



Patterns of decomposition rates in central European forests differ among carrion, leaf litter and deadwood

Marit L. Hertlein^{a,*}, Philip S. Barton^b, Christian Ammer^c, Matthias-Claudio Loretto^d, Peter Schall^c, Simon Thorn^{e,f,g}, Sebastian Seibold^a

^a TUD Dresden University of Technology, Forest Zoology, Tharandt 01737, Germany

^b School of Life and Environmental Sciences, Deakin University, Geelong Warrnambool Campus, Victoria 3216, Australia

^c Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Göttingen 37077, Germany

^d Research Institute of Wildlife Ecology, Department of Interdisciplinary Life Sciences, University of Veterinary Medicine Vienna, Vienna 1160, Austria

^e Department of Biology, Philipps Universität Marburg, Marburg 35043, Germany

^f Hessian Agency for Nature Conservation, Environment and Geology, Biodiversity Center, Giessen 35394, Germany

^g Czech Academy of Sciences, Biology Centre, Institute of Entomology, České Budějovice 37005, Czech Republic

ARTICLE INFO

Keywords:

Necromass
Coarse woody debris
Forest gap
Canopy cover
Arthropods
Decomposition

ABSTRACT

Decomposition of dead organic matter is essential for ecosystem functioning and nutrient cycling, but carrion, leaf litter, and deadwood vary in their physicochemical characteristics, associated decomposer communities, and consequently in the rates at which they are decomposed. Despite being well studied separately, how carrion, leaf litter, and deadwood decompose under similar conditions is less well known. We conducted an experiment to quantify the effects of arthropods, canopy openness, and forest-management intensity (ForMI) on decomposition rates of carrion, leaf litter, and deadwood in temperate forests. We found that carrion decomposition was up to 90 times faster than decomposition rates of leaf litter and deadwood, which decomposed at similar rates. The presence of arthropods accelerated the decomposition of carrion by 2.8 times relative to when they were absent, highlighting how arthropods are an important driver of carrion decomposition. Canopy openness increased leaf litter decomposition when arthropods were present, and it mediated effects of arthropods: For leaf litter, arthropods accelerated decomposition in gaps but had a marginally decelerating effect in closed forest. For deadwood in canopy gaps, arthropods marginally decelerated decomposition. ForMI had no effects on any decomposition. Our findings demonstrate that arthropods and canopy openness interactively shape decomposition processes, but their relative effects differ between carrion, leaf litter, and deadwood. This highlights that patterns of decomposition rates in response to environmental drivers cannot be generalized across different types of dead organic matter. Increasing natural disturbances and harvesting leading to increased canopy openness will most likely affect the decomposition processes of leaf litter positively and deadwood negatively.

1. Introduction

Biomass is a major pool of global carbon (Bar-On et al., 2018; Xu et al., 2021). Yet only a small portion of plant biomass is thought to be consumed by herbivores, and the majority is recycled via decomposers and the brown food web as necromass, i.e., dead biomass (Gessner et al., 2010; Zou et al., 2016). The decomposition of necromass is therefore a significant source of global carbon flux (Benbow et al., 2019; Xu et al., 2021), but is likely underrepresented in ecosystem models due to challenges in quantifying processes and drivers for the large variety of

necromass types, such as soil microbes, carrion, root or leaf litter, or deadwood (Berg, 1984; Yoshitake et al., 2014; Barton et al., 2019; Wang et al., 2021a; Wijas et al., 2024). There are many studies that focus on the decomposition processes of specific types of necromass (Barton et al., 2013; Krishna and Mohan, 2017; Bauhus et al., 2018), but these studies use a range of methods and ecosystem contexts. This limits our ability to directly compare decomposition rates across different types of necromass or identify general drivers of decomposition. Necromass represents an important carbon stock in forest ecosystems (Thurner et al., 2014; Barbosa et al., 2017) and can be broadly categorized into

* Corresponding author.

E-mail address: marit.hertlein@tu-dresden.de (M.L. Hertlein).

Peer review under the responsibility of Editorial Office of Forest Ecosystems.

<https://doi.org/10.1016/j.fecs.2026.100468>

Received 21 January 2026; Received in revised form 23 March 2026; Accepted 8 April 2026

