conversion into faeces, and following further microbial decomposition, allowing us to test a different set of hypotheses.

In brief, we collected six detritivore species in the Scottish Lowlands in May–June 2018, including three millipede species (*Glomeris marginata*, *Ommatoiulus sabulosus*, *Tachypodoiulus niger*), two woodlouse species (*Armadillidium vulgare*, *Porcellio scaber*) and one snail species (*Cepaea nemoralis*). In parallel, we collected decomposing leaf litter from six tree species (*Acer pseudoplatanus*, *Aescusulus hippocastanum*, *Corylus avellana*, *Fagus sylvatica*, *Quercus robur*, *Tilia platyphyllos*). These detritivore and tree species were selected as they are common and abundant throughout Europe and constitute large phylogenetic and functional gradients: detritivore species vary in their metabolic rates (consumption rates, assimilation efficiency (David 2014) and litter of the selected tree species vary in physicochemical characteristics which control litter decomposition. We deliberately selected decomposing litter for improved realism as detritivores prefer feeding on decomposed rather than fresh litter (David and Gillon 2002). We paired, in plastic boxes, litter from each species with each animal species, separately, to obtain faeces from each combination of litter and detritivore species and prepared control treatments without detritivores to produce intact litter under identical conditions, for a total of 42 treatment combinations (6 litter species × (6 detritivore species + 1 control without detritivores)). These plastic boxes (30 × 22 × 5.5 cm) were filled with ca 30 g of air-dry leaf litter and ca 50 individuals from each detritivore species separately or no

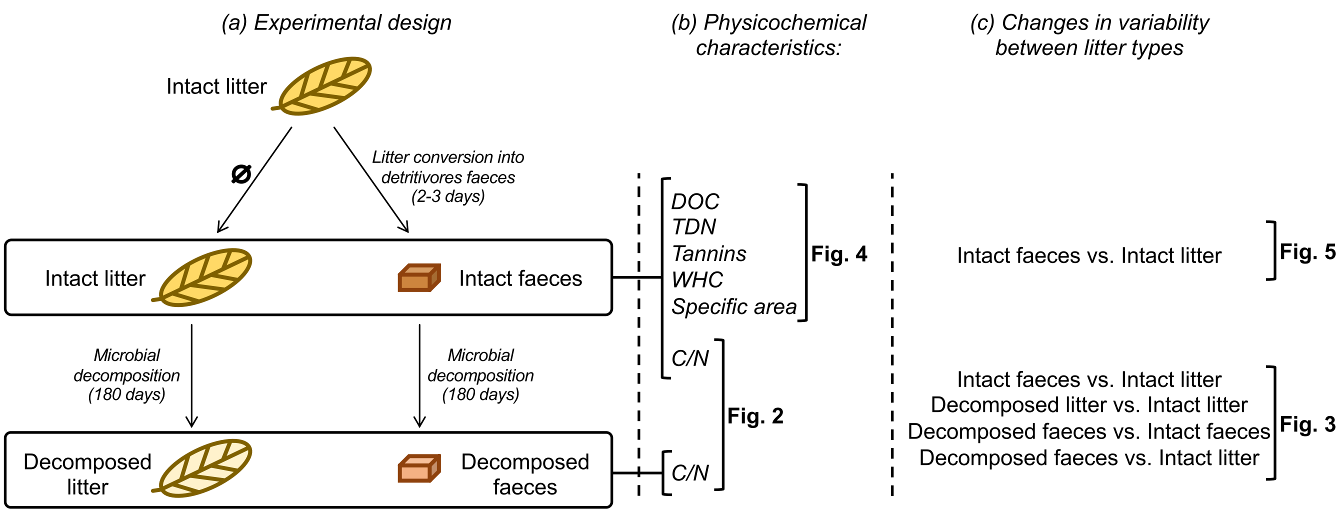

Figure 1. (a) Experimental design tracking changes in plant litter physicochemical parameters following litter conversion into detritivore faeces, and following microbial decomposition of intact litter or detritivore faeces, done for litter of six tree species, and following litter conversion in faeces by six detritivores species. We calculated the variability in physicochemical parameters amongst the six different litter species, by measuring (b) six physicochemical parameters on intact litter and detritivore faeces, and by measuring the C/N ratio as well on the microbially decomposed litter and faeces. We only measured the C/N ratio on the microbially decomposed litter and faeces due to the limited amount of material left after decomposition. We then determined how the variability in physicochemical parameters amongst the six different litter types changed throughout these steps by comparing (c) the variability in all parameters between intact faeces and intact litter, and the variability in C/N ratio between decomposed litter and intact litter, decomposed faeces and intact faeces, and between decomposed faeces and intact faeces.

detritivore for the intact litter treatment. Substrates (intact litter or faeces) were collected from the boxes twice a week for four weeks to produce sufficient quantities for physicochemical analyses and incubation. All collected substrates were dried at 30°C upon collection. As detritivores feed on leaf lamina and leave veins uneaten, we cut out veins from intact leaf litter. See Joly et al. (2020) for further details on substrate collection.

