Carrion decomposition in a subtropical forest biodiversity experiment

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Abstract

Tree species richness promotes the diversity of higher trophic levels and ecosystem functioning. Tree species richness may thus also affect communities of insect decomposers, and through this, accelerate the decomposition of animal carrion. However, these effects might be masked by other factors driving decomposition, such as forest structure, topography, and competition between different decomposer groups.

We placed 1728 dead mice and observed their decomposition for up to seven days, and captured carrion decomposers with mouse-baited traps across 96 plots in the worldwide largest forest biodiversity experiment (BEF-China) in subtropical China in May 2023 and July 2024.

We sampled 30,975 decomposer invertebrates from at least 65 species of nine orders. The abundance, species richness, and composition of decomposer groups (flies, ants, other arthropods) was related to sampling year, canopy cover and slope steepness, but not to tree species richness. Flies (Calliphoridae, Sarcophagidae and Muscidae) were nine times more abundant and were more often the primary decomposer of carrion in 2023 than in 2024, especially in closed forests. In contrast, when flies were rare in 2024, ants primarily decomposed carrion, especially in areas with more ants or fewer flies, independently of environmental factors or tree species richness.

Carrion decomposition was accelerated in 2023 compared to 2024, in closed forests and partially on steeper slopes, but was not influenced by tree species richness. Carrion decomposition was faster when flies instead of ants were the primary decomposers. When both insect groups co-occurred on carrion, ants typically outcompeted flies, resulting in slower decomposition.

This study shows that carrion decomposers were largely unaffected by tree species richness, and consequently, carrion decomposition also appeared to be insensitive to bottom-up effects of tree species richness. Instead, our results highlight the interactive effects of temporal and environmental factors on decomposer communities of small vertebrate carrion, the competitive interactions between decomposer groups, and decomposition rates. Our findings thus challenge the general expectation that tree diversity promotes higher-trophic diversity and ecosystem functioning.

Keywords: biodiversity-ecosystem functioning, carcass decay, cadaver, necromass, scavenger, postmortem interval, forensic entomology, nutrient cycling, tree species richness, trophic interactions

Introduction

Tree diversity can enhance ecosystem functioning through mechanisms such as niche partitioning, facilitation, and multitrophic interactions, which improve the efficiency of resource use and promote the stability of ecological functions (Trogisch et al., 2021). For example, biodiversity-ecosystem functioning (BEF-)experiments have shown that mixtures of tree species, in particular those with complementary traits, can increase forest productivity and carbon sequestration (Bongers et al., 2021; Depauw et al., 2024; Huang et al., 2018; Liu et al., 2018), and promote the diversity of other organisms (Chen et al., 2023; Fornoff et al., 2019; Schuldt et al., 2019) and their functions (Beugnon et al., 2023; Fornoff et al., 2019; Plath et al., 2012; Schnabel et al., 2025; Vehviläinen & Koricheva, 2006). This has made BEF-research a key contributor to forest restoration strategies (Baeten et al., 2019) and has helped justifying biodiversity conservation to society and policymakers beyond purely ethical and aesthetic arguments (Messier et al., 2022). Yet despite these insights, many ecological functions, particularly those not centered on trees, remain understudied in BEF-experiments (Grossman et al., 2018). One such example is animal carrion decomposition, a key process in nutrient cycling and food web dynamics.

When an animal dies, its body becomes a concentrated, ephemeral and spatially unpredictable source of energy and nutrients, which is attractive to a diverse community of decomposers and scavengers throughout the food web (Carter et al., 2006; Wilson & Wolkovich, 2011). Among them, arthropods are central to carrion decomposition (Amendt et al., 2004; Büchner et al., 2024; Paula et al., 2016; Payne, 1965; Wierer et al., 2024), and this role has been amplified by the decline of vertebrate scavengers in many regions (Oaks et al., 2004; Sonawane et al., 2025). Flies, especially blow and flesh flies, lay eggs in natural openings, from which larvae emerge and rapidly consume the tissue. As they feed, the larvae secrete digestive enzymes that break down proteins and fats, causing the carrion to soften, liquefy, and essentially ‘melt’ into the ground (Fig. 1). Ants and beetles also feed on the carrion and preying on fly larvae as they compete for dominance. When ants act as primary decomposers, they often cover the carrion with soil or suppress other decomposers, which can result in a drying and eventual mummification of the carrion (Fig. 1). Interspecific competition and predation among decomposers can therefore influence both the rate of decomposition and the community structure of arthropods present on carrion (de Jong et al., 2021; Wei et al., 2023). Although animal carrion represents a relatively small portion of the total detritus pool in forest ecosystems (Barton et al., 2019), it is a local hotspot of arthropod activity and exerts a disproportionately large influence on the diversity of consumers and nutrient cycling (Carter et al., 2006; Johnson-Bice et al., 2023), ultimately enhancing the functioning of forests.

Tree diversity positively affects arthropod diversity through increased habitat complexity and resource availability (Schuldt et al., 2019; Wang et al., 2025), but the strength of this effect likely depends on mobility and habitat use of arthropods (Guo et al., 2021; Staab et al., 2014) and may weaken with increasing trophic levels (Scherber et al., 2010; Schuldt et al., 2019). Because animal carrion decomposition is related to the diversity and community composition of arthropods in forest ecosystems (Barton & Evans, 2017; Farwig et al., 2014; Marschalek & Deutschman, 2022), positive tree diversity effects on arthropod decomposers may indirectly accelerate the decomposition of carrion in diverse forests. However, testing effects of tree diversity on animal carrion decomposition in forests is challenging because other abiotic and biotic factors may interact with tree diversity in complex ways.

Microclimatic conditions, shaped by canopy structure (Schnabel et al., 2025), may play a particularly important role in carrion decomposition. In open forests, higher temperatures may attract a more diverse arthropod community, and thus, could accelerate decomposition rates directly and indirectly (Achury et al., 2023). In contrast, drying (or ‘mummification’) of carrion may limit microbial activity and access for some decomposers, potentially slowing the process (Finaughty & Morris, 2019). In closed forests, cooler and moister conditions may either reduce decomposer activity or, by preserving moisture, make carrion more accessible to arthropods and hence promote decomposition. The direction and magnitude of microclimatic effects on decomposition may therefore depend on interactions between the forest environment, the arthropod community and seasons (de Carvalho & Linhares, 2001; Farwig et al., 2014; Finaughty & Morris, 2019; Paula et al., 2016).

Not only microclimate, but also topography, such as slope steepness, can influence carrion decomposition. Steeper slopes often differ in humidity and exposure compared to ridges and shallow slopes, which may alter arthropod activity and carrion drying. In addition, rainfall and runoff on steep terrain can displace carrion or fragment the soft tissues, thereby increasing surface area and exposure. Both microclimatic variation and mechanical processes may enhance microbial colonization and arthropod access, ultimately accelerating decomposition. However, to our knowledge, the effects of slope steepness on carrion decomposition have not been studied.

Ants have also been shown to control animal carrion decomposition (Eubanks et al., 2019), and can both impede (e.g., disruption of fly egg-laying and predation of fly larvae) and expedite (e.g., direct consumption) the decomposition process (Lindgren et al., 2011; Nooten et al., 2022; Paula et al., 2016; Wei et al., 2023). Studying animal carrion and associated arthropods in BEF-experiments provide a compelling model to better understand the contribution of tree diversity to food webs and nutrient cycling in forests, but requires a holistic and detailed analysis of a suite of biotic and abiotic variables in forest ecosystems (Dawson et al., 2024).

The BEF-China experiment (Bruelheide et al., 2014), with its experimental manipulations of tree species richness and topography, provides an ideal setting to address these questions combined. In this study, we investigated how the forest environment, particularly tree species richness, influences decomposer communities and animal carrion decomposition. We analyzed the relative importance of tree diversity effects in comparison to other factors, including canopy cover, forest slope steepness, and the role of primary decomposers. Furthermore, we explored how environmental effects on carrion decomposition were mediated by their effects on the decomposer community. We hypothesized that (i) tree species richness increases the diversity of carrion decomposers, either by providing a wider range of resources and habitats, or by altering forest structure and microclimate, and thereby, accelerate the decomposition of animal carrion; (ii) canopy cover influences decomposer diversity and carrion decomposition rates, with the direction of this effect being dependent on season, arthropod communities, or their interaction; (iii) slope steepness affects decomposition directly by increasing carrion fragmentation and aeration and indirectly via impacts on microclimatic conditions or the decomposer communities; and (iv) carrion decomposition strongly depends on the main decomposer groups, especially ants, whose effects could be either negative (through competition with other decomposers) or positive (through direct consumption), depending on local context and time.

Material and methods

Study area

This study took place in the BEF-China experiment, which is located in a hilly region near Xingangshan, Jiangxi Province, China (117°54′ E, 29°07′ N) between 28 May – 5 June 2023 and 30 June – 25 July 2024. The mean annual temperature and precipitation are 16.7°C and 1800 mm. The natural vegetation of this region is a subtropical broad-leaved forest with evergreen tree species being predominant. BEF-China encompasses two study sites which were established in 2009 (site A) and 2010 (site B), are 4 km apart from each other and together occupy 50 ha. This makes BEF-China the worldwide largest tree diversity experiment (www.treedivnet.ugent.be) (Paquette et al., 2018). A total of 566 study plots of

25.8 m × 25.8 m were set up with 400 tree seedlings in a 20 × 20 grid with a spacing of 1.29 m between each seedling (i.e. a density of 0.6 trees per m²). The gradient of tree species richness comprises 1, 2, 4, 8, 16, and 24 tree species per plot, obtained from a pool of 40 tree species. Each site has a pool of 24 broad-leaved native tree species, with eight tree species shared between sites. All trees are represented in monocultures and all higher diversity mixtures represent randomly assigned mixtures of tree species according to a broken-stick design. The position of individual trees within plots, as well as the different levels of tree species richness among plots were randomly assigned. All plots were initially weeded twice a year to reduce growth of competing forbs between trees. Site A ranges in altitude from 105 m to 275 m a. s. l. and site B from 105 m to 190 m a. s. l.. Slopes have an inclination of 0°-45° (site A = 25°, site B = 30°). An extended description of the BEF-China experiment is provided in Bruelheide et al. (2014). In our study, we used a subset of 96 plots (48 plots for site A, 48 plots for site B), with tree species richness levels represented as follows: 30 monocultures, 16 two-species mixtures, 17 four-species mixtures, 16 eight-species mixtures, 13 sixteen-species mixtures, and four twenty-four-species mixtures. This ensured a balanced representation of each tree species level across the gradient.

Carrion decomposition experiment

To measure decomposition of vertebrate carrion, we purchased frozen carrions of white *Mus musculus* (house mouse) through an online retailer in China. We stored the frozen mice in a deep freezer (-18°C), and weighed them before the experiment. Initial mass of frozen mice was on average 34.7 g, with 95% of values ranging from 24.5 g to 50.8 g. Mice used for the experiment in 2023 were c. 16% heavier than those used in 2024 (37.2 g vs 32.2 g; Supplementary Figure S1).

To study carrion decomposition along the experimental tree diversity gradient, we laid out three mouse carrion around each of three trees in a plot (n = 9 carrion per plot). The location of trees around which the carrion was placed was assigned randomly in the field, avoiding the intensively studied centres of the plots to reduce spatial overlap with other experiments in BEF-China (Fig. S2). In 2023, the decomposition experiment spanned nine days (28 May–5 June) and was completed quickly with assistance from local helpers. In 2024, the experiment was conducted over 27 days (30 June–25 July), and initiated on eleven separate days, covering an average of nine plots per session (range: 6–17 plots). The extended time frame in 2024 resulted from the experiment being conducted by a single researcher without additional support.

In total, we laid out 1728 carrions (3 mice × 3 trees × 96 plots across the two sites × 2 years). The carrion was not protected from scavenging by vertebrates. During the experiment, a total 88 mice (10.2%) in 2023 and 215 mice (24.9%) in 2024 were lost. Complete loss of all nine carrion occurred at one plot in 2023 and at eight plots in 2024. To monitor carrion decomposition, we took photos of decomposing carrion twice during the experiment; one photo was taken usually two days after deployment (± 1 d, mean ± 95% CI, but see 'Statistical methods), and a second photo after 4.5 days (± 1 d). Time intervals for photos were based on the observation of a pilot study in 2023 indicating that many carrions were fully decomposed after 7 days.