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autotrophic (plant-derived) and heterotrophic (fungi or animal-derived) forms. Examples of plant-derived necromass include deadwood and leaf litter, whereas animal-derived necromass is typically referred to as (invertebrate or vertebrate) carrion (Benbow et al., 2019). Compared to autotrophic biomass, carrion is present less frequently in ecosystems (Benbow et al., 2019), and its occurrence is patchy and often ephemeral and unpredictable (Butterworth et al., 2023). By contrast, leaf litter is more abundant and in temperate ecosystems spatially much more evenly distributed, while deadwood may also occur aggregated but has a high longevity (Barton et al., 2024). In terms of nutrient values, carrion is considered higher quality due to its lower C:N ratio (Benbow et al., 2019). This ratio increases in leaf litter necromass and is usually highest in deadwood, which contains more tissues that are resistant to decomposition and are more difficult and less rewarding for most organisms to digest. The decomposition rate of carrion is (during warmer months) driven mainly by arthropods, particularly Coleoptera and Diptera (Barton et al., 2013), and moderated by temperature and precipitation (Turner et al., 2017). Decomposition of leaf litter can be driven by environmental conditions (globally) and by leaf litter quality (locally), but the magnitude of both factors can vary and is dependent on the ecological context (Lavelle et al., 1993; Cornwell et al., 2008; Canessa et al., 2021). Environmental factors, especially temperature and soil moisture, regulate the metabolism of bacteria and fungi, followed by chemical composition (Krishna and Mohan, 2017). Deadwood decomposition is mainly driven by microclimate, and the most important decomposer groups are insects and fungi (Stokland et al., 2012; Harmon, 2021). The decomposition of different forms of necromass can range from a few days or weeks for carrion (DeVault and Rhodes, 2002; Schwegmann et al., 2023) to years and decades for deadwood (Shorohova and Kapitsa, 2014; Harmon, 2021; Edelmann et al., 2023). This gradient in necromass quality and resistance to decomposition, and the relative importance of different biota and environmental drivers provides a general framework to build predictions of necromass decomposition rates (Benbow et al., 2019). Based on this, decomposition rates are expected to be slower with decreasing resource quality and increasing resistance to decomposition from carrion to leaf litter to deadwood.

At the same time, the relative importance of arthropods for decomposition generally decreases and the importance of environmental drivers increases with decreasing resource quality (Benbow et al., 2019; von Hoermann et al., 2023). Note that the importance of arthropods can vary during the whole decomposition process and differ between ecosystems (Sánchez-Galindo et al., 2022), as e.g., termites enhance deadwood decomposition compared to ecosystems without termites (Ulyshen, 2016; Griffiths et al., 2019). Quantitative assessments of these predictions, however, are still lacking for a spectrum of necromass types within the same ecosystem, leaving a clear gap in our knowledge of relative rates of decomposition. These data are needed from a range of ecosystems and biomes to develop more complete energy and nutrient turnover models.

The decomposition process is continuous but passes through broad decay stages, with each stage also affected differently by arthropods and various abiotic factors (Payne, 1965; Berg, 2000; Mäkinen et al., 2006; Michaud et al., 2015; Purahong et al., 2016b). Decomposition rates are not constant in general and vary between habitats differing in environmental conditions, such as microclimate, vegetation cover, or composition. In forests, canopy cover is a major driver of microclimatic conditions as temperatures and vapor pressure deficit are, on average, higher and also more variable in gaps than under a closed canopy (Ritter et al., 2005; Thom et al., 2020). Gaps with open canopy additionally increase solar radiation (Wang et al., 2022). In addition, forest management alters tree species composition and other structural characteristics (Hämäläinen et al., 2014; Brockerhoff et al., 2017). These differences in environmental conditions related to canopy openness and forest management can cause differences in decomposer communities and alter decomposition rates (Aerts, 1997; Barton and Evans, 2017; von

Hoermann et al., 2020; Edelmann et al., 2022, 2023), but differences can diminish as decomposition processes (Castillo-Figueroa, 2025). Yet, our understanding of whether the effects of canopy openness and forest management are similar across necromass types remains unclear. Such better understanding is particularly relevant since climate-change induced increases in forest disturbances and changing forest management lead to increasing canopy openness in forests in many regions (Park et al., 2014; Senf et al., 2020).

Arthropods are a key driver of necromass decomposition, yet their contribution to decomposition differs between necromass types. For example, they are important for the decomposition of carrion (Englmeier et al., 2023) or leaf litter (Burtis et al., 2024), but for deadwood fungi play a more dominant role (Bani et al., 2018; Seibold et al., 2021). Not only is arthropod activity moderated by temperature and humidity (Sharanowski et al., 2008; Barton and Bump, 2019) but it can also be affected by forest structure, such as canopy openness. Microclimatic conditions can also shape arthropod community structure, which indirectly can also influence the decomposition process (Castillo-Figueroa and Castillo-Avila, 2025a). For deadwood, increasing forest-management intensity (ForMI) can positively affect the diversity of wood-decomposing insects (Edelmann et al., 2022), and also canopy openness affects community composition and diversity of saproxylic beetles (Seibold et al., 2016). Deadwood decomposition rates can thus differ between gaps and closed forest, related to arthropod activity, as shown for tropical forest (Griffiths et al., 2021). The effect of increased temperature (due to gaps) on the contribution of arthropods to leaf litter decomposition remains unclear, as heterogeneous results have been found (Ferreira and Canhoto, 2014; Figueroa et al., 2021). Arthropods are typically affected by canopy openness and forest management, but how this affects the relationship between the decomposer communities and decomposition rates remains poorly understood (Gessner et al., 2010; Barton and Evans, 2017; Junggebauer et al., 2024).