Effect of detritivore conversion of litter into faeces on organic matter quality

To evaluate the effect of detritivore conversion of litter into faeces on physicochemical variability among litter species, we measured the quality of faeces and intact litter on all 42 substrates (6 litter species + 36 faeces types) by measuring the carbon to nitrogen ratio (C:N), dissolved organic carbon (DOC) and total dissolved nitrogen (TDN), total tannins concentrations, water-holding capacity (WHC) and specific area (surface area per unit of mass) measured at the scale of the faecal pellets and faecal particles constituting the pellets. All measurements were done on three subsamples per substrate, using standard analytical procedures detailed in Joly et al. (2020).

Cascading effect of faunal-driven changes on microbially-driven changes

To evaluate the cascading effect of detritivore conversion of litter into faeces on changes in C:N ratio variability following microbial decomposition, we incubated all 42 substrates in microcosms under controlled conditions for six months. Microcosms consisted in 250 ml plastic containers filled with 90 g of air-dry soil from a temperate grassland (thereby avoiding any potential home-field advantage). We added ca 120 mg of substrate within a small PVC tube (30 mm diameter × 30 mm height) closed in the bottom with a 100-µm, open on top, and placed the tube on top of the soil within the microcosm. We prepared five replicates per substrate for a total of 210 microcosms (42 substrates × 5 replicates). Microcosms were watered at 70% soil WHC, incubated in a controlled environment chamber at 22°C and 70% relative humidity with replicates on separate shelves according to a complete randomized block design, and watered weekly so as to reach 70% of soil WHC. At the end of the six-month incubation, we collected the remaining decomposed substrates, dried them at 30°C for 48 h, ground them with a ball mill and measured their C and N concentrations with a CHN elemental analyser. See Joly et al. (2020) for more details on substrate incubation and decomposition rates.

Data analyses

We quantified the absolute and relative variability in organic matter quality by calculating the standard deviations and variation coefficients, respectively. The absolute variability was quantified with the standard deviation (SD) calculated according to the following equation: $SD = \sqrt{\frac{\Sigma\left(X - \bar{X}\right)^2}{N}}$ where X is a given value of one organic matter quality parameter of one plant species, $\bar{X}$ is the mean value across plant species and N the number of plant species. For the relative variability, we used the coefficient of variation (cv) calculated according ot the following equation: $cv = \frac{SD}{\bar{X}}$. By dividing the absolute variability by the mean value, the variation coefficient corrects for difference in absolute values and thus strictly reflects the relative variability. We measured these two parameters on all physicochemical characteristics, amongst substrates derived from the six litter species (i.e. amongst the six intact litter species, amongst the six faeces types resulting from each detritivore feeding on the six litter species, amongst the six microbially-decomposed litter species and amongst the six microbially-decomposed faeces types resulting from each detritivore feeding on the six litter species). For intact litter and fresh faeces, this was done for all measured physicochemical characteristics. For microbially-decomposed substrates (faeces and litter), this was done for the C/N ratio as the only measured characteristic.

We quantified changes in the absolute and relative variability in organic matter quality by calculating the ratio of standard deviations, and ratio of variation coefficients, respectively, between faeces of each detritivore species and intact litter, for each detritivore species and all physicochemical characteristics. To compare the changes in variability following microbial decomposition of intact litter or faeces, we calculated these ratios between microbially-decomposed litter and intact litter, fresh faeces and intact litter, microbially-decomposed faeces and fresh faeces, and between microbially-decomposed faeces and intact litter. A ratio lower than one indicates a convergence while a ratio higher than one indicates a divergence. We identified significant convergence or divergence by testing if the standard deviation or variation coefficient ratios significantly differed from one across detritivore species, using two-sided one-sample T-tests. We identified differences between ratios using one-way ANOVAs followed by Tukey HSD tests. To test if ratios between fresh faeces and intact litter significantly differed from the equivalent ratios between microbially-decomposed litter and intact litter (a single value), we used one-sample T-tests. Similarly, we used one-sample T-tests to test if ratios between microbially-decomposed faeces and intact faeces significantly differed from the equivalent ratios between microbially-decomposed litter and intact litter.