Decomposition scores and relative mass loss

Based on the appearance of carrion in photos, four observers (for photos taken in 2023) or two observers (for photos taken in 2024) assigned a decomposition score from 1 (fresh) to 7 (only remains) to each photo (Fig. 1). This scoring system followed the general structure of previously established carrion decomposition stages (Farwig et al., 2014; Payne, 1965), but adapted to seven stages. In addition to assigning scores of decomposition, we noted the dominant decomposer for each photo: flies were assigned when carrion showed signs of liquefication ('melting', Fig. 1) or maggots were visible in the photographs; ants were assigned when signs of mummification or visible ant activity were present ('mummification'). If both, ants and flies

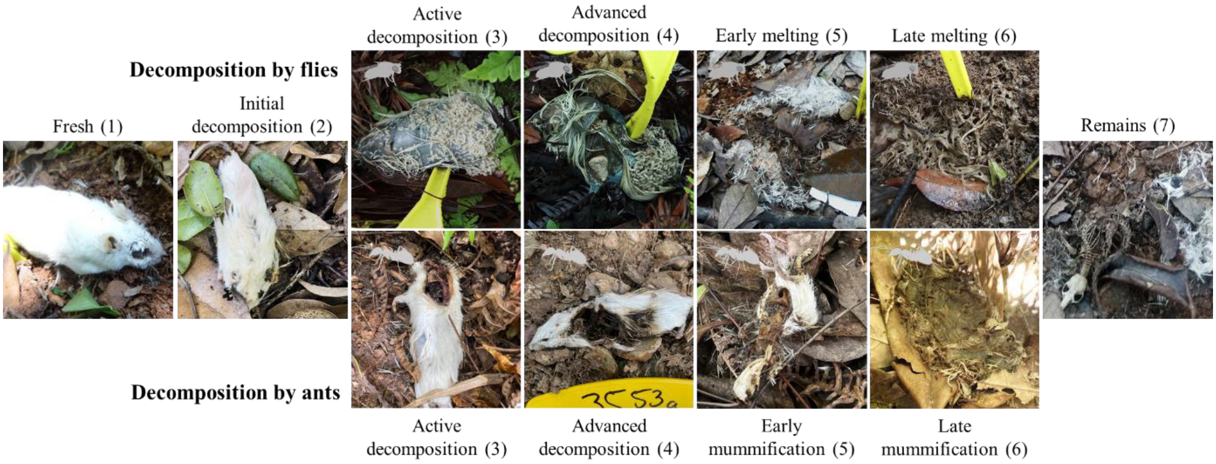


Figure 1: Decomposition pathways of mouse carrion over time, primarily decomposed by either flies ('melting') or ants ('mummification') decomposition. Based on the observed decomposition stages in the images, carrion was assigned a decomposition score ranging from 1 to 7 (see Table S1). When flies decompose carrion, their larvae secrete digestive enzymes that break down proteins and fats, causing the carrion to soften and liquefy, effectively 'melting' into the ground. In contrast, when ants dominate decomposition, they often cover the carrion with soil or suppress other decomposers, which can lead to mummification of the carrion. Please note that although these pathways are typically distinct, decomposition by flies can also lead to mummification of a carrion under dry conditions (e.g., in open forests). Images by Finn Rehling and Marc Nagel; icons of the fly and ant from Phylopic (www.phylopic.org).

were observed on photos, we recorded both as decomposers. More detailed information on characteristics of each state of the decomposition succession is provided in electronic supplementary material (Fig. 1, Table S1, Supplementary text S1). Observers were trained on test photos to harmonize criteria before scoring all images independently. Agreement among observers was near-perfect across years and sites (Cronbach's $\alpha = 0.97$, $n = 2615$). In 2023, when photo quality was occasionally compromised (in 27 cases for photos after two days, Text S1), we averaged scores if at least two observers rated the same photo (98.4% of cases), excluding the remainder.

In 2023, we freshly weighed a subset of 176 carrion samples (site A: $n = 75$, site B: $n = 101$) from 25 plots after two days. Relative (fresh) mass loss was strongly correlated with photo-based decomposition scores (GLMM with betabinomial log link: $R^2 = 0.965$, $\chi^2 = 290.7$, $p < 0.001$; Fig. 2), confirming the validity of the scoring approach. We converted ordinal scores (x) into a continuous measure of relative carrion mass using the GLMM parameters (Fig. 2):

$$relative\ carrion\ mass\ (x) = \frac{1}{1 + e^{-(3.6540 - 0.8644 * x)}} \quad (1)$$

More detailed information on the decomposition scores and the calculation of relative mass loss is provided in electronic supplementary material (Supplementary text S1).

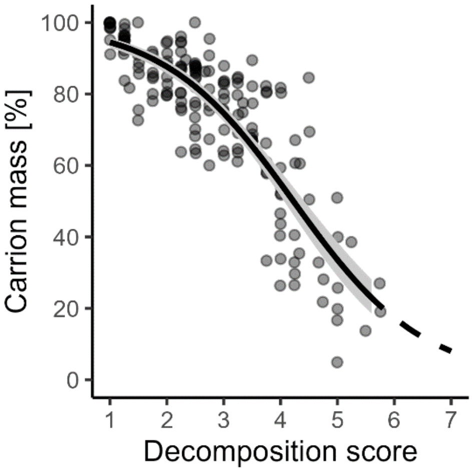


Figure 2: Relationship between the (fresh) remaining mass of carrion [%] and the assigned decomposition score based on the appearance of the mouse carrion in a photograph taken after two days of decomposition in the experiment in 2023 in BEF-China. Predicted mean ± 95% CI.

Sampling and identification of arthropod decomposers

In the week after we completed the decomposition experiment, we exposed one trap baited with mouse carrion at the center of each plot to sample carrion-associated arthropod communities (Fig. S4, Fig. S5). The trap consisted of a large plastic container (5 L) and a small plastic bottle (0.5 L). The barrel was cut at the lower middle to allow arthropods access to the carrion, and the small bottle had a hole in the bottom, allowing it to be placed on top of the large barrel to capture flying arthropods. The carrion was placed on a mesh wire in 2023, and in plastic cups in 2024 inside the large bottle (Fig. S4). The traps were partially buried in the soil to protect them from vertebrate scavengers, and the bottles were filled with salt-soap water, with detergent added to break surface tension. After two days, we emptied the bottles and removed the remaining carrion. For both years, we collected all arthropods from the traps, cleaned the specimens with 100% ethanol and stored them in 100% ethanol (changed after the first 24 and 72 hours) in a deep freezer until species identification.

All collected specimens were initially sorted into distinct morphotypes, and their abundance was recorded. Specimens were then identified to the most precise taxonomic level possible, using dichotomous keys when these were available (e.g., for ants). In cases where morphological characteristics were insufficient to achieve species-level identification, DNA barcoding was used. For each morphotype to barcode, tissue samples (specifically, one leg from two representative individuals) were removed. Subsequently, DNA extraction, PCR amplification of the mitochondrial Cytochrome c oxidase subunit I (COI) gene through LCO1490 and HCO2198 primers, and sequencing were conducted following the Sanger sequencing protocol (Hebert et al., 2003; Sanger et al., 1977). The sequences were then compared against records published in the core nucleotides database of NCBI platform (https://www.ncbi.nlm.nih.gov/).

Due to methodological limitations of the trap design used in 2023, not all arthropod data were included in the final analysis (see Supplementary Text S2). Specifically, the design in 2023 allowed decomposing carrion to leak into the preservative fluid, compromising arthropod sampling and reducing the efficiency of collecting ants and other ground-dwelling arthropods. Consequently, the abundance and community composition of non-flying arthropods were substantially lower in 2023 than in 2024 (Fig. S5). To ensure data quality and comparability, we restricted the analysis of non-flying arthropods to the 2024 dataset, which used a revised trap design. In addition, we excluded arthropod by-catch from the traps because they also captured carrion-associated predators that were hunting flies, for instance nine spider species, two wasp species (*Vespa velutina* and *Vespula flaviceps*), one fly species (Asilidae), and a mantis (*Statilia maculata*). Traps from four of 96 plots in 2023 were destroyed, presumably by wildlife, and were excluded from the analyses.

We quantified sample coverage of our carrion-baited traps (Chao et al., 2020) and found that the carrion-baited traps captured nearly complete necrophagous communities of flies and ants (Fig. S6), while other decomposers were somewhat underrepresented, particularly at shallow forest slopes (GLM, Wald-$\chi^2 = 5.27$, $p = 0.022$; Fig. S7). Mean sample coverage was 99.1% for flies in 2023, 96.2% for flies in 2024, 97.4% for ants in 2024, and 77.6% for other decomposers in 2024, considering only traps that collected at least five individuals of at least two species of a decomposer group (see Statistical analysis). For further details on trap design and associated issues are provided in Supplementary Text S2.

Canopy cover

Canopy cover was estimated for each plot using elevation-normalized LiDAR point clouds collected in 2023. We acquired drone-based LiDAR data during the leaf-on season of September 2023 using a Hesai Pandar40P laser scanner (LiAir 220N system, GreenValley International). The drone flew at an average altitude of 100 m above the ground and at a velocity of 8 m/s, resulting in an average point density > 164.6 points m^{-2}. Most flight lines overlapped > 50% and the maximum scan angle was ± 15°. The LiDAR data were pre-processed using LiDAR360 software (GreenValley International, Beijing, China) following a standardized workflow (Liu et al., 2024). Canopy cover was approximately the inverse of the gap fraction and estimated as the proportion of the ground covered by forest canopy (above 2 m) in percentage.

Statistical analysis

While the preceding sections followed the chronological order of data collection, the remainder of the manuscript is structured ecologically, from decomposer communities to their effects on carrion decomposition to better align results and interpretation.

Decomposer abundance

Because the contribution of arthropods to animal carrion decomposition differs between groups of decomposers, we analyzed the effects of the forest environment on arthropods separately for necrophagous flies, ants and other decomposers. To avoid bias from undersampling, we a priori excluded traps from the analysis of a given decomposer group if they contained no species, only one species, or fewer than five individuals of that group (i.e., five traps for flies in 2023, 16 traps for flies in 2024, 12 traps for ants in 2024, and 30 traps for other decomposers in 2024), and retained the trap for analyses of other groups. We analyzed the relationship between the abundance of arthropods and log2-transformed tree species richness, canopy cover and forest slope steepness with (generalized) linear mixed effect models (type III sums of squares). In models of arthropod abundance, we used a negative binomial error distribution with a log link to account for overdispersion in count data. Because the group of other decomposers was partially undersampled by our traps, we used estimated species richness values derived from iNEXT (Hsieh et al., 2016) to account for potentially undetected species. We calculated estimated diversity for a standardized sample coverage of 80% for flies and ants, and a coverage of 60% for other decomposers. In these models, we used a gamma error distribution with a log link. Because the models with flies included data from two sampling years, we included two-way interactions with year and modelled year-specific overdispersion to account for differences in variability between years. We included the experimental site (i.e., A or B) as a random intercept in the models, z-transformed all continuous fixed factors (to mean = 0 and SD = 1) and checked for multicollinearity visually and using variance inflation factors before analyses. In addition, community composition of decomposer arthropods was analyzed using PERMANOVA based on Bray-Curtis dissimilarities and visualized with NMDS to assess relationships with environmental factors. Further methodological details are provided in the appendix (Supplementary text S3).

Analysis of primary decomposer

We analyzed the probability that either flies (in 2023) or ants (in 2024) were the primary decomposers during early decomposition stages using binomial generalized linear mixed-effect models (type III sums of squares). As fixed effects, we included z-standardized measures of canopy cover, forest slope steepness, and the abundances of flies (from traps in 2023 and 2024, respectively) and ants (only from traps in 2024), and log2-transformed tree species richness. We included experimental site as a random intercept. We checked for collinearity among predictors using Pearson correlation and variance inflation factors, and checked model diagnostics.

Carrion decomposition analysis

There were two important caveats in the analysis of carrion decomposition. Firstly, carrion decomposed much more quickly in 2023 compared to 2024 (see Results). As a consequence, approximately 40% of mice were already fully decomposed by the time the second photo (after 4-5 days) was taken in 2023 (see Fig. S8). This posed a problem for the analysis because the high proportion of fully decomposed mice led to right-skewed censoring and a loss of variation. This loss of variation may have affected the results qualitatively, as the effect sizes of the tested variables (canopy cover, steepness of forest slope, tree species richness) were smaller in models that included interaction effects with year and experiment duration of carrion decomposition (Fig. S9). To avoid potential problems associated with a partial right censoring of the data, we decided to analyze only the decomposition of mice after two days.