We investigated the effects of arthropods, canopy openness, and ForMI on decomposition rates of three necromass types: carrion, leaf litter, and deadwood. These necromass types represent a wide range of key characteristics of necromass and were used to test for generalities in patterns and drivers across necromass types. Standardized substrates to represent a commonly sized carcass (rat (*Rattus norvegicus*) carcasses) or dead plant material from the most common tree species in the study region (leaf litter and deadwood of European beech *Fagus sylvatica*) were exposed at paired plots representing a contrast in canopy cover (experimental gap vs. closed forest) along a gradient of ForMI in three regions in Germany. As the contribution of arthropods to decomposition differs per necromass type, we contrasted treatments that either allowed arthropods to access the necromass or restricted the access for arthropods to quantify the contribution along necromass types (Fig. 1). We tested the following predictions:

- 1) Decomposition rates differ between necromass types, with the fastest decomposition for carrion, intermediate for leaf litter, and slowest for deadwood because resource quality decreases across these forms of necromass.
- 2) The presence of arthropods positively affects decomposition rates of all necromass types, but their contribution to the decomposition process is relatively greater for carrion necromass.
- 3) Forest attributes, i.e., canopy gaps and ForMI, affect decomposition rates, but the direction and magnitude of these effects vary among necromass types with weaker effects for carrion than leaf litter and deadwood.
- 4) The interaction between canopy openness and the presence of arthropods enhances decomposition rates, whereas the direction of the interaction of ForMI and the presence of arthropods has a negative effect on the decomposition rates. The effect size is relatively greater for carrion necromass.

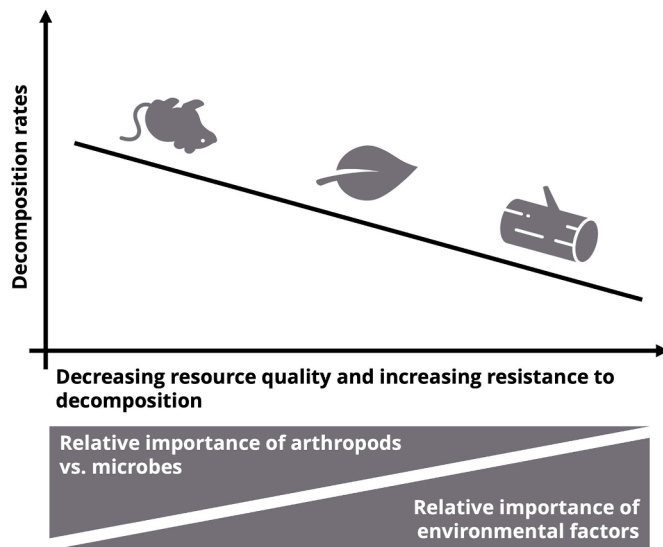


Fig. 1. Conceptual visualisation of decomposition rates decreasing with decreasing resource quality increasing resistance to decomposition among necromass types (carrión, leaf litter, and deadwood). With increasing resistance to decomposition, the relative importance of arthropods vs. microbes decreases whereas the relative importance of environmental factors increases. Icons from thenounproject.com, created by Vectorstall, Firman, and Muhammad Arifin respectively.

2. Methods

2.1. Study area

This study was embedded in the Biodiversity Exploratories Framework (www.biodiversity-exploratories.de, Fig. 2a) comprising three study regions located in different parts of Germany with different geology and climate characteristics: Schorfheide-Chorin in the northeast (geology: young glacial landscape, soil characteristics: sandy loam to pure sand with Dystric Cambisol as main soil type, mean annual temperature: 8–8.5 °C, elevation of 3–140 m a.s.l., precipitation:

500–600 mm), Hainich-Dün in central Germany (Calcareous bedrock, loam to clay, Eutric Cambisols, Luvisols, and Stagnosols, 6.5–8 °C, 280–550 m a.s.l., 500–800 mm) and Swabian Alb in the southwest of Germany (Calcareous bedrock with karst phenomena, rich in clay, Eutric Cambisols, and Leptosols, 6–7 °C, 460–860 m a.s.l., 700–1,000 mm) (Fischer et al., 2010).

In each region, plots cover a gradient of ForMI from extensively managed European beech forests to mixed stands to intensively managed conifer (Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*) stands. ForMI was quantified by a compound index calculated as the sum of the proportion of harvested tree volume, the proportion of tree species that are not part of the natural forest community, and the proportion of deadwood showing signs of saw cuts (Kahl and Bauhus, 2014). Data used for calculating ForMI were derived from a forest inventory conducted at each 1-ha plot in 2016 (Schall et al., 2018).

This study covered 26 paired plots (nine in Schorfheide and Hainich and eight in Swabian Alb), each including one plot with a closed canopy and one plot with a gap. Experimental gaps were installed in January–March 2020 to create a contrast in canopy openness. Before creating a gap, all trees were inventoried on an area of 0.5 ha (71 m × 71 m). (Staab et al., 2022). In this area, trees were felled within a circular area with a diameter of approximately 25–37 m (mean = 31.0 ± 3.2 m SD), depending on stand height. Trees were removed, and gap size varied between approximately 500 and 1,000 m². The distance between the plot with closed canopy and the gap at each site was at least 100 m while minimizing variation in topography and exposition (Staab et al., 2022). The canopy cover of both the plots with closed canopy and the gaps (no trees in the gap centre) was quantitatively determined using terrestrial laser scanning and differed significantly.