We determined the relative importance of organic matter identity (litter species) and decomposer identity (animal species) on organic matter quality (faeces traits) following detritivore conversion of litter into faeces (all physicochemical characteristics), and following further microbial decomposition of faeces (C/N ratio), using two-ways ANOVAs. We then calculated the variance associated with each term (litter species; detritivore species; interaction) by dividing the sum of squares by the total sum of squares, indicating the relative importance of litter identity, decomposer identity and their interactions on faeces quality.

We checked all data for normal distribution and homoscedasticity of residuals. We used R ver. 4.1.0 (<www.r-project.org>) for all data analyses.

Results

Changes in C/N ratio variability throughout decomposition

The variability in C/N ratio between the six litter species decreased following 180 days of microbial decomposition (Fig. 2) with relative and absolute reduction of variability by 28.5% and 34.5% on average (Fig. 3). Similarly, the variability in C/N ratio between the six litter species consistently decreased following litter conversion into detritivore faeces, for all detritivore species (Fig. 2), leading to significant relative and absolute convergence, with significant reductions of relative and absolute variability by 47.6% ($p < 0.001$) and 55.0% ($p < 0.001$) on average (Fig. 3), respectively. These fauna-driven changes in C/N variability were significantly stronger than microbial-driven changes, both in relative ($p < 0.05$) and absolute terms ($p < 0.05$). Interestingly, the subsequent microbial decomposition of faeces led to further relative and absolute reductions in variability by 19.3% ($p < 0.05$) and 32.3% ($p < 0.01$) (Fig. 3), and these reductions were not significantly different from the relative ($p = 0.26$) and absolute ($p = 0.76$) reductions observed following microbial decomposition of intact litter. Overall, the litter conversion into detritivore faeces and the subsequent microbial decomposition of the faeces reduced the variability in C/N ratio (Fig. 2), with reduction in relative and absolute variability by 57.5% ($p < 0.001$) and 69.3% ($p < 0.001$), respectively (Fig. 3a, b).

Detritivore-driven changes in organic matter quality variability

In addition to changes in C/N ratio, the conversion of litter into detritivore faeces significantly reduced the variability in most other chemical characteristics (Fig. 4a–c, 5). The relative and absolute variability in dissolved organic carbon concentrations both increased, by 18.5% ($p < 0.05$) and 57.5% ($p < 0.01$) respectively. For dissolved organic nitrogen, the relative variability reduced by 36.8% ($p < 0.001$) while the absolute variability did not decrease significantly ($p = 0.23$). For tannins, both relative and absolute variability decreased significantly, with reductions by 61.9% ($p < 0.001$) and 81.3% ($p < 0.001$) respectively.

The conversion of litter into detritivore faeces also largely reduced the variability in physical characteristics, also with some exceptions (Fig. 4d–e, 5). The relative and absolute variability in water-holding capacity reduced by 48.1% ($p < 0.01$) and 52.0% ($p < 0.01$) respectively. When comparing the variability in specific area between litter and faecal pellets, we observed declines in relative and absolute variability of 62.9% ($p < 0.001$) and 87.2% ($p < 0.001$) respectively. However, when comparing the variability in specific area between litter and faecal particles, we observed a reduction by 38.7% ($p < 0.001$) for the relative variability, and an increase by 92.2% ($p < 0.001$) for the absolute variability.