Second, when we took photos of a decomposing mouse for the first time, we photographed the decomposing mice after one ($n = 82$), two ($n = 1574$), three ($n = 63$) or four days ($n = 9$). The number of days until the first photo was taken had a strong influence on the score of decomposition of the mouse, with later photos corresponding to more advanced decomposition (GLMM, Wald-$\chi^2 = 55.7$, $p < 0.001$). To account for this, based on this model, we adjusted the scores of decomposition for differences in the number of days so that all scores reflected the expected state for photos taken on the second day. Scores from the one plot in 2024, where we took photos only on the fourth day, were divided by two (Fig. S10).

After converting the scores into values of relative mass loss using Eq. (1), we used a generalized linear mixed model to investigate the relationship between the proportion of carrion mass lost after two days and initial carrion mass, log2-transformed tree species richness, canopy cover, slope steepness and the identity of primary decomposer, each in interaction with year to account for temporal variation. We used a beta-binomial error distribution with a logit link to account for normality and homoscedasticity of variances. We included plots nested within sites (i.e., A or B), and the tree species around which the carrion was placed as orthogonal random intercept. Dispersion was modelled as a function of year, canopy cover and primary decomposer to account for heterogeneity in variability. All continuous predictors were z-transformed (to mean = 0 and SD = 1) before analysis.

All statistical analyses were done with R program version 4.4.1 (R Core Team, 2021). Generalized linear mixed models were constructed using the R-package ‘glmmTMB’ version 1.1.10 (Brooks et al., 2017). Multicollinearity among predictor variables was assessed using ‘performance’ version 0.12.4 (Lüdecke et al., 2021). Significance values were obtained using Wald-χ^2-tests in the package ‘car’ version 3.1.2 (Fox & Weisberg, 2019). Model performance was evaluated using the R-package ‘DHARMa’ version 0.4.7 (Hartig, 2021). Species richness estimation and sample coverage calculations were performed using the R-package ‘iNEXT’ version 3.0.1 (Hsieh et al., 2016). The multivariate analysis was conducted using the R-packages ‘vegan’ version 2.6.6.1 (Oksanen et al., 2020), with ‘RVAideMemoire’ version 0.9.83.7 (Hervé, 2022) used for type II PERMANOVA tests and permutation.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used large language models to assist with language, grammar, spelling, and overall readability. All content was reviewed and edited by the authors, who take full responsibility for the accuracy and integrity of the article.

Results

Decomposer diversity

We collected a total of 25,027 flies, representing 16 species (including three morphospecies), from 9 genera and 5 families, with 192 carrion-baited traps in BEF-China in 2023 and 2024. The five most abundant species were *Chrysomya megacephala* (46.0%), *Lucilia porphyrina* (31.4%), *Hemipyrellia ligurriens* (6.9%), *Sarcophaga peregrina* (6.5%), and *Chrysomya pinguis* (5.0%). Other carrion-associated flies constituted ~1.5% or fewer individuals (see Supplementary table S2). Flies of the family Calliphoridae (n = 22,709) were an order of magnitude more frequent than those of Sarcophagidae (n = 1,643) or Muscidae (n = 617).

We collected almost 7.5 times more flies and also more fly species in May 2023 (22,075 individuals from 16 species) than in June 2024 (2,952 individuals from 11 species, see Table 1). The abundance of flies was not influenced by tree species richness in the two-study years (Fig. 3a). The abundance of flies was positively associated with canopy cover in 2023, but negatively in 2024 (Fig. 3b). Slope steepness of forests was positively related to the abundance of flies in 2023, but there was no relationship in 2024 (Fig. 3c). Species richness of flies was associated with their abundance at the plot level and decreased with canopy cover in 2023 (Fig. S11 a-d). The community composition of flies was strongly associated with year and canopy cover in 2023 (Table S3, Fig. S12).

We collected a total of 4,946 ants, representing 13 species from 11 genera and four subfamilies, in BEF-China in 2024. The five most abundant species were *Crematogaster cf.*

rogenhoferi (26.2%), *Pheidole nodus* (17.3%), *Polyrhachis illaudata* (sensu lato, 14.7%), *Polyrhachis dives* (10.2%), and *Lepisiota* sp. (7.6%). Other carrion-associated ants each accounted for less than 7% of the total (see Supplementary Table S2). The abundance of ants in carrion-baited traps did not change with tree species richness or canopy cover, but increased with slope steepness of forests in 2024 (Table 1, Fig. 3 d-f). Species richness of ants was strongly associated with their abundance at plot-level, and increased with canopy cover (Fig. S11 e-h). The community composition of ants was related to slope steepness and canopy cover (Table S3, Fig. S12).

In addition to flies and ants, we collected a total of other 1,002 invertebrates in 2024 from carrion-baited traps in BEF-China, spanning at least 36 taxa across 10 insect orders and one centipede family. The majority belonged to Coleoptera (67.2%), Lepidoptera (14.7%), and Orthoptera (12.7%). The most abundant beetles were *Onthophagus* sp. (37.4%), *Aleochara postica* (11.4%), and *Copris* sp. (9.6%). Among Lepidoptera, the most common were an unknown morphospecies (4.7%), *Glyphodes* sp. (3.5%), and *Sypnoides fumosa* (2.2%). Orthopteras included *Xenogryllus marmoratus* (6.0%) and *Diestramima excavata* (3.3%), with other species present in lower abundances. Other taxa of cockroaches, hemipterans, dermapterans, and scutigerid centipedes were also collected in low abundance (see Supplementary Table S2). The abundance of other decomposers was positively associated with canopy cover, but was not related to tree species richness or slope steepness of forests (Table 1, Fig. 3 g-i). Species richness of other decomposer was strongly associated with their abundance at the plot level, but did not depend on the forest environment (Fig. S11 e-h). The community composition of other decomposer was variable and not related to the forest environment (Table S3).

Table 1: Mixed-model analyses of variance of the effects of tree species richness, canopy cover, slope steepness, abundance on the abundance and species richness of flies, ants, and other decomposers sampled from carrion-baited traps over two days in the subtropical forest of BEF-China. For flies, all interactions between year (2023 vs. 2024) and the main predictors were tested. Bold Wald-χ^2 values with an asterisk indicate significant effects ($p < 0.05$).

	Flies		**Ants**		**Other decomposers**	
Predictors	**Abundance Chisq**	**Richness Chisq**	**Abundance Chisq**	**Richness Chisq**	**Abundance Chisq**	**Richness Chisq**
Tree richness (log)	0.05	1.28	0.26	0.61	0.91	0.21
Canopy cover	**4.74***	**4.59***	0.99	**3.90***	**8.38***	0.13
Slope steepness	**4.65***	0.04	**5.03***	0.02	1.39	0.16
Abundance (log)		**7.20***		**3.89***		**9.84***
Year	**187.94***	**12.60***				
Year × Tree richness	1.29	0.05				
Year × Canopy cover	**15.97***	**4.52***				
Year × Slope steepness	**4.70***	0.25				
Year × Abundance		**14.76***				

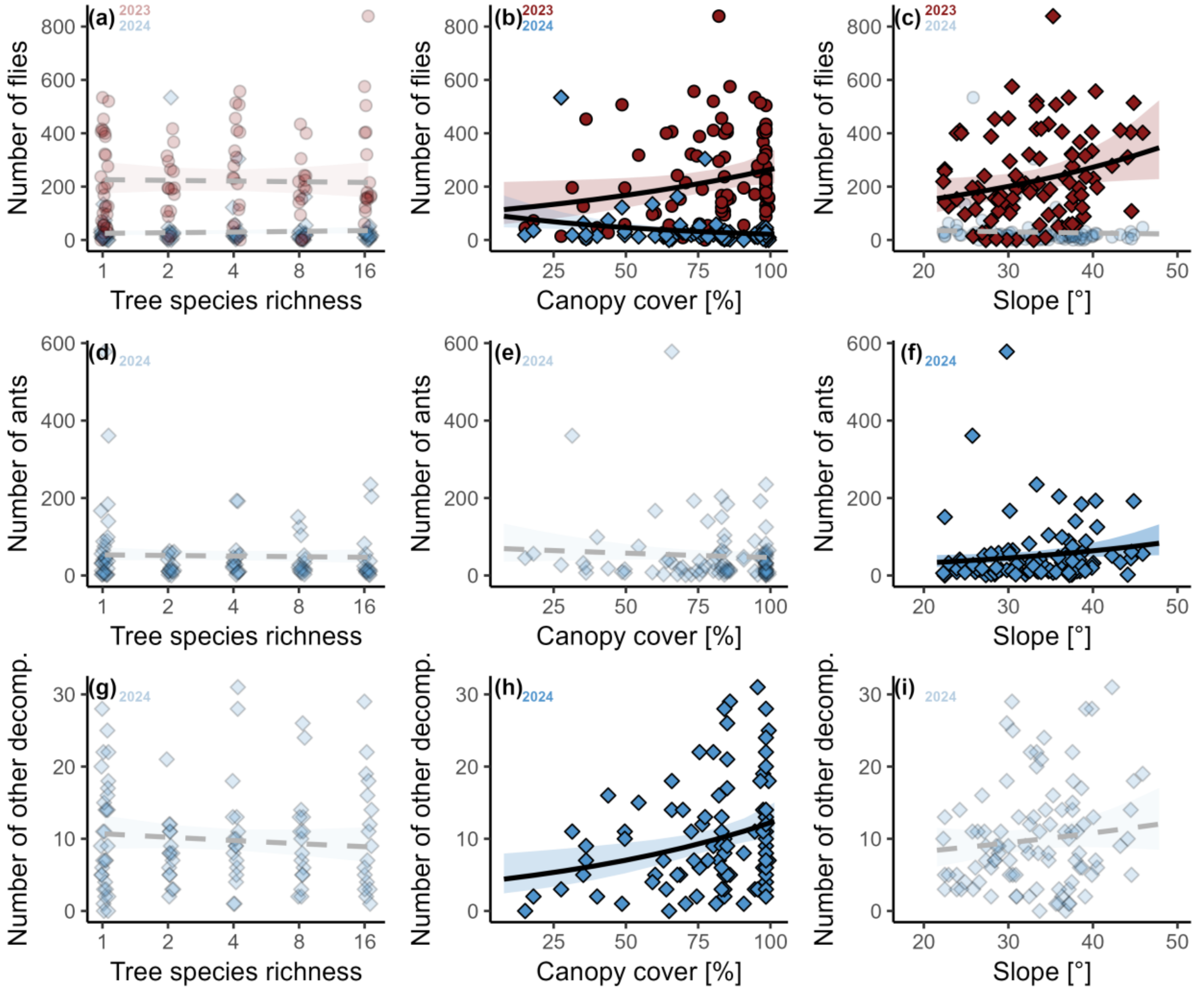


Figure 3: Relationship between the abundance of (a-c) flies, (d-f) ants and (g-i) other decomposer in carrion-baited traps after two days in the subtropical forest of BEF-China in 2023 (red circles) and 2024 (blue diamonds) and forest environmental factors: (a, d, g) tree species richness (log2-transformed), (b, e, h) canopy cover and (c, f, i) slope steepness. Solid lines with coloured intervals indicate statistically significant relationships ($p < 0.05$), while grey dashed lines with blurred points represent non-significant relationships. Lines show model predictions (mean), and shaded polygons indicate 95% confidence intervals (mean ± 95% CI).

Primary decomposer of mouse carrion

We identified ants as the primary decomposers in 903 carrion samples, flies in 385 samples, and both flies and ants together in 70 samples. For 495 carrion samples, the primary decomposer could not be determined from photographs or decomposition succession (Fig. 1). In 2023, carrion was primarily decomposed by flies (34%), while in 2024 ants were the main decomposers (39%; Fig. 4a).

The proportion of carrion decomposed by flies in 2023 was not influenced by tree species richness (Wald-$\chi^2 = 1.65$, $p = 0.199$, Table S3) and was not related to the abundance of ants (Wald-$\chi^2 = 0.56$, $p = 0.454$, Fig. 4b), the abundance of flies (Wald-$\chi^2 = 0.64$, $p = 0.422$, Fig. 4c) or slope steepness (Wald-$\chi^2 = 0.99$, $p = 0.319$). However, as canopy cover increased from 10% to 100%, the proportion of carrion decomposed by flies rose from 8% to 52% (Wald-$\chi^2 = 24.08$, $p < 0.001$, Table S3). In 2024, the proportion of carrion decomposed by ants was strongly related to the abundance of ants (Wald-$\chi^2 = 11.02$, $p < 0.001$, Fig. 4d) and flies (Wald-$\chi^2 = 6.42$, $p = 0.011$, Fig. 4e) at the plot level, but not to other forest variables ($p > 0.05$, Table S3).