2.2. Decomposition experiment

2.2.1. Carrión

We used frozen dead rats (*R. norvegicus*, 350–450 g), bought from a pet food supplier (XCLUSIVE SNAKES, Reilingen, Germany) as small-sized standardized carrión. Before the installation of the experiment, the carrión was defrosted for 24 h. Two rats were deployed per plot, resulting in 104 rats in total. Each rat was placed on the ground on a 15 cm × 15 cm metal grid with a mesh size of 6.3 mm × 6.3 mm, to be

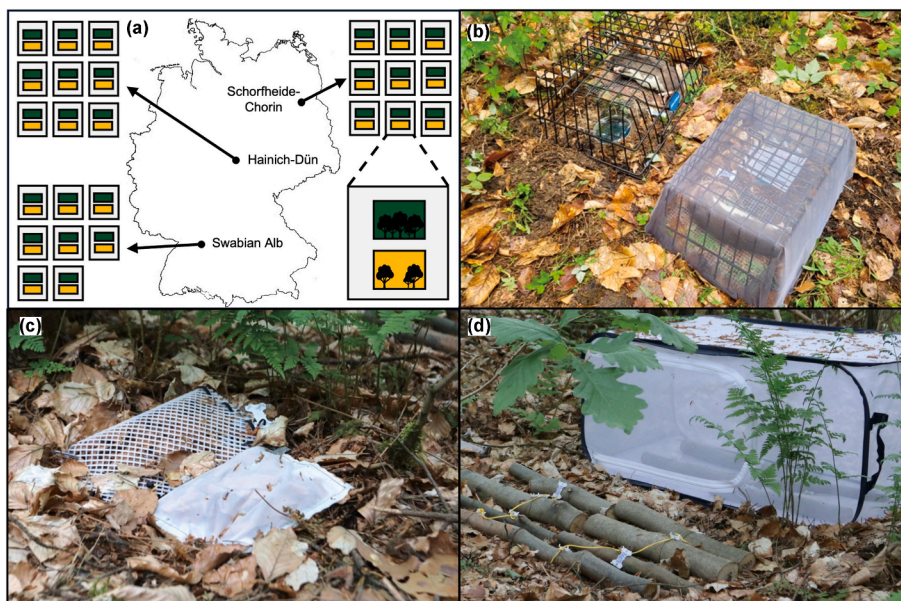


Fig. 2. (a) Overview sampling regions across Germany with research plots on a gradient of ForMI with each a forest plot with closed canopy and a forest gap with open canopy. Pictures of the experimental setup of different necromass types with arthropod exclusion setup: (b) carrión (rats) in cages (against vertebrate scavengers) and with additional fine mesh to exclude arthropods (right cage), (c) one pair of leaf litter bags with coarse mesh (left) and finer mesh to exclude arthropods (right), and (d) deadwood either for arthropods to access or in a cage to restrict arthropod access.

able to weigh the rat even at an advanced decomposition stage. A metal cage with 2.0 cm × 2.0 cm openings was put on top and secured tightly to the ground with tent pegs to secure the rat from vertebrate scavengers. In addition, one cage on each plot was covered with a fine nylon mesh (0.70 mm × 0.70 mm mesh size) to exclude arthropods from the decomposition process (Fig. 2b). The rats were weighed at the start of the treatment and six times during a six-week frame: on day 5 (due to access restrictions in Hainich on day 4 and 6), on day 9 (due to weather conditions partly on day 8 in Swabian Alb), on days 14, 21, 30 and 42 (day 41 due to logistic reasons in Schorfheide).

2.2.2. Leaf litter

Freshly fallen beech leaves without any visual damage were collected in leaf litter traps in one forest stand in autumn 2022 and dried at 65 °C until mass remained constant. Approximately 4.86 ± 1.12 g of dry leaves were filled into leaf litter bags (size: 20 cm × 10 cm, Fig. 2c) consisting of either a coarse plastic mesh (10 mm × 10 mm mesh size) allowing arthropods to enter, or into leaf litter bags with fine nylon fabric (0.07 mm × 0.07 mm mesh size) to exclude arthropods. Dry weight of leaf litter bags was measured. We deployed three pairs of leaf litter bags (each pair consisted of one coarse-meshed and one fine-meshed leaf litter bag) at each plot. In April 2023, leaf litter bags were placed on the forest floor and secured with tent pegs to the ground, removing moss or dense leaf litter layers to ensure soil contact. The three pairs were placed with a 1–1.5 m distance from each other in a triangle around the deadwood samples. Any abnormalities or special microsites were avoided. In September 2024, all leaf litter bags were collected, transported in separate plastic bags, and stored below 10 °C. Leaf litter bags were carefully cleaned from soil, moss, or any plant material that entered the bags during the exposure time without removing the original leaf litter. Afterward, leaves were dried at 65 °C for at least 72 h until constant weight and weighed.

2.2.3. Deadwood

Straight beech stems of young trees with a diameter between 2.0 and 8.0 cm and without any visual damage were cut in one forest stand in March 2023. All logs were weighed within 48 h after sawing and stored in a cold room until placed outside in early April 2023. Dry mass was estimated from a wood section cut from each log (Section S1). At each plot, four logs were placed on the forest floor, and four within a fine mesh cage (mesh size 0.5 mm × 0.5 mm, Fig. 2d). Moss or dense leaf litter layers were carefully removed to ensure contact with the forest floor. Logs were collected in July 2024 and transported in separate bags for each plot and treatment until further processing. They were dried at 105 °C for at least 96 h until constant weight to calculate the weight loss.