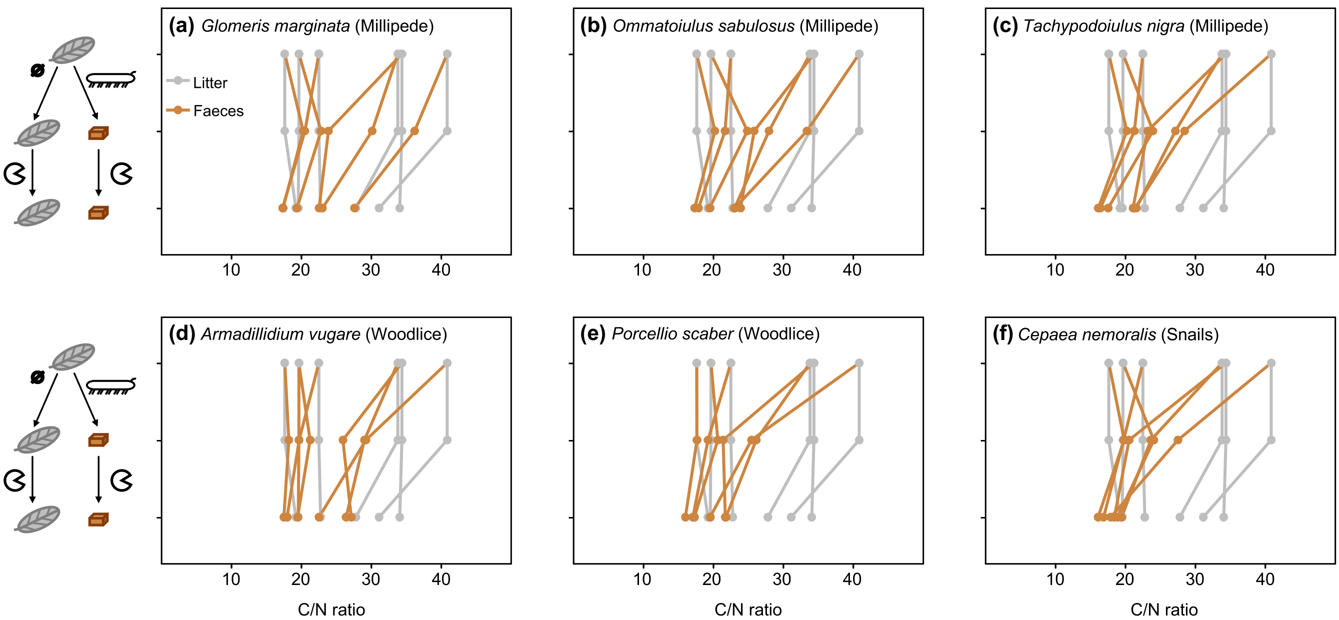

Figure 2. Visual representation of the changes in C:N ratio value distribution, and thus of the variability amongst litter species, from intact litter (top) to detritivore faeces (middle) to microbially-decomposed litter or faeces (bottom). Each panel displays changes by a given detritivore species. Each point represents the average value ($n = 5$) of replicate measures for each litter (intact litter), or each litter × animal combination (faeces).

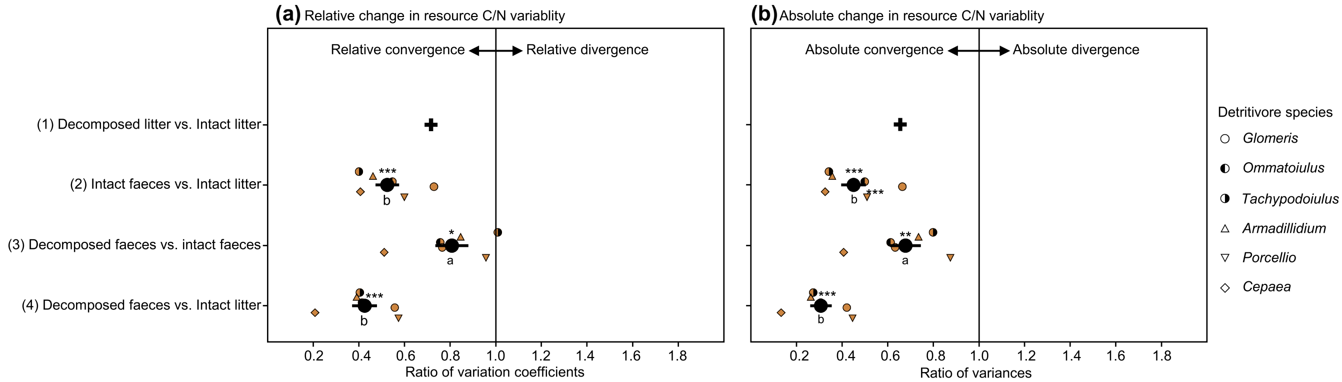

Figure 3. (a) Relative and (b) absolute changes in C/N variability, following (1) microbial decomposition of intact litter, (2) conversion of litter into faeces, (3) microbial decomposition of faeces and (4) conversion of litter into faeces followed by microbial decomposition of faeces, quantified by ratios of (a) variation coefficients and (b) standard deviations, for each animal species. Black crosses represent the average ratios following microbial decomposition of intact litter, while black dots represent the average ratio across animal species (mean ± SE). Asterisks indicate ratios significantly different from 1 (n.s. non-significant; *p < 0.05; **p < 0.01; ***p < 0.001). Letters indicate differences amongst paths 2–4 (Tukey HSD tests).