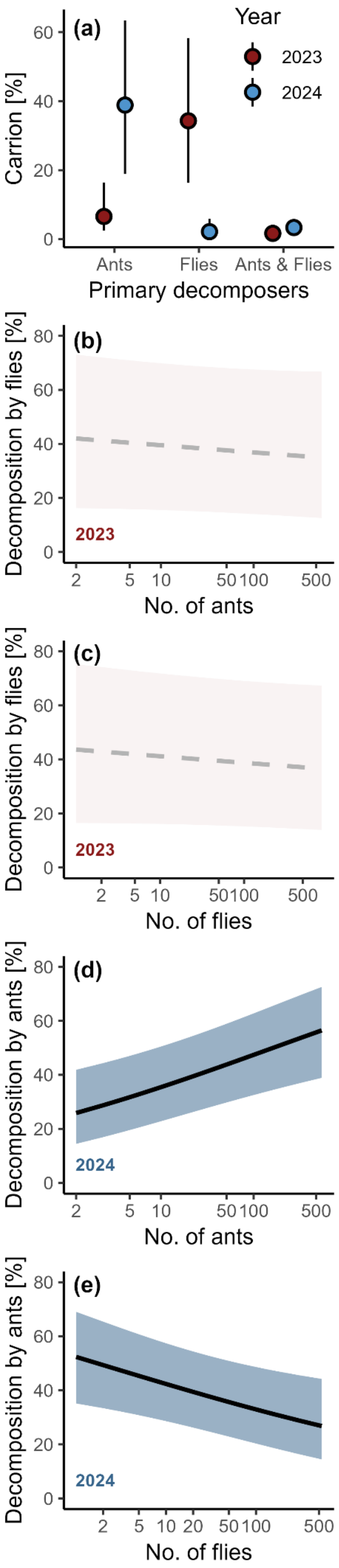
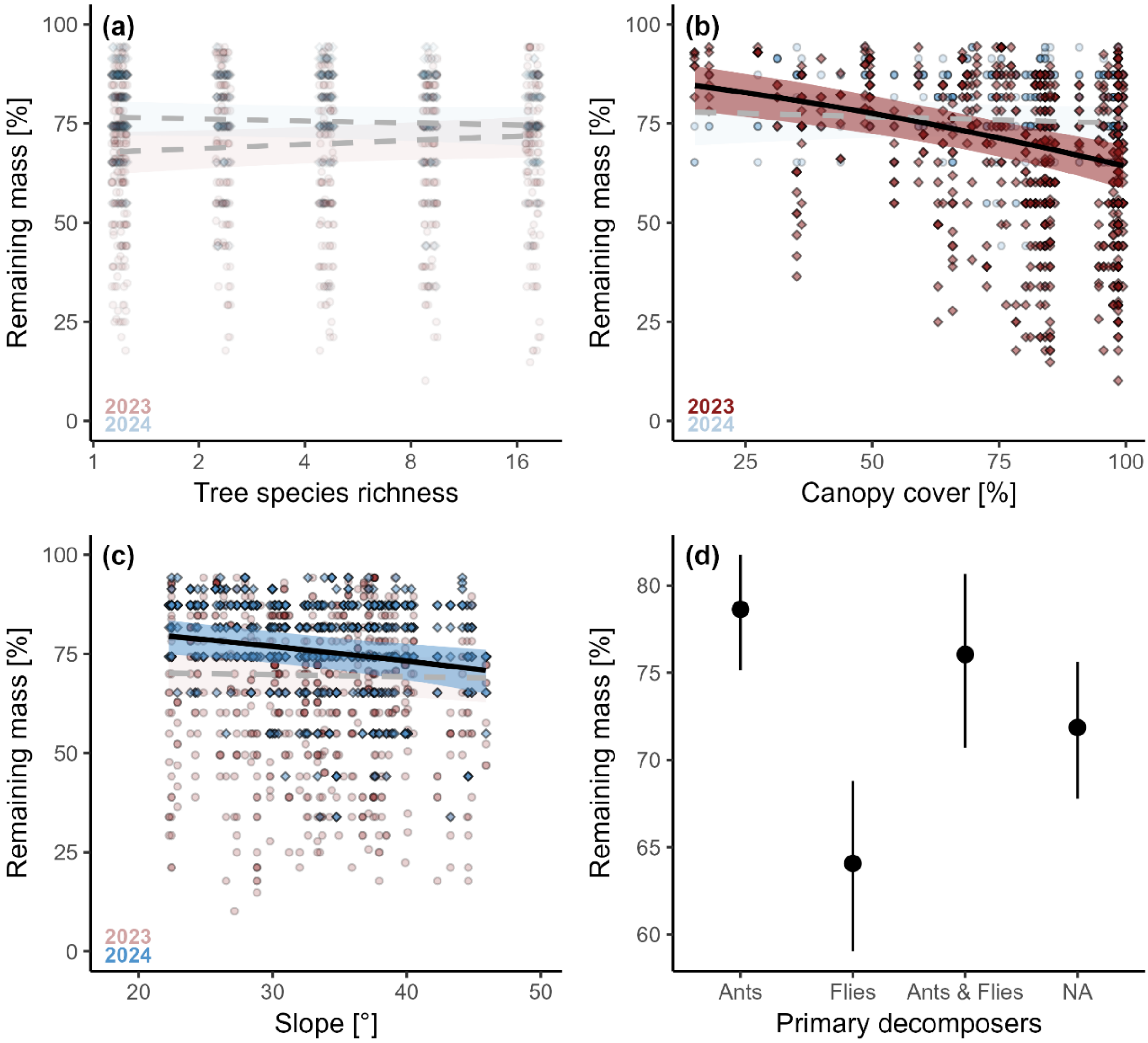


Figure 4: Relationship between the proportion of carrion primarily decomposed by (a, b, c) flies or (a, d, e) ants and three explanatory variables: (a) sampling year, (b, d) fly abundance and (c, e) ant abundance in carrion-baited traps in 2023 and 2024. In (a), the values do not sum to 100% because the primary decomposer was not clear in the other cases. Please further note, ants were not considered in 2023; therefore in (b), ant abundances from 2024 were paired with the decomposition by flies in 2023. Solid lines with coloured intervals indicate statistically significant relationships ($p < 0.05$), while grey dashed lines with pale intervals represent non-significant relationships. Mean ± 95% confidence intervals.

Carrion decomposition

The relative mass of carrion lost after two days in the subtropical forest of BEF-China was strongly influenced by the initial mass, study year, forest variables, and their interactions (Table S4, Fig. 5). Overall, carrion was 6.4% more decomposed after two days in 2023 than in 2024. Tree species richness did not have a significant effect on carrion decomposition in either year (Wald-$\chi^2 = 2.59$, $p = 0.108$). The relationship between tree species richness and decomposition differed significantly between years, but the slopes did not differ from zero in both years (Wald-$\chi^2 = 9.90$, $p = 0.002$; Fig. 5a). Carrion decomposition was accelerated in closed forests in 2023 (year × canopy cover interaction: Wald-$\chi^2 = 33.09$, $p < 0.001$; Fig. 5b), and increased on steep slopes in 2024 (year × slope interaction: Wald-$\chi^2 = 9.59$, $p = 0.002$; Fig. 5c).

Carrion decomposition was strongly dependent on the primary decomposer. In our study, ants fully buried carrion with soil in 53 cases (6 in 2023, 47 in 2024). Buried carrion represented 3.9% of all cases, and 10.5% of cases dominated by ants, and in 89% of these cases, the burial of carrion effectively excluded flies. Regardless of the year, carrion decomposed by ants were c. 15% less decomposed after two days than carrion decomposed by flies (Fig. 5d). When ants and flies co-occurred on carrion, the decomposition rate was similar to that of carrion dominated by ants.



450 **Figure 5**: Relationship between the remaining mass of decomposing carrion after two days in the subtropical forest of BEF-China and (a) tree species richness, (b) canopy cover, (c) slope steepness, and (d) the primary decomposer. Solid lines with coloured intervals indicate statistically significant relationships ($p < 0.05$) with 95% CI as shaded polygons, while grey dashed lines with pale intervals represent non-significant relationships. In (d), the error bars indicate 95% CI.

Discussion

Our study demonstrates that decomposition of small vertebrate carrion in subtropical forests is primarily explained by interactions between the identity and abundance of decomposers and temporal variability. In spring 2023, when flies were abundant, carrion decomposition was faster and mostly decomposed by flies. In summer 2024, when flies were relatively rare in the samples, decomposition was slower and ants were the main decomposer. These patterns were positively influenced by canopy cover and slope steepness, but not by tree species richness, highlighting a predominant role of seasonal differences, environmental variation and interspecific interactions for carrion decomposition compared to that of tree diversity.

Lack of effect of tree species richness

Animal carrion decomposition has received little attention in biodiversity–ecosystem functioning (BEF-)research, which has predominantly focused on plant-derived substrates such as leaf litter in decomposition studies (Desie et al., 2023; Scherer-Lorenzen, 2008; Seidelmann et al., 2016). Our study is the first to investigate effects of tree species richness on animal carrion decomposition.

We found no effect of tree species richness on the decomposer community, competitive interactions, or the rate of carrion decomposition. This result contrasts with many BEF-studies, which commonly report positive effects of tree diversity on the diversity of higher trophic levels and their associated ecosystem functions. For instance, tree diversity has been shown to enhance arthropod diversity by increasing habitat complexity and resource heterogeneity (Schuldt et al., 2019; Wang et al., 2025). However, recent work highlights that BEF relationships are context-dependent: diversity effects differ between ecosystem functions (Tang et al., 2022), can vary over space and time (Amyntas et al., 2023; Bongers et al., 2021; Trogisch et al., 2021), and may be overridden by abiotic conditions or biotic interactions (Li et al., 2023). As a result, BEF-relationships may weaken or vanish at certain ecological scales, which challenges the application of BEF-principles in real-world ecosystems (Manning et al., 2019).

Mobility and habitat use may explain the lack of a tree diversity effect on decomposers. While most BEF effects are related to effects at the local scale, multitrophic interactions often operate at broader scales (Fichtner et al., 2018; Yu et al., 2024). For instance, carrion flies are known to move more than 2 km per day, especially species that rely on carrion for oviposition (Braack & Retief, 1986; Smith & Wall, 1998; Spradbery et al., 1995). Because flies need to find carrion over large areas, they may respond to the environment at a larger scale, rather than to local tree neighborhoods (Johnson-Bice et al., 2023). This mismatch in spatial scale potentially explains the absence of localized effects of tree species richness on fly diversity and decomposition. Similar scale mismatches might also influence other ecosystem functions carried out by highly mobile organisms, such as pollination, seed dispersal or predation (Jordano et al., 2007; Pasquet et al., 2008; Tucker et al., 2018).

Ants, the second most important group of decomposers, are less mobile and more locally bound. Canopy and litter ant richness often increases with tree diversity (Skarbek et al., 2020), yet this pattern is weaker or absent for ground-dwelling, omnivorous ants, which often remain diverse even in disturbed forests (Staab et al., 2014). Their broad diets and flexible nesting behavior (Blüthgen & Feldhaar, 2009) likely reduce the dependence of omnivorous ants on the resources (e.g. leaf litter) provided by specific tree species.

Tree diversity also did not show any effect on other decomposers, although grouping these taxa may have masked more nuanced, taxon-specific relationships (e.g. in Lepidoptera, Coleoptera or Orthoptera). Nonetheless, any subtle positive effects were likely too weak to lead to changes in carrion decomposition. Moreover, flies or ants may have further outcompeted other decomposers or suppressed their activity (Trumbo & Bloch, 2000). Finally, tree species richness also did not influence carrion decomposition indirectly via microclimatic buffering, such as temperature or moisture moderation (Schnabel et al., 2025). Taken together, our findings suggest that tree species richness neither supports decomposer diversity nor enhances carrion decomposition, directly or indirectly. This challenges the widespread assumption that tree diversity generally promotes diversity of higher trophic levels and ecosystem functioning.