2.3. Statistical analyses

We used the exponential mass loss model in (Olson, 1963; Berg, 2000; Purahong et al., 2016b) with a daily time step. Here, the decomposition rate, k -rate, was calculated based on the exponential model $y_t = a_0 e^{-kt}$, with t being the exposure time of the decomposition in days, y_t the weight at time t , and a_0 the initial weight, to obtain comparable decomposition rates for all three necromass types. Leaf litter and deadwood were exposed for approximately 18 and 16 months, respectively. For carrion, the various measurements taken along the exposure time were used to calculate k . All statistical analyses were conducted in R (version 4.4.2, R Core Team, 2023).

To address the first hypothesis, we tested whether there was a difference in decomposition rates when arthropods were present for the three different necromass substrates. The model included the decomposition rate as dependent variable and necromass type (factorial variable with three levels: deadwood, leaf litter, and carrion) as predictor. A plot nested in a region was used as a random effect to account for the

spatially nested design. We used a linear mixed effect model (function *lmer* in package *lme4* (Bates et al., 2015) and function *cftest* in package *multcomp* (Hothorn et al., 2008)) and Tukey post-hoc test (function *glht* in package *multcomp*) for pairwise comparisons.

For hypotheses 2 to 4, we tested whether forest attributes (canopy and forest management) and arthropod exclusion treatment affected the decomposition rates. The model included decomposition rate as response, and canopy (factor with two levels: gap vs. closed forest), arthropod exclusion (factor with two levels: with arthropods vs. without arthropods), and ForMI (continuous, range: 0–3) as explanatory variables. In addition, the three regions (Schorfheide-Chorin, Hainich-Dün, and Swabian Alb) and plots nested within regions were added as a random factor in both models. To test for the interaction of forest attributes and arthropod exclusion without overfitting models, we run each model twice, first including an interaction between ForMI and arthropod exclusion and second, an interaction between canopy and arthropod exclusion. Since interactions with canopy were significant, we tested effects of arthropods on decomposition rates separately for gaps and closed forest (model code: $k \sim \text{ForMI} + \text{canopy} + \text{canopy}:\text{arthropod} + (1|\text{region}/\text{plot})$). For each substrate separately, we used a linear mixed effect model (functions *lmer*, *cftest* in package *multcomp*, and *confint* in package *stats*).

2.4. Data availability

Data are publicly available in the Biodiversity Exploratories Information System (<http://doi.org/10.17616/R32P9Q>). This work is based on data collected within the CaFoDec project (ID 32178, version 1 (Hertlein and Seibold, 2025); and forest structure (core) project (ID 24646, version 4; Schall et al., 2019) of the Biodiversity Exploratories Program (DFG Priority Program 1374), funded by DFG.

3. Results

The mean decomposition rate across gaps and closed canopy with arthropods present was $k = 0.090 \pm 0.0061$ SE ($n = 46$) for carrion, 0.0010 ± 0.0052 ($n = 150$) for leaf litter, and 0.0026 ± 0.0054 ($n = 121$) for deadwood. Note that in some cases, we measured a positive rate in leaf litter. Across all necromass types, we found that carrion decomposition rates per day were approximately 35 to 90 times faster than those of leaf litter (estimate = -0.0553 , z -value = -21.2 , $P < 0.001$) and deadwood (estimate = -0.0548 , z -value = -20.8 , $P < 0.001$). Decomposition rates of leaf litter and deadwood did not differ significantly from each other (estimate = -0.000506 , z -value = -0.272 , $P = 0.959$).

Linear mixed-effect models per necromass type indicated that canopy openness had no significant main effect on decomposition rates of any of the three necromass types. Yet, the significant and marginally significant interaction of canopy and arthropod exclusion for leaf litter and deadwood, respectively, indicates that canopy mediates the effect of arthropods on decomposition rates of these two necromass types (Table S1). Moreover, the significant interaction between canopy and the effect of arthropods indicates that for leaf litter, decomposition rates are higher in gaps than in closed forest, but only when arthropods were present (Fig. 3 and Table S1). ForMI had no significant effect on decomposition rates of any of the three substrates and also did not interact significantly with arthropod exclusion (Table S2).

Arthropods positively affected decomposition rates of carrion, similarly for gaps and closed forests (Figs. 3 and 4 and Table S3), accelerating decomposition rates by a factor of 2.8. For leaf litter, arthropods had a significantly positive effect in gaps (Figs. 3 and 4 and Table S3), but arthropods tended to decelerate leaf litter decomposition in closed forest ($p = 0.09$; Table S3). For deadwood, arthropods tended to have negative effects in gaps ($p = 0.06$, Table S3) and no significant effect in closed forest (Figs. 3 and 4 and Table S3).