Drivers of organic matter quality variability

The modification in variability of physicochemical characteristics between litter species conversion of the six different litter species into detritivore faeces appears to be driven by litter identity, detritivore identity and their interaction (Fig. 6). The relative importance of these drivers on faeces quality varied depending on which physicochemical characteristic is considered. For physical characteristics such as specific area, either measured at the scale of faecal pellets (Fig. 6a) or at the scale of faecal particles (Fig. 6b), or water-holding capacity (Fig. 6b), litter species only played a limited role on faeces quality, explaining 19.3–24.4% of the variance. Meanwhile, detritivore species, and the interaction between detritivore species and litter species explained most of the variance. In turn, apart from tannin contents (Fig. 6d), chemical characteristics such as DOC (Fig. 6e), TDN (Fig. 6f) and C/N ratio (Fig. 6g) were predominantly driven by the identity of the litter species from which the faeces were derived, which explained 58.6% (TDN) to 85.5% (DOC) of the variance, while the identity of the detritivore species producing the faeces and its interaction with litter species explained 15–40% of the variance. Notably, the part of the variance in faeces C/N ratio explained by litter species decreased from 75 to 50%

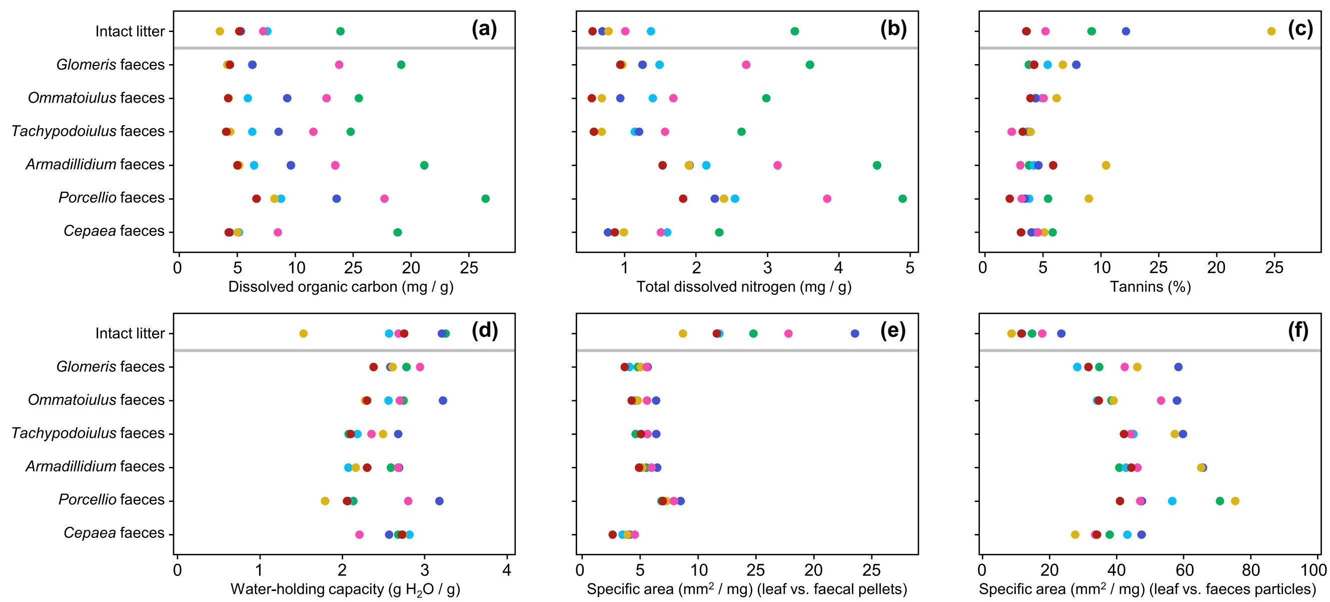

Figure 4. Visual representation of the changes in organic matter quality parameter value distribution, and thus of the of the variability amongst litter species, from intact (top section) and detritivore faeces (bottom section) of each animal species, including (a) dissolved organic carbon, (b) total dissolved nitrogen concentrations, (c) tannin content, (d) water-holding capacity, (e) specific area (litter versus faecal particles), (f) specific area (leaf versus faecal pellets). Each point represents the average value (n = 3) of replicate measures for each litter (intact litter), or each litter × animal combination (faeces).