Competition between flies and ants for carrion

It is well established that flies and ants are among the most dominant invertebrate decomposers of carrion and that they often compete directly for access to this ephemeral resource (Eubanks et al., 2019). Our results show that the outcome of the fly-ant competition over carrion is strongly influenced by temporal variation in decomposer abundance and local forest conditions in a subtropical forest.

In our study, carrion was primarily decomposed by flies in spring 2023. This period was characterized by high temperatures (mean: 27.5 °C; max: 35.7 °C), relatively dry conditions, and more sunlight compared to the wet season. Such seasonal environmental conditions generally favor flies by enhancing their activity, dispersal, and reproductive output (Arnaldos et al., 2001; de Carvalho & Linhares, 2001; Shi et al., 2009), ultimately leading to increased fly dominance over carrion. Fly communities in 2023 were not only more abundant but also more species-rich, which may have increased their ability to locate and monopolize carrion.

In contrast, ants dominated carrion decomposition in summer 2024. This period marks the early wet season, when monsoonal conditions intensify. The period experienced increased rainfall, persistently high humidity, slightly elevated temperatures, and more cloud cover than in 2023. These conditions may reduce fly activity and abundances (Arnaldos et al., 2001; de Carvalho & Linhares, 2001; Shi et al., 2009). For instance, we sampled nine times fewer flies in summer 2024 than in spring 2023 (n = 21,242 vs. n = 2,402), indicating a decline in fly abundance and dominance. Although slightly different trap designs were used in the second year (Supplementary text S2), the large differences in fly abundance between spring 2023 and summer 2024 are unlikely to be explained by trap design alone. In contrast, it has been often demonstrated that ant abundance in (sub-)tropical forests increases during the wet season (Kass et al., 2023; Levings, 1983; Queiroz et al., 2023; Suwabe et al., 2009). The combination of reduced fly abundance and increased ant abundance may have contributed to the observed shift in decomposer dominance between spring 2023 and summer 2024.

In addition, when flies were abundant and species-rich, as in spring 2023, neither fly nor ant abundance was related to their dominance on carrion. Under such conditions, a single carrion may host between 100 and 1,000 flies. Ovipositing sarcophagids and calliphorids typically produce ~20–40 live larvae per cycle (Knipling, 1936), which could result in comparably high numbers of larvae per mouse carrion (Archer & Elgar, 2003). Such saturation likely makes resource control less sensitive to small changes in fly or ant abundance. In contrast, when flies were relatively rare, ant dominance on carrion was strongly associated with the abundance of both ants and flies at the plot level. Together, these results indicate that decomposer interactions are shaped by local densities when flies are rare, but when flies are super-abundant, fly dominance is less dependent on local competition between decomposer groups and potentially more influenced by factors such as early arrival or environmental conditions that promote fly activity (Brundage et al., 2014; Dawson et al., 2022; Michaud & Moreau, 2017). These findings highlight that decomposer interactions are strongly abundance-driven and shaped by seasonal and environmental filters (Farwig et al., 2014; Hernández-Ortiz et al., 2022). However, because ant sampling was limited in the first year, further replicated studies are needed to better understand how seasonal dynamics and environmental conditions influence decomposer competition and decomposition rates in subtropical forests (Barton et al., 2013; Eubanks et al., 2019; Kishimoto-Yamada & Itioka, 2015).

Figure 6: An unsuccessful attempt of ants to bury a carrion to protect it from flies.

Ants used a range of physical and behavioral strategies to interfere with flies. In our study, ants buried carrion with soil in about 3.9% of all cases (10.5% of cases dominated by ants), and in 89% of these instances, the burial of carrion effectively excluded flies (but see Fig. 6) (Cornaby, 1974; Lindgren et al., 2011). When carrion remained uncovered, we observed ants attacking adult flies, likely reducing oviposition and larval development (Stoker et al., 1995). Ants also preyed on fly larvae from carrion, as previously reported (Barton & Evans, 2017; de Jong & Hoback, 2006; Early & Goff, 1986; Stoker et al., 1995). These behaviors influenced the decomposition process, and likely depend on ant species. Carrion dominated by ants decomposed more slowly than carrion dominated by flies, allowing ants to exploit the resource over a longer period. Even when both groups co-occurred, decomposition rates resembled those of ant-dominated carrion, suggesting strong suppression of fly activity by ants. However, ants might only be able to compete successfully with flies if they discover carrion early and are able to quickly recruit nestmates. This study is among the first to show that interspecific competition among decomposers is strongly related to their abundances and can shape carrion decomposition across environmental gradients (Barton & Evans, 2017; Fernandes et al., 2024).

In addition, our results on the decomposition by ants are consistent with studies showing that ants mostly slow down carrion decomposition by disrupting necrophagous communities (Barton & Evans, 2017; de Jong & Hoback, 2006; Lin et al., 2022; Pereira et al., 2017; Wei et al., 2023), while only a few studies point out positive effects of ants on carrion decomposition through facilitating decomposition (Meyer et al., 2020). However, different ant species employ different ecological strategies (Nooten et al., 2022), highlighting the need for further research into tri-trophic interactions among ants, flies, and other carrion-associated arthropods (Alvarado-Montero et al., 2021). Such studies are essential to understand when and how ants influence decomposition, and its effects on ecosystem functioning (Fornoff et al., 2019; Tiede et al., 2017). Our findings emphasize the role of ants in decomposer interactions and carrion decomposition, particularly in tropical and subtropical forests (Amendt et al., 2004; Paula et al., 2016; Stoker et al., 1995).

The role of forest structure

Open forests are typically warmer and drier, potentially promoting insect activity and diversity (Achury et al., 2023; Perry et al., 2018; Rothacher et al., 2025). In case of carrion decomposition, open forests probably also facilitate carrion detection by decomposers through improved volatile emissions (Von Hoermann et al., 2022). In our experiment, however, warm and dry conditions in open forests accelerated carrion drying, which reduced its suitability for colonization by decomposers (cf. Staab et al., 2022). Fly abundance and fly-dominated carrion declined in open forests in 2023. In contrast, cooler, moister conditions in closed forests likely favored colonization and larval development. This potentially resulted in the consistently faster decomposition of carrion in closed forests in our experiment.

Beyond flies, canopy cover also influenced the community composition of ants and beetles, in line with previous findings that these groups differ in their associations between forests and grasslands (Barton & Evans, 2017). Seasonal variation further modulated these patterns. For example, fly abundance on carrion was generally higher in spring 2023 than in summer 2024, but canopy effects differed between the two time periods. While Barton & Evans (2017) observed no canopy effect on fly community composition, we found clear compositional shifts, suggesting environmental filtering may vary in strength across seasons or years

(Farwig et al., 2014) and systems. Overall, our results align with previous evidence that decomposition proceeds more rapidly in closed compared to open forests (Alvarado-Montero et al., 2021; de Carvalho & Linhares, 2001). Nonetheless, very few studies have directly linked decomposer diversity, forest structure, and decomposition outcomes. The results of this study highlight the context-specific role of forest canopy in controlling decomposer interactions and carrion decomposition.

The role of topography

Topography, particularly slope steepness, affected decomposer communities and carrion decomposition in our study. In 2023, fly abundance was positively associated with steeper slopes. The abundance and composition of ant communities also shifted towards steeper slopes, whereas the group of other decomposers did not show a clear response. Notably, carrion decomposition in 2024 was faster at steeper slopes, suggesting a link between topographic variation and ecosystem functioning.

Several mechanisms may explain these patterns. First, microclimatic variation along slopes likely plays a key role. In BEF-China, slope steepness correlates with local humidity (Figure S13) during the experiment, with shallower slopes typically located at hill ridges, where they are drier and more exposed to the sun. These conditions are similar to those found in open forests, which were also associated with carrion drying and limited decomposer activity. In line with this, we observed higher fly and ant abundances on steeper slopes and accelerated decomposition in early summer 2024, when humidity was high, possibly due to increased moisture buffering and a slower drying of carrion.

Second, erosion and physical movement of carrion on slopes may influence carrion decomposition. On steep terrain, rainfall and runoff can displace carrion, damage them or fragment soft tissues, increasing surface area and exposure. Such physical changes likely enhance microbial colonization and arthropod access, and ultimately accelerate decomposition. Such mechanical processes may interact with the biological factors, reinforcing the functional importance of slope gradients.

We did not find studies that have examined topographic effects on carrion decomposition. However, topography is known to shape other biotic processes, including biocrust development (Seitz et al., 2017), sediment redistribution from animal burrowing (Grigusova et al., 2023) or tree growth via nutrient and water fluxes (Scholten et al., 2017). Our findings extend this understanding by showing that slope steepness can also influence decomposer diversity and decomposition rates, likely through combined microclimatic and mechanical effects. This highlights topography (here, slope steepness) as an often-underappreciated dimension in BEF-research.

Conclusion

Our study has provided comprehensive insights into carrion ecology in subtropical forests. We found that tree species richness had little influence on decomposer diversity, their interactions, or carrion decomposition. This lack of effect may stem (i) from the weak dependence of carrion decomposers on trees, and/or (ii) from a mismatch in spatial scale between local tree neighborhoods and the scales at which decomposer communities respond to environmental variation. In contrast, carrion decomposition was primarily related to the abundance-dependent interactions between flies and ants, with their competition modulated by seasonal and environmental variability. Forest canopy and topography influenced decomposer communities and their interactions. Future research could investigate whether other animal groups and ecosystem functions exhibit similar scale mismatches, and whether some functions remain sensitive to local tree diversity despite the broad movement ranges of the organisms involved. Studies could also test whether different necromass types respond similarly to tree species richness, forest conditions, topography, and decomposer competition

(Barton et al., 2024; Benbow et al., 2019). These insights will help predict and preserve key ecosystem functions of multi-trophic communities in forests.

Author Contributions

Finn Rehling: conceptualization (lead), data curation, formal analysis (lead), investigation (equal), methodology (equal), formal analysis (lead), visualization (lead), writing - original draft preparation. **Matteo Dadda**: investigation (equal), methodology (equal), writing - review & editing (equal). **Marc Nagel**: investigation (equal), methodology (equal), writing - review & editing (equal). **Georg Albert**: formal analysis (support), writing - review & editing (equal). **Helge Bruelheide**: project administration (equal), resources (equal), writing - review & editing (equal). **Jing-Ting Chen**: investigation (support), writing - review & editing (equal). **Heike Feldhaar**: validation (equal), writing - review & editing (equal). **Felix Fornoff**: conceptualization (support), writing - review & editing (equal). **Arong Luo**: project administration (equal), resources (equal), writing - review & editing (equal). **Massimo Martini**: investigation (support), writing - review & editing (equal). **Xiao-Yu Shi**: project administration (equal), resources (equal), writing - review & editing (equal). **Michael Staab**: validation (equal), writing - review & editing (equal). **Xianglu Deng**: investigation (support), writing - review & editing (equal). **Xiao-Juan Liu**: investigation (support), methodology (equal), project administration (equal), resources (equal), writing - review & editing (equal). **Qing-Song Zhou**: project administration (equal), writing - review & editing (equal). **Chao-Dong Zhu**: project administration (equal), resources (equal), supervision (equal), writing - review & editing (equal). **Alexandra-Maria Klein**: funding acquisition, project administration (equal), supervision (equal), writing - review & editing (equal).

Conflict of interest statement

The authors declare that they have no conflict of interest.

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Data availability statement

The dataset is available at Figshare (dx.doi.org/10.6084/m9.figshare.30490391) and via the BEF-China data portal (https://data.botanik.uni-halle.de/bef-china). Data and code can also be accessed for the review via GitHub (https://github.com/nature-rehling/). A permanent option for code sharing will be implemented before publication.