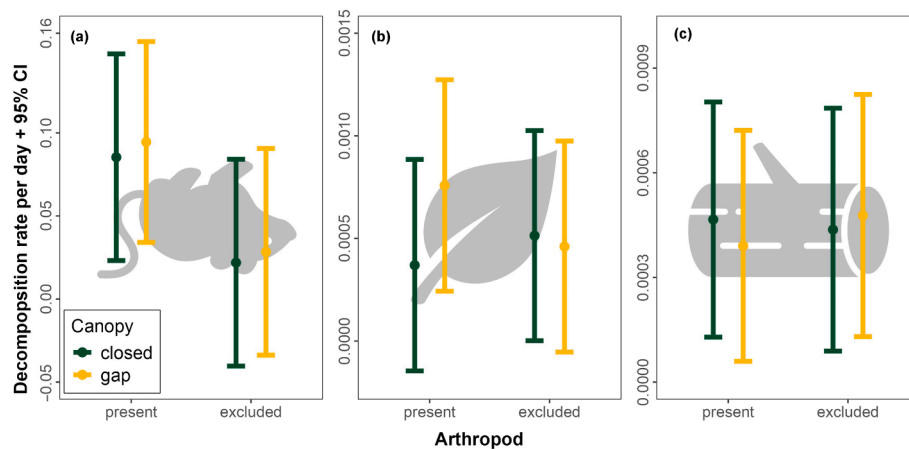


Fig. 3. Predicted decomposition rates (mean + 95% confidence intervals) of (a) carrion, (b) leaf litter, (c) deadwood for the two arthropod and canopy treatments based on separate linear mixed models for each necromass type. Model code: $k \sim \text{ForMI} + \text{canopy} + \text{canopy} \times \text{arthropod} + (1|\text{region/plot})$. Note: Y axes are on different scales. Icons from thenounproject.com, created by Vectorstall, Firman, and Muhammad Arifin respectively.

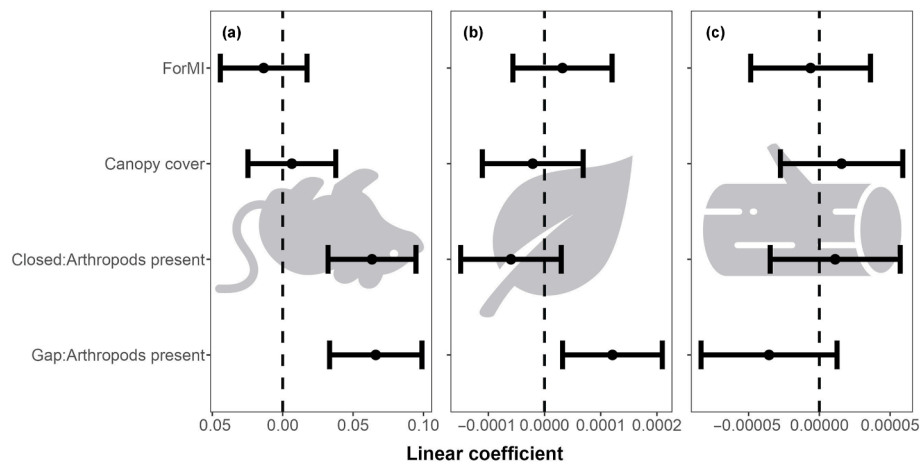


Fig. 4. Linear coefficients of the effects of ForMI, canopy openness (gap vs. closed) and the effect of arthropods on the decomposition rates of (a) carrion, (b) leaf litter, and (c) deadwood derived from linear mixed-effects models. Model code: $k \sim \text{ForMI} + \text{canopy} + \text{canopy}:\text{arthropod} + (1|\text{region/plot})$. Note that x axes are on different scales. Icons from thenounproject.com, created by Vectorstall, Firman, and Muhammad Arifin, respectively.

4. Discussion

To assess the generality of patterns and drivers of decomposition across different types of necromass, we studied the effects of canopy openness, ForMI, arthropod exclusion, and their interactions on decomposition rates of carrion, leaf litter, and deadwood. Carrion decomposition was up to 90 times faster than the decomposition of leaf litter or deadwood when arthropods had access. Canopy openness had no effects on carrion decomposition, but increased leaf litter decomposition when arthropods were present, and it mediated the effects of arthropods on leaf litter and deadwood decomposition. Arthropods accelerated carrion decomposition clearly and irrespective of canopy openness. For leaf litter and deadwood, arthropod effects were weaker and included accelerating and decelerating effects.

4.1. Decomposition rates differ between necromass types (hypothesis 1)

Carrion decomposes quickly within several weeks (Barton et al., 2013), whereas leaf litter and deadwood (depending on size, characteristics, and environment) need from months to decades (Shorohova and Kapitsa, 2014; Edelmann et al., 2023). These differences can be explained by higher nutrient and protein content and lower resistance to decomposition of carrion compared to the other two substrates (Benbow

et al., 2019). Our data support this general trend, as we found that carrion decomposed up to 90 times faster than leaf litter or deadwood. This highlights that carrion decomposition is a highly dynamic process and its characteristic of being an ephemeral resource patch (Butterworth et al., 2023). Decomposition rates of leaf litter and deadwood did not differ significantly, although we expected leaf litter to decompose faster. One reason could be that we only studied the initial phase of the decomposition process, and the slopes of decomposition rates are not distinguished in this phase, as deadwood decomposes faster in the beginning and rates slow down later (Bani et al., 2018). Moreover, beech leaf litter decomposes more slowly compared to leaf litter from some other tree species (Berger et al., 2015; Stuckenberg et al., 2025), whereas beech deadwood has comparatively high decomposition rates (Edelmann et al., 2023).