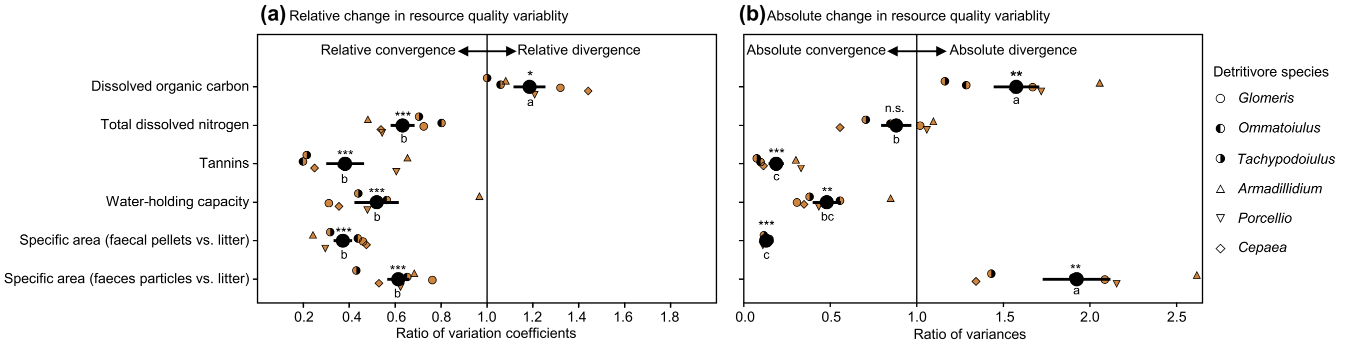

Figure 5. (a) Relative and (b) absolute changes in organic matter quality variability following litter conversion into detritivore faeces, quantified by ratios of faeces to litter trait (a) variation coefficients and (b) standard deviations, for each animal species. Thick black dots represent the average ratio across animal species (mean ± SE, n = 6). A ratio below one indicates a convergence, while a ratio above one indicates a divergence. Asterisks indicate ratios significantly different from 1 (n.s. non-significant; *p < 0.05; **p < 0.01; ***p < 0.001). Letters indicate differences amongst organic matter quality parameters (Tukey HSD tests).

following microbial decomposition, with the cumulative relative importance of detritivore species, and the interactions between detritivore species and litter species, increasing from 23.5 to 36.6% (Fig. 6h).

Discussion

The view that differences in organic matter quality amongst different litter types converge throughout decomposition is a central paradigm in decomposition ecology (Fierer et al. 2009), but previous studies did not assess organic matter variability changes quantitatively, and there is so far a lack of focus on different decomposer organisms to support this view. Focussing on the C/N ratio (a common litter characteristic and predictor of decomposition) and on its absolute and relative variability across plant litter from different tree species, we found clear evidence that 1) the microbial degradation of the litter, and 2) the detritivore conversion of the litter into faeces by diverse detritivores as different as millipedes or snails, both reduced the C/N variability in relative and absolute terms, albeit to varying degrees (Fig. 3; see level 1 and 2). While this is in line with our first hypothesis, this finding conflicts with the recent challenge of the convergence paradigm (Wickings et al. 2012). Yet, without variability metrics presented in this and other previous studies, it is difficult to compare findings. Here, regardless of the metric used, our findings suggests that decomposer organisms as distinct as microorganisms and detritivores, using litter as a resource differently, impose similar trajectories to organic matter quality, in line with the assumption underlying the convergence paradigm (McGill 2007, Fierer et al. 2009). This could be