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Supplementary Material: **Carrion decomposition in a subtropical forest biodiversity experiment**

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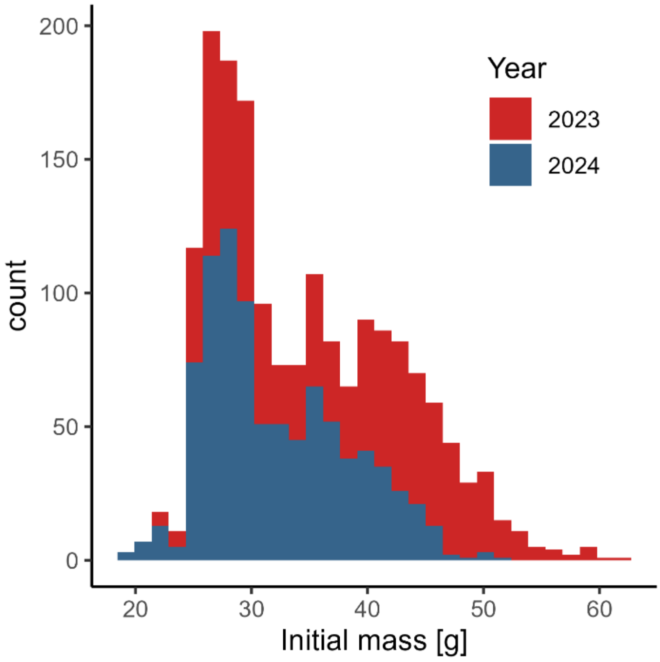

Figure S1: Distribution of initial mass of mice carrion in the BEF-China experiment in 2023 (red) and 2024 (blue). Mice in 2023 weighted ~16% more than mice in 2024 ($\chi^2 = 220.4$, $p < 0.001$).

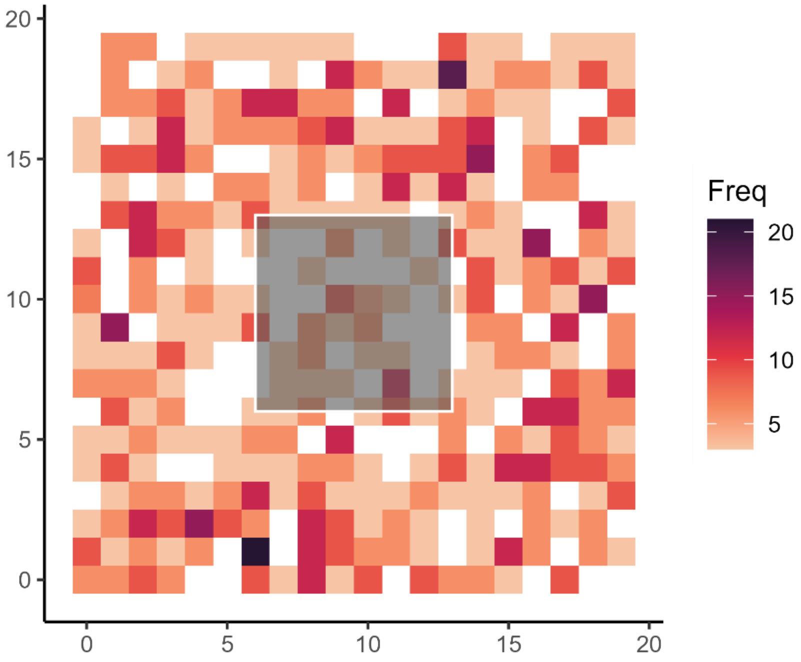

Figure S2: The frequency of locations (i.e. where mice carrions were placed around trees) at the 96 plots of BEF-China. Each plot consists of a grid of 20 × 20 planted trees, and three mice were laid out around each of three trees. The grey shaded area represents the intensively investigated center of the plots, which was largely avoided in order to prevent olfactory conflicts between multiple, co-occurring experiments.

Table S1: Decomposition scoring scheme for mouse carrion decomposition: A seven-stage classification, depending on mouse carrion was primarily decomposed by flies or ants.

Fresh – Score 1 - Eyes decomposed - Fur intact	
Initial decomposition – Score 2: - Fur starts to get loose - Body often bloated - With few, small (< = 2) holes	

Active decomposition – Score 3:

Decomposition by flies:
- Fur mostly loose
- Meat is largely remaining
- Flesh is colored light grey
- Many small maggots visible

Decomposition by ants:
- Dry (but if it was rainy)
- Opened up clean
- Tissue with many (> 2) holes
- Sometimes fur intact, but mostly loose
- Rarely skeleton visible
- If large holes exist, they occur only on one part of the body

Advanced decomposition – Score 4:

Decomposition by flies:
- Intermediate-sized maggots
- Tissue largely gone
- Mouse-like structure often gone
- Meat often dark grey

Decomposition by ants:
- Skeleton is partially visible
- Meat often gone, or black
- Tissue with large hole (1/4 body)

Early melting – Score 5 –

Decomposition by flies:
- Carrion melts into the ground
- Large maggots
- Tissue is still remaining and wet (!)
- Skeleton often detached from tissue
- Often spread in larger area

Early mummification – Score 5:

Decomposition by ants:
- Skeleton / spine visible without flesh
- Meat largely gone
- Often some fur remains

Advanced melting – Score 6:

Decomposition by flies:
- Tissue largely gone
- Parts of soil moist (!) because maggots

  went into ground
- Almost no signs of maggots

Advanced mummification – Score 6:

Decomposition by ants:
- Mummified, dry
- Low activity, few organisms
- Some few

Remains – Score 7:

Decomposition by flies:
- Everything is gone
- No activity of any organism
- Skeleton, fur and small parts of tissue remain
- Soil around the carrion is dry

Supplementary text S1: Extended method description on decomposition scores and relative mass loss

Based on the appearance of carrion in photos, four observers (for photos taken in 2023) or two observers (for photos taken in 2024) assigned a decomposition score from 1 (fresh) to 7 (only remains) to each photo. This scoring system followed the general structure of previously established carrion decomposition stages (Payne et al. 1965, Farwig et al. 2014), but adapted to seven stages. However, as we repeated the experiment across two years, we noticed marked differences in the succession of decomposition between years. In 2023, decomposition was primarily dominated by flies and their larvae, whereas in 2024 decomposition was primarily dominated by ants. Accordingly, the decomposition succession (and the interpretation of scores) was linked to the presumed dominant decomposer.

In addition to assigning scores of decomposition, we noted the dominant decomposer for each photo: flies were assigned when carrion showed signs of liquefication (‘melting’, Fig. 1) or maggots or adult flies were visible in the photographs; ants were assigned when signs of mummification or visible ant activity were present (‘mummification’, Fig. 1). If both, ants and flies were observed on photos, we recorded both as decomposers. More detailed information on characteristics of each state of the decomposition succession is provided in electronic supplementary material (Fig. 1, Table S1).

To ensure a low inter-rater variability in the scoring of photos, all four observers were trained with a test set of random 50 photos from 2023. Observers cross-checked their initial scores, discussed discrepancies, and refined the scoring criteria. After recalibration, the observers evaluated their scoring with another test set of 50 photos and achieved improved consistency. Subsequently, the observers scored independently all photos, and achieved a low inter-rater variability with a near-perfect agreement across years and sites (Cronbach’s $\alpha = 0.97$, $n = 1172$ for four observers, total $n = 2669$). We averaged the decomposition scores across observers per year. However, the quality of photographs from the 2023 experiment was partially compromised due to three main issues: (1) some images did not clearly capture the carrion, (2) others were blurred, and (3) in certain cases, it was unclear whether the carrion was fully decomposed or had been scavenged, leaving only fur behind. As a result, some observers assigned decomposition scores to these photos, while others did not. To address this inconsistency, we only averaged decomposition scores for photos when at least two observers had independently assigned a score. Unfortunately, these issues were only identified after the field season had concluded in 2023. In response, we ensured higher photo quality in the experiment in 2024. To ensure robust scoring despite these limitations, we only averaged decomposition scores when at least two observers had rated the same photo from 2023 (which applied to 96.3% of photos), and excluded photos of carrion with less than two assigned scores from further analysis.

In 2023, we freshly weighed a subset of 176 carrion samples (site A: n = 75, site B: n = 101) from 25 plots (with at least 3 plots per tree species richness level) after two days. Relative (fresh) mass loss after two days was strongly correlated with the assigned decomposition score (GLMM with a betabinomial log link, $R^2 = 0.965$, $\chi^2 = 290.7$, $p < 0.001$; Fig. 2), indicating that carrion decomposition was accurately captured by the photo-based score. To allow for analysis of carrion decomposition on a continuous scale, we converted the decomposition score x into relative (fresh) carrion mass based on the parameters from the GLMM, using the following formula:

$$relative\ carrion\ mass\ (x) = \frac{1}{1 + e^{-(3.6540 - 0.8644 * x)}} \tag{1}$$

Supplementary text S2: Trap nest design and associated issues

Figure S4: Photograph of a baited trap used to sample carrion-associated arthropods in 2023 (left) and 2024 (right). The trap consisted of a large (5 L) and a small plastic bottle (0.5 L). Small openings at ground level allowed arthropods to access the carrion, while the small bottle at the top of the large bottle collected flying insects. Both bottles were filled with 70% ethanol to preserve the arthropods, and traps were emptied after two days. The design of the traps from the two years differs only in how the mice were placed: in 2023, we placed the mouse on a metal grid, while in 2024 we placed it in plastic cups.

In 2023, the carrion was placed on a mesh wire inside the large bottle (Fig. S4). This original design is based on traps described by Farwig et al. (2014). However, the carrion decomposed in our experiment so quickly that it leaked through the grid into the ethanol, making the sampling of arthropods unpleasant. However, due to the decomposition of the carrion, sampling arthropods became particularly unpleasant, as the carrion often leaked into the trap water. The contamination of the water with carrion made it impossible to collect arthropods using a filter, so we had to collect them by hand instead.

In 2024, we revised the trap design by placing the carrion in plastic cups held by a fine metallic wire at the top of the large barrel (Fig. S5). This allowed for cleaner handling of the decomposed mice during sampling and facilitated arthropod collection with a filter as no carrion remains could leak into the preservation fluid. For both years, we collected all arthropods from the trap and brought them to the laboratory at the field station, where we cleaned the specimens with tap water and stored them in 100% ethanol in a deep freezer until species identification.

Upon further analysis, we observed that the number of non-flying arthropod was lower in 2023 than in 2024 across all orders (Fig. S5). In addition, the number of non-flying arthropod in 2023 poorly rank-correlated with those from the same plots in 2024, maybe due to the issues with the unpleasant, and therefore insufficient collection of arthropods in 2023 (carrion leakage). We believe the revised design in 2024 resulted in more accurate sampling and a more comprehensive arthropod assemblage. For this reason, we decided to exclude the samples with non-flying arthropods (ants and the group of other arthropods) from 2023, and focus the analysis only on the samples from 2024. In addition, we excluded arthropod by-catch from the traps because they also captured carrion-associated predators that were hunting flies, for instance nine spider species, two wasp species (*Vespa velutina* and *Vespula flaviceps*), one fly species (Asilidae), and a mantis (*Statilia maculata*). Traps from four of the 96 plots were pushed over and excluded from the analyses.

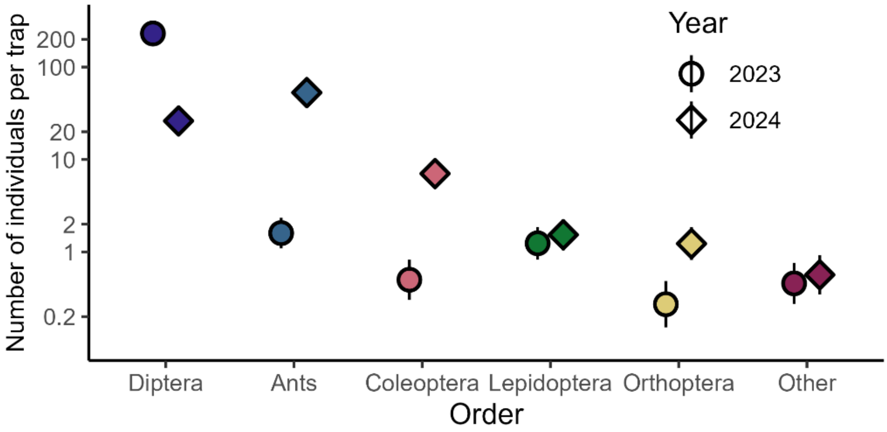

Figure S5: Number of individuals for mice carrion-feeding arthropods; here orders of diptera, ants (Hymenoptera), coleoptera, lepidoptera, orthoptera and other arthropods in baited traps with carrion in 2023 and 2024. Predicted mean ± 95%-CI. Note that the y-axis is on a log-scale.

The carrion-baited traps captured nearly complete necrophagous communities of flies and ants, while other decomposers were somewhat underrepresented, particularly at shallow forest slopes (Table S2, Fig. 6-7). Mean sample coverage was 98.2% for flies in 2023, 96.3% for flies in 2024, 96.0% for ants in 2024, and 76.7% for other decomposers in 2024, considering only traps that collected more than one species of a decomposer group (see Statistical analysis in main text).