Moreover, in some cases, we measured an increase in the weight of leaf litter bags. Increasing weight is regularly observed in decomposition experiments for slowly decomposing necromass types, such as leaf litter and deadwood (Edelmann et al., 2022; Zeng et al., 2024). A potential ecological explanation for leaf litter bags with fine mesh is that the gain could be caused at first by fungal decomposers' growth, hence an increase in biomass, to decompose the leaf litter, and hence before mass loss can be observed (Voříšková and Baldrian, 2013). Secondly, the gain could be caused by stronger growth of microbial biomass in absence of

arthropods feeding on fungal biomass (Parkinson et al., 1979). Thirdly, we only used beech leaf litter; many studies, however, show that mixed leaf litter is decomposed faster (Steinwandter et al., 2019; Li et al., 2023). Nevertheless, by conducting an experiment studying decomposition across necromass rates simultaneously, a comparison that has rarely been addressed, we can show that necromass types decompose at different rates. We found a clear distinction between slower autotrophic (plant derived) and faster and very dynamic heterotrophic (fungal or animal derived) necromass types.

4.2. Arthropod contribution to decomposition (hypothesis 2)

Arthropods are important drivers for carrion decomposition (Payne, 1965; Kočárek, 2003; Barton et al., 2013; Pechal et al., 2014), and they can affect decomposition of leaf litter and deadwood, but their effects are variable and more pronounced in the tropics (Griffiths et al., 2021; Seibold et al., 2021; Zeng et al., 2024). However, some studies also found a rather minor effect of arthropods on the decomposition process (Sánchez-Galindo et al., 2022; Castillo-Figueroa and Castillo-Avila, 2025b). This is confirmed by our results, which showed that decomposition of carrion was 2.8 times faster when arthropods were present, but we did not find such a strong effect of arthropods on leaf litter or deadwood decomposition rates. Besides directly consuming the necromass, arthropods also indirectly influence the decomposition process by physically fragmenting necromass and making parts of the necromass available for smaller decomposers and microbes. In line with Pechal et al. (2014), we observed that without arthropods present, carrion remained longer in the bloated phase (Payne, 1965). Normally, carrion beetles, fly larvae, or vertebrate scavengers would open the carcass, leading to the active decay stage of the carcass. Remaining in the bloated phase results in slowing down the decomposition rates as flesh is not consumed by arthropods. Similarly, arthropods physically fragment leaf litter and deadwood (Ulyshen, 2016), resulting in a higher surface-to-volume ratio, which promotes microbial activity (Frouz, 2018). With this study, we underlined that arthropods are a major driver of decomposition rates of carrion, but many interactions or dependencies between arthropods and other decomposer groups of different necromass types are not fully understood.

4.3. Effects of canopy openness and ForMI on decomposition rates (hypothesis 3) and interaction with the contribution of arthropods (hypothesis 4)

Forest management shapes forests in species composition, understorey vegetation, and structural heterogeneity (Ehbrecht et al., 2017; Brockerhoff et al., 2017). Previous studies conducted at the same sites observed no or varying effects of forest management intensity on decomposer communities for carrion (von Hoermann et al., 2018, 2020), leaf litter (Purahong et al., 2016a; Pollierer et al., 2021), and deadwood (Blaser et al., 2013; Edelmann et al., 2022). In line with some of these studies, we did not find any effect of ForMI on decomposition rates among all necromass types. This indicates that either ForMI does not affect decomposer communities or decomposition rates, such as for carrion beetles (von Hoermann et al., 2018), or effects on decomposer communities like those found for deadwood-inhabiting beetles (Edelmann et al., 2022) do not translate into effects on decomposition rates. The latter case could be explained by different communities contributing similarly to the decomposition process, thus indicating functional redundancy (Mori et al., 2015). Overall, our results suggest that decomposition rates of carrion, leaf litter, and deadwood are not sensitive to the forest management that is practiced in the study region. For non-managed forests, it was found that degradation and fragmentation can affect decomposition rates of leaf litter (Moreno et al., 2014; Leal et al., 2024). Therefore, more research is needed to assess whether the same is true also for other necromass forms, such as large-diameter deadwood and large carrion, and for longer exposure time. Future

research should also try to link decomposition rates and decomposer communities in the same necromass objects more explicitly.