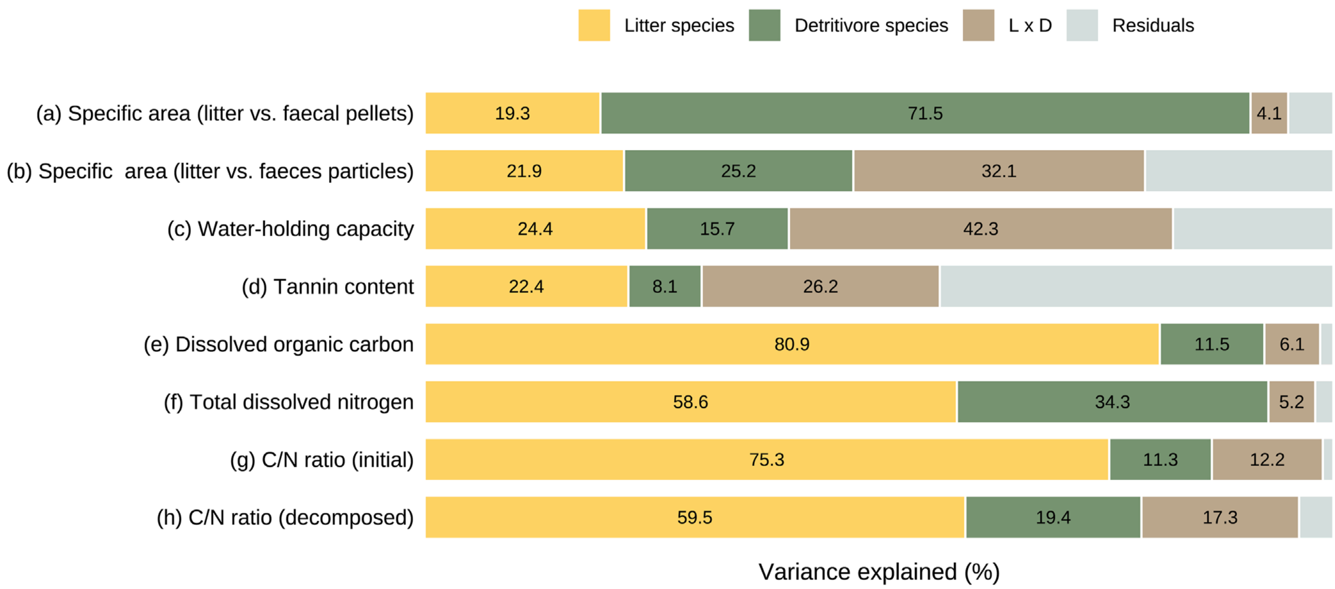

Figure 6. Relative importance of litter identity (litter species), decomposer identity (detritivore species) and their interaction (L × D) on the variability in organic matter quality following detritivore conversion of litter into faeces (a–g), and following microbial decomposition of faeces (h).

due to similar stoichiometric constraints or metabolic abilities shared between soil microorganisms and detritivores, or between soil microorganisms and microorganisms living in detritivore guts. Overall, the similar response of organic matter quality variability to microbial- versus faunal-decomposition is noteworthy, and future studies should investigate whether this similar convergence amongst decomposer pathways also applies to other organic matter quality parameters that could not be measured here for lack of remaining material.

Interestingly, though, while both detritivore and microbial activities led to a convergence of the C/N ratio, it is important to note the detritivore conversion of litter into faeces, which typically takes place over a few days, led to a stronger convergence than did 180 days of microbial degradation (Fig. 3; compare level 2 to level 1). A potential explanation for this may be related to the proportion of the resource used by microorganisms versus detritivores. In the 180 days of microbial degradation, the litter lost on average 23.8% of its initial C, while detritivores can assimilate higher proportion of the ingested litter (David 2014, Coulis et al. 2015). In fact, differences in assimilation efficiencies between detritivore species may explain the varying levels of convergence observed for the different species included in the study. These varying levels of convergence could also be due to differences in the parts ingested by the detritivore, differences in the gut microbiome community composition with varying metabolic abilities, or stoichiometric constraints. Regardless of the mechanisms underlying the differences amongst detritivores species, and between detritivores and microorganisms, our results clearly indicate that detritivore conversion of litter into faeces leads to a stronger and much faster convergence of organic matter quality than microbial decomposition.

What is more, we found that microbe- and fauna-driven convergence of the C/N ratio were additive, with a comparable level of convergence following microbial decomposition of intact litter and following microbial decomposition of detritivore faeces (Fig. 3; compare level 3 to level 1). This suggests that potential stoichiometric constraints that lead to this microbial convergence of C/N ratio amongst contrasting resources are not dependent on values of C/N ratio and are largely conserved, regardless of the C/N level of the organic matter. This could mean that the number of trophic levels using litter and its transformed forms as a resource determines the level of convergence, and that ultimately, the complexity of soil food webs determines the fate of organic matter. Evaluating how convergence is affected by further use of organic matter by other decomposers (e.g. soil animals feeding on detritivore faeces) would allow testing this hypothesis. We encourage the further determination of how organic matter quality, beyond C/N ratio, changes during its passage through the soil food web, by focussing on the changes in the form of organic matter (detritivore faeces; leachates; microbial necromass), rather than on remaining undecomposed litter material, to disentangle the changes in organic matter quality and their effect on SOM formation.

Our results provide some insights into the role of organic matter form by documenting changes in other physicochemical characteristics following litter conversion into detritivore faeces. We focused on this step for these characteristics as the remaining material following microbial decomposition was not sufficient for the determination of quality parameters other than the C/N ratio presented above. Our results indicate that detritivores as different as millipede and snails induce a strong reduction in the variability of most physico-chemical characteristics between different litter species. With strong convergence in tannin concentration, water-holding capacity, specific area, and to a lesser extent also dissolved total nitrogen, our results support the general convergence of litter physico-chemical characteristics for a large diversity of detritivore species. Strikingly, such reduction in characteristics can occur within a few days during which litter is ingested and returned to the soil as faeces. Given the strong control of physicochemical characteristics on SOM formation, detritivore activity may importantly affect the reduction in the variability of the decomposing organic matter, and therefore the characteristics of the resulting SOM. However, we also report a divergence with an increase in the variability in DOC concentrations following litter conversion into faeces, both in relative and absolute terms. This divergence has potentially far-reaching consequences, as leachates can be readily mineral-stabilised, through incorporation into microbial biomass, and thus contribute to the formation of stable SOM (Sokol and Bradford 2019). Detritivore-driven divergence of DOC concentrations could thus exacerbate differences in litter DOC concentrations amongst species and their contribution to stable SOM formation.