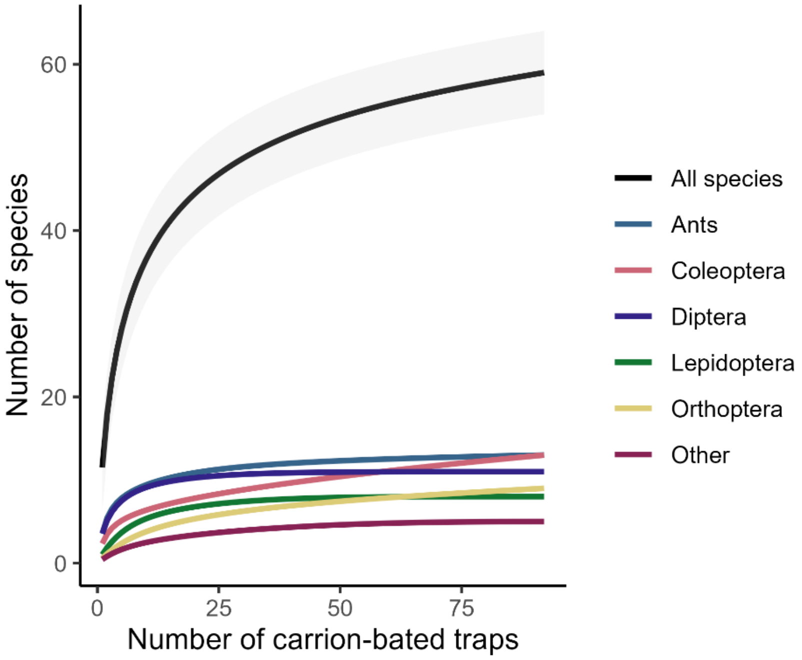

Figure S6: Rarefaction curves showing species richness of different groups of decomposers in relation to the number of carrion-baited traps, after two days of trap presence in the forest in 2023 and 2024 in BEF-China. Predicted mean ± 95% CI.

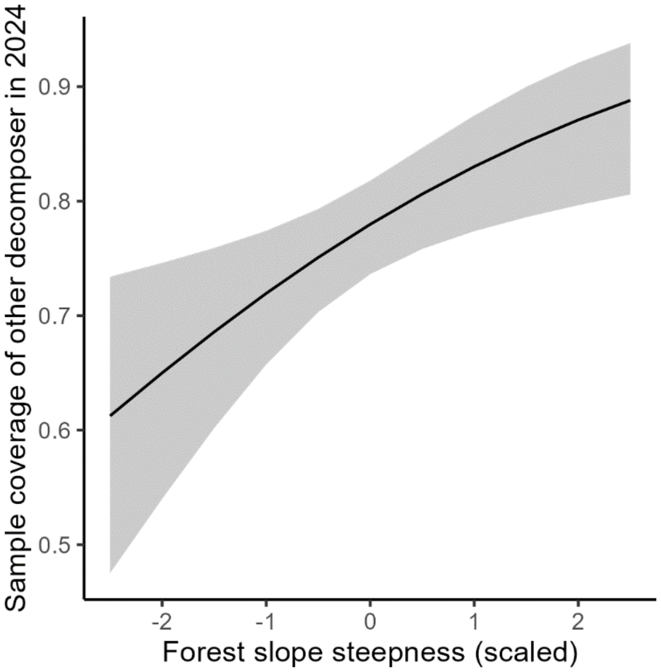

Figure S7: Sample coverage of other decomposers in mice carrion-baited traps along the forest slope gradient in BEF-China in 2024. Predicted mean ± 95% CI.

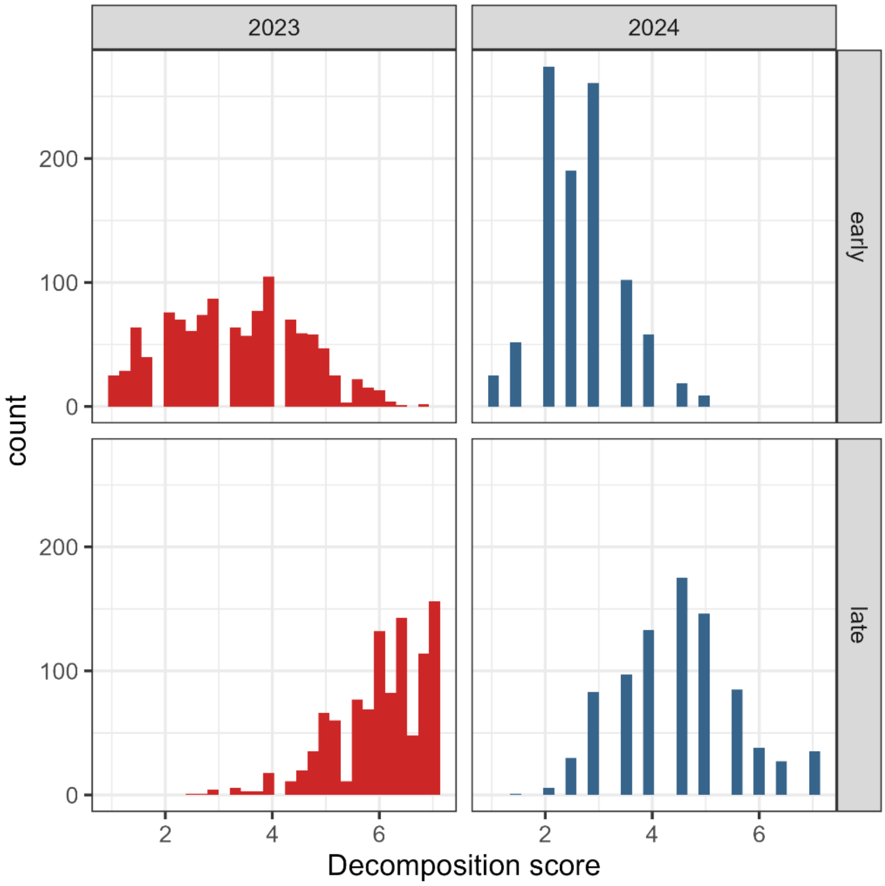

Figure S8: Distribution of mice carrion decomposition scores after the first photo survey (‘early’; i.e. 1-3 days), and the second survey (‘late; 4-7 days). There is a strong left-skewed distribution of scores in the second survey in 2023, with c. 40% of mice being fully decomposed (i.e. a score ≥ 6.5).

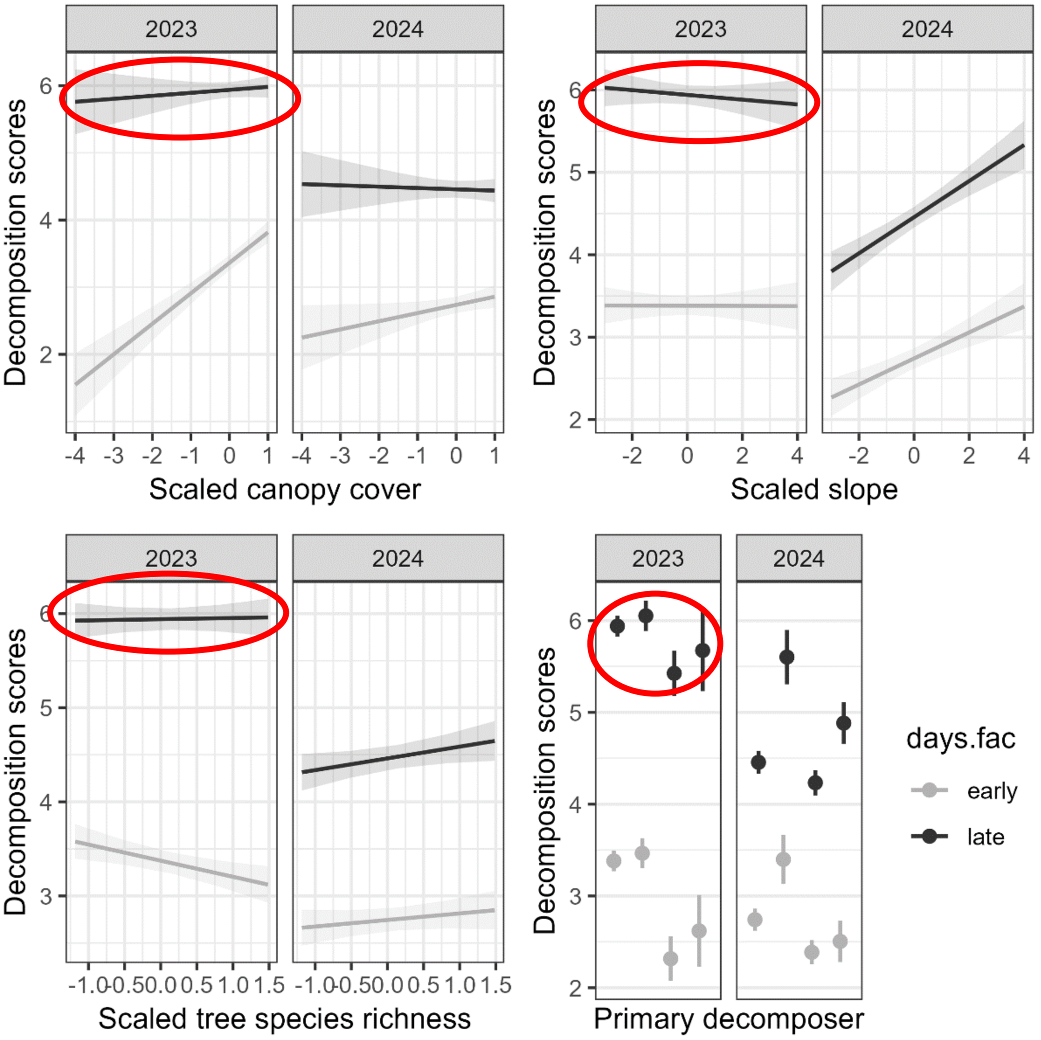

Figure S9: The effect of canopy cover, slope, tree species richness and primary decomposer on the decomposition of mice carrion after 1-3 days (‘early’, light grey) and 4-7 days (‘late’, dark grey). The strong left-skewed distribution of scores in the late survey in 2023 (Fig. S8) led to right censoring and a loss of variation, potentially reducing the effect size of the factors (red circle) in the model that included interaction effects of a factor with experiment duration (‘days.fac’) and year on mice decomposition. Mean ± 95%CI.

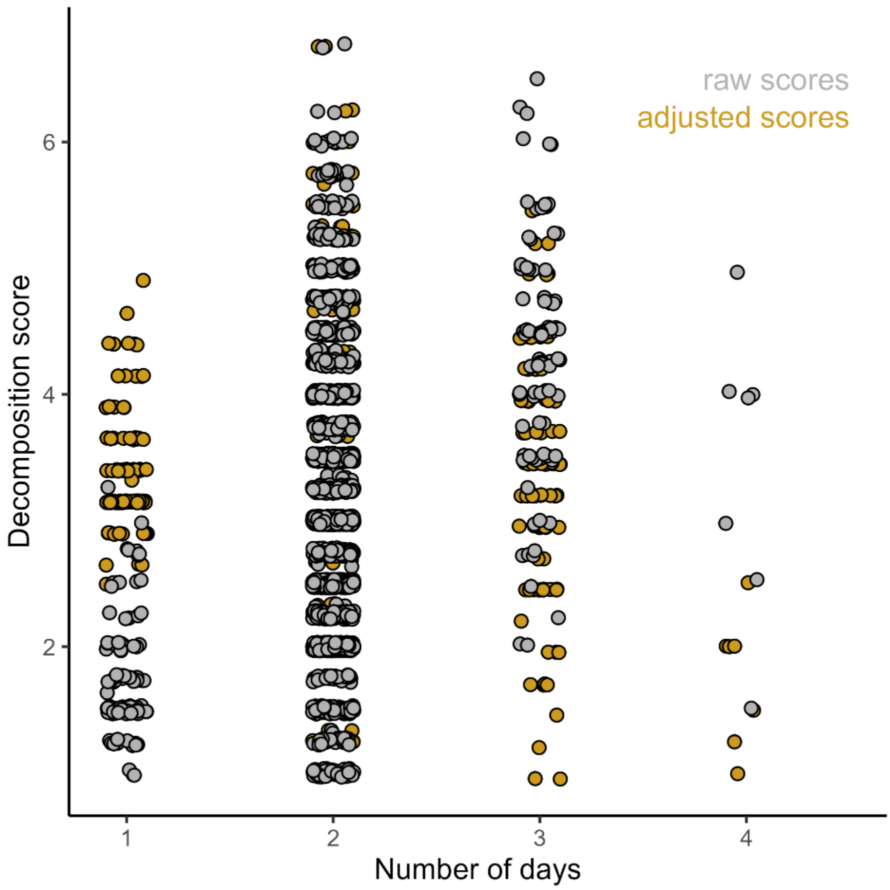

Figure S10: The effect of number of days until a photo was taken on the decomposition stage (i.e. the score) of mice carrions on photos. There was a strong positive relationship between the number of days until a photo of was taken and the decomposition score of a mouse (Wald-$\chi^2 = 55.7$, $p < 0.001$). We therefore adjusted the scores for differences in the number of days between photos so that scores were representative for photos taken on the second day.