In gaps with open canopy, microclimatic temperatures are on average higher and moisture is lower (Thom et al., 2020). Warmer temperatures can promote arthropod activity and microbial growth (Griffiths et al., 2021) and thus higher decomposition rates (Ritter, 2005; Barton and Bump, 2019), given that microclimatic conditions are not too dry and hence unfavorable for microbial activity (Bani et al., 2018). We expected increased decomposition rates in gaps. Although carrion decomposition can be sensitive to climatic conditions (Englmeier et al., 2023), the differences in microclimatic conditions and other habitat characteristics between gaps and closed forest (Thom et al., 2020) did not affect carrion decomposition. This might be explained by the high dispersal ability of carrion-decomposing arthropods and their high efficiency in locating carrion (Barton and Bump, 2019). Consistent with our hypotheses, we did observe higher decomposition rates for leaf litter in gaps when arthropods were present, as indicated by the significant interaction between canopy and the arthropod treatment. This suggests that higher arthropod activity or abundance in gaps or different arthropod communities in gaps compared to closed forest (Seibold et al., 2016) can lead to faster leaf litter decomposition. Next to temperature and moisture, with an open canopy, more solar radiation reaches the forest floor (Ritter et al., 2005). Solar radiation can physically break down necromass (photodegradation) and contribute to the decomposition process (Austin et al., 2016; Wang et al., 2021b; Austin and Ballaré, 2024). Hence, if exposed to direct sunlight, decomposition rates could be accelerated in our gaps. Given the experimental setup with leaf litter bags, photodegradation could explain increased decomposition rates, too, but only for the top leaves in the leaf litter bags. In contrast to leaf litter, deadwood decomposition rates were slowed down in gaps with an open canopy when arthropods were present. Besides temperature, moisture is another important driver for decomposition (Sierra et al., 2015). While soil moisture is usually lower in forest gaps (Ritter et al., 2005; Gálhidy et al., 2006) than in closed forests, deadwood in gaps is subject to a stronger change of drying out and rewetting than under closed canopies. This may lead to unfavorable conditions which can limit fungal activity (Wallace et al., 2018) and the decomposition processes in general (Erickson et al., 1985; Parmenter and Macmahon, 2009). Necromass, especially deadwood can hold water (Klamerus-Iwan et al., 2020), which can function as a buffer in drier conditions, but the capacity is related to the size of the log and the stage of decomposition (Erickson et al., 1985). For larger deadwood logs, studies found that decomposition rates increase under open canopy with moderate moisture (Shorohova and Kapitsa, 2014). However, it is likely that our deadwood objects were too small and had not decomposed enough to have sufficient water-holding capacity to buffer the drier conditions in gaps with open canopy, resulting in arthropod and microbial decomposer activity being halted. So even though higher temperatures in gaps can accelerate decomposition rates, lower moisture content can limit the decomposition rates at the same time. Future research is needed to investigate the interaction of microclimatic temperature and moisture on the decomposition process (Sierra et al., 2015).

4.4. Remarks concerning study limitations

The decomposition process is structured into different decay stages with each specific characteristic and long-term studies incorporating the whole decomposition process of experimentally placed slower-decomposing necromass experimentally are very rare. Given the different magnitudes of our decomposition rates, we were able to assess nearly the whole decomposition process of carrion, but not for leaf litter, and we only studied the initial phase of the deadwood decomposition. Additionally, for slowly decomposing necromass types, such as leaf litter and deadwood, increasing weight is regularly observed in decomposition experiments (Edelmann et al., 2022; Zeng et al., 2024). In line with

that, we measured some positive decomposition rates for leaf litter. Although also ecological reasons (mycorrhiza growth) could explain this, gains could also be a methodological artifact, since particles from outside could have entered coarse leaf litter bags. Even though we carefully removed particles, such as sand or needles of coniferous tree species, this effect cannot be ruled out completely. Regarding the ForMI of our study stands, please note that it does not reflect the entire range of intensity levels because unmanaged and more intensive forms of management, such as clear-cutting and soil cultivation, were not included. Further studies should therefore include more intensively managed plantations and primary forests. Finally, as here, we did not assess the (arthropod) decomposer community. Future research is required to study these interactions and dependencies and how they affect the decomposition process.

5. Conclusions

This study evaluates the decomposition of different necromass types and quantifies how decomposition rates are affected by forest attributes and the contribution of arthropods by studying different necromass types within one experiment, an approach rarely applied in previous studies. Our results highlight that decomposition processes differ strongly between carrion and autotrophic necromass (i.e., leaf litter and deadwood), which is likely linked to differences in nutrient content and physio-chemical resistance to decomposition. Moreover, the results demonstrate that arthropods play a major role in the decomposition of carrion but have a much smaller role in the decomposition of leaf litter and deadwood in temperate European forests. While ForMI had no significant effects on decomposition rates of any necromass type, effects of canopy openness differed between necromass types. Effects of canopy openness on decomposition rates were linked to arthropods for leaf litter and deadwood, which is most likely linked to microclimatic conditions in gaps. Considering increasing canopy openness due to climate change-induced higher tree mortality, decomposition rates in forests, and the contribution of arthropods might thus also change. Assessing patterns and drivers of decomposition rates across necromass types revealed few similarities across necromass types. This highlights that more comparative studies across necromass types are needed to better understand why processes differ between necromass types. Moreover, differences between necromass types also indicate that a better understanding of each necromass type is needed to account for them in carbon models and ecosystem theory.

CRediT authorship contribution statement

Marit L. Hertlein: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Philip S. Barton:** Writing – review & editing, Writing – original draft, Formal analysis. **Christian Ammer:** Writing – review & editing, Methodology. **Matthias-Claudio Loretto:** Writing – review & editing, Funding acquisition, Conceptualization. **Peter Schall:** Writing – review & editing, Methodology. **Simon Thorn:** Writing – review & editing, Formal analysis. **Sebastian Seibold:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the managers of the three Exploratories, Julia Bass, Max Müller, Sven Pompe, Anna K. Franke and Melissa Jüds, and all former

managers for their work in maintaining the plot and project infrastructure; Victoria Griefmeier for giving support through the central office, Andreas Ostrowski for managing the central database, and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze, Wolfgang W. Weisser and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. We thank the administration of the Hainich national park, the UNESCO Biosphere Reserve Swabian Alb and the UNESCO Biosphere Reserve Schorfheide-Chorin as well as all land owners for the excellent collaboration. The work has been funded by the DFG Priority Program 1374 “Biodiversity- Exploratories” (project number 512286464). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2026.100468>.

Data availability

RData are publicly available (ID 32178 and ID 24646) in the Biodiversity Exploratories Information System: <http://doi.org/10.17616/R32P9Q>.

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