Notably, we observed conflicting results on the changes in variability for the total dissolved nitrogen and specific area measured at the scale of faecal particles, depending on whether we used the relative or absolute variability, which lead to both relative convergence and absolute divergence (Fig. 5). While both metrics seemed to be in broad agreement for other characteristics, either showing a divergence (DOC concentrations) or convergence (all other characteristics), the contrasted outcomes for TDN concentrations and specific area highlight the importance of defining organic matter variability and the limits of past reports. One of the main obstacles to settling the convergence versus divergence debate lies in the lack of clearly defined metrics to quantify changes in organic matter variability. To date, most studies used changes in the range of organic matter characteristics across studied species throughout decomposition as evidence for convergence or divergence or organic matter quality (Wickings et al. 2012). However, this metric only captures the variability in organic matter quality amongst the litter species at each end of the gradient. Reporting the change in standard deviation of organic matter quality between studied species rather than the absolute range provides a better proxy of variability. Yet, both the range and the standard deviation are sensitive to the magnitude of the values, which can limit their use as proxies of variability. If all values of an organic matter quality parameter increase by the same percentage throughout decomposition, then the range and standard deviation would also increase, but this should not necessarily be considered as a divergence, as in turn, the coefficient of variation (standard deviation corrected by the mean) could stay the same or even decrease. This is the case in our study with an increase in specific area following litter conversion into faecal particles (Fig. 4f), which leads to a divergence when considering the absolute variability, but a convergence when considering the relative variability (Fig. 5). This may be even more important when reporting parameters that are expressed as relative abundance (e.g. % cellulose and lignin), as any decrease in one parameter (leading to a decrease in absolute variability) inevitably leads to an increase in the values of the other parameters (leading to an increase in absolute variability). This may explain why Wickings et al. (2012) observed a divergence of litter chemistry based on py-GCMS spectra. To avoid these pitfalls, we advocate for the use of ratios of relative variability between different stages of decomposition to determine convergence and divergence.

The partitioning of variability in faeces quality parameters revealed that both initial litter identity and detritivore identity explained the variability in faeces physicochemical characteristics, albeit to varying degrees. Interestingly, the physical parameters of faeces were predominantly explained by the detritivore identity and its interactions with litter identity. With 71.5% of the variability in faeces specific area explained by the detritivore identity, it appears that the shape and size of detritivore faeces are species-specific and little affected by litter identity. This could be due to differences in biomechanical aspects amongst detritivore species, such as the organs used for feeding (mandibles for arthropods versus radula for snails) that may dictate the size and shape of ingested fragments, or the shape and size of the anal part that may dictate the physical form of faecal pellets. Chemical parameters such as C/N ratio or concentrations of dissolved organic carbon and nitrogen in turn were largely explained by the litter identity, but detritivore identity still explained a non-negligible part of the variance, indicating the decomposer community plays a key role in determining the organic matter quality throughout decomposition.

In summary, our study provides strong evidence for the gradual convergence of the physicochemical characteristics of plant litter as it is processed in soil food webs. Our results show that detritivores, by transforming plant litter into faeces within a few days, induce a rapid and important convergence of multiple physicochemical characteristics. Importantly, the convergence induced by this detritivore pathway does not replace the convergence induced by the microbial pathway, as microbial degradation induces similar convergence when decomposing either intact litter or detritivore faeces. While decomposition studies typically focus on the control of initial litter quality on litter decay (Aerts 1997, Cornwell et al. 2008, Zhang et al. 2008, Makkonen et al. 2012), our results show that the variability in initial litter quality amongst litter type can rapidly decrease following detritivore processing, which potentially limits the control of initial litter quality on further decomposition. We thus advocate for more reports of litter quality throughout decomposition, and for the report of changes in relative variability (e.g. ratios of variation coefficients) as we do here. This would facilitate comparisons amongst studies and provide a common framework for the study of the fate of organic matter quality throughout decomposition – an aspect of decomposition that remains poorly documented despite its importance for SOM formation.

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Author contributions

François-Xavier Joly: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **Sylvain Coq**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Jens-Arne Subke**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the University of Stirling's online data repository (<http://hdl.handle.net/11667/161>).

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