Table S2: Taxonomic list of invertebrate decomposer species collected in carrion-baited traps in the BEF-China experiment (2023–2024, see supplementary text S2).

Order	Family	Genus	Species	2023	2024
Flies					
Diptera	Calliphoridae	Chrysomya	*Chrysomya megacephala*	10825	676
Diptera	Calliphoridae	Lucilia	*Lucilia porphyrina*	7672	177
Diptera	Calliphoridae	Hemipyrellia	*Hemipyrellia ligurriens*	1008	725
Diptera	Sarcophagidae	Sarcophaga	*Sarcophaga peregrina*	619	1024
Diptera	Calliphoridae	Chrysomya	*Chrysomya pinguis*	1213	55
Diptera	Muscidae	Dichaetomyia	*Dichaetomyia* sp.	340	47
Diptera	Calliphoridae	Lucilia	*Lucilia bazini*	252	106
Diptera	Muscidae	Hydrotaea	*Hydrotaea chalcogaster*	6	106
Diptera	Muscidae	Atherigona	*Atherigona* sp.	40	11
Diptera	-	-	Morphospecies #3	51	0
Diptera	Muscidae	Dichaetomyia	*Dichaetomyia bibax*	4	21
Diptera	Muscidae	Dichaetomyia	*Dichaetomyia* sp.	21	0
Diptera	-	-	Morphospecies #1	11	0
Diptera	-	-	Morphospecies #2	7	0
Diptera	Stratiomyidae	Ptecticus	*Ptecticus aurifer*	3	4
Diptera	Limoniidae		Limoniidae	3	0
Ants					
Hymenoptera	Formicidae	Crematogaster	*Crematogaster cf. rogenhoferi*	sampled	1294
Hymenoptera	Formicidae	Pheidole	*Pheidole nodus*	sampled	857
Hymenoptera	Formicidae	Polyrhachis	*Polyrhachis illaudata* (sensu lato)	sampled	729
Hymenoptera	Formicidae	Polyrhachis	*Polyrhachis dives*	sampled	503
Hymenoptera	Formicidae	Lepisiota	*Lepisiota* sp. (potentially *xichangensis*)	sampled	375
Hymenoptera	Formicidae	Camponotus	*Camponotus pseudorritans*	sampled	342
Hymenoptera	Formicidae	Pheidole	*Pheidole pieli*	-	342
Hymenoptera	Formicidae	Ectomomyrmex	*Ectomomyrmex astutus*	sampled	211
Hymenoptera	Formicidae	Aphaenogaster	*Aphaenogaster* sp.	-	199
Hymenoptera	Formicidae	Tetramorium	*Tetramorium wroughtonii*	-	69
Hymenoptera	Formicidae	Leptogenys	*Leptogenys kitteli*	-	12
Hymenoptera	Formicidae	Odonthomachus	*Odonthomachus monticola*	-	11
Hymenoptera	Formicidae	Anochetus	*Anochetus risii*	-	2
Other decomposer					
Blattodae	Blattidae	Periplaneta	*Periplaneta fuliginosa*	-	3
Blattodae	Blaberidae	Pseudoglomeris	*Pseudoglomeris* sp.	-	3
Coleoptera	Staphylinidae	Aleochara	*Aleochara postica*	sampled	111
Coleoptera	Carabidae	Brachinus	*Brachinus sp.*	-	1
Coleoptera	Scarabaeidae	Copris	*Copris* sp. 1	-	8
Coleoptera	Scarabaeidae	Copris	*Copris* sp. 2	-	93
Coleoptera	Passalidae	Diamesus	*Diamesus osculans*	-	1
Coleoptera	Silphidae	Necrophila	*Necrophila cyaniventris*	sampled	-
Coleoptera	Silphidae	Necrophila	*Necrophila jakowlewi*	-	1
Coleoptera	Silphidae	Nicrophorus	*Nicrophorus nepalensis*	sampled	-
Coleoptera	Scarabaeidae	Onthophagus	*Onthophagus* sp. 1	-	364
Coleoptera	Scarabaeidae	Onthophagus	*Onthophagus* sp. 2	-	48
Coleoptera	Scarabaeidae	Paragymnopleurus	*Paragymnopleurus* sp.	sampled	19
Coleoptera	Curculionidae	Phytoscaphus	*Phytoscaphus* sp.	-	4
Coleoptera	Staphylinidae	Platydracus	*Platydracus brevicornis*	sampled	2
Coleoptera	Scarabaeidae	Sophrops	*Sophrops* sp.	-	1
Coleoptera	Carabidae	Trigonotoma	*Trigonotoma lewisii*	-	1

Table S2 (cont.): Taxonomic list of invertebrate species collected in carrion-baited traps in the BEF-China experiment (2023–2024, see supplementary text S2).

Order	Family	Genus	Species	**2023**	**2024**
Other decomposer					
Dermaptera	Anisolabididae	Gonolabis	*Gonolabis* sp.	-	14
Hemiptera	Rhyparochromidae	Metochus	*Metochus* sp.	sampled	30
Lepidoptera	Geometridae	Amblychia	*Amblychia angeronaria*	-	8
Lepidoptera	Crambidae	Glyphodes	*Glyphodes* sp.	-	34
Lepidoptera	Nymphalidae	Lethe	*Lethe syrcis*	3	-
Lepidoptera	Geometridae	-	Morphospecies #4	45	46
Lepidoptera	-	-	Morphospecies #5	9	17
Lepidoptera	Nymphalidae	Mycalesis	*Mycalesis mineus*	4	5
Lepidoptera	Geometridae	Ophthalmitis	*Ophthalmitis* sp. 1	3	7
Lepidoptera	Nymphalidae	Panthema	*Panthema adelma*	18	4
Lepidoptera	Geometridae	Parapercnia	*Parapercnia giraffata*	1	-
Lepidoptera	Geometridae	Plagodis	*Plagodis* sp.	17	-
Lepidoptera	Erebidae	Spirama	*Spirama retorta*	7	-
Lepidoptera	Erebidae	Sypnoides	*Sypnoides fumosa*	10	22
Orthoptera	Tettigoniidae	Atlanticus	*Atlanticus fengyangensis*	sampled	10
Orthoptera	Acrididae	Ceracris	*Ceracris kiangsu*	-	6
Orthoptera	Tettigoniidae	China	*China mantispoides*	-	1
Orthoptera	Rhaphidophoridae	Diestramima	*Diestramima excavata*	-	33
Orthoptera	Acrididae	Hieroglyphus	*Hieroglyphus annulicornis*	-	4
Orthoptera	Tettigoniidae	Mecopoda	*Mecopoda niponensis*	-	1
Orthoptera	Tettigoniidae	Meloimorpha	*Meloimorpha japonica*	-	9
Orthoptera	-	-	Morphospecies #6	-	1
Orthoptera	Gryllidae	Xenogryllus	*Xenogryllus marmoratus*	-	59
Scutigeromorpha	Scutigeridae	-	Morphospecies #7	-	2

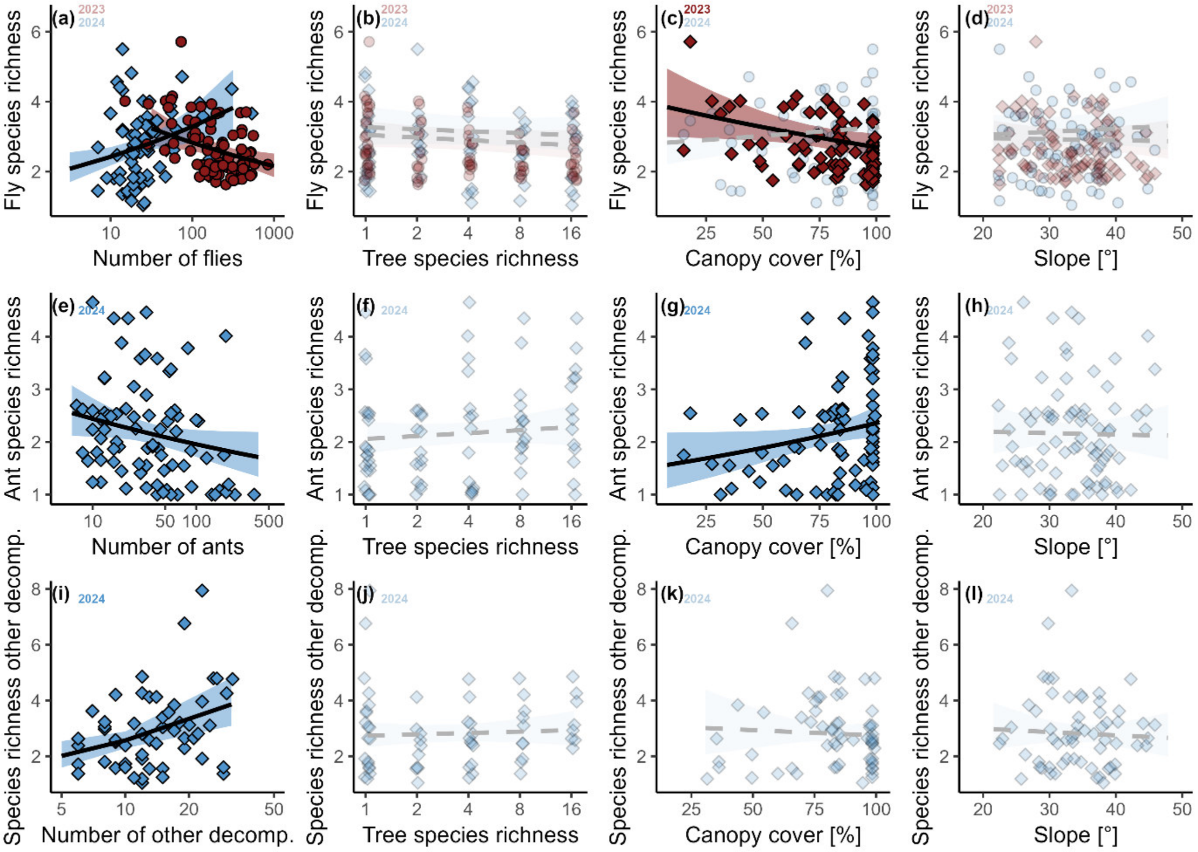

Figure S11: Relationship between the expected richness of species (i.e. species richness corrected for differences in sampling coverage) of (a-d) flies, (e-h) ants, (i-l) and other decomposers in mice carrion-baited traps after two days in the BEF-China experiment in 2023 (red circles) and 2024 (blue diamonds) and their abundances (a, e, i) or forest environmental factors: (b, f, j) tree species richness (log2-transformed), (c, g, k) canopy cover and (d, h, l) slope steepness. Solid lines with colored intervals indicate statistically significant relationships ($p < 0.05$), while grey dashed lines with blurred points represent non-significant relationships. Lines show model predictions (mean), and shaded ribbons indicate 95% confidence intervals (mean ± 95% CI)

Supplementary text S3: *Community composition analysis of decomposers*

The relationship between the species composition of different groups of arthropods (flies, ants, and other decomposers) in carrion-baited traps (response variable) and log2-transformed tree species richness, canopy cover, and forest slope steepness (fixed factors) was analyzed using permutational analysis of variance (PERMANOVA) (Anderson 2017). All continuous fixed factors were z-transformed before analysis. Because the models with flies included data from two sampling years, year was included as a factor. The abundance of species was Hellinger-transformed before analysis. The Bray-Curtis index was calculated as a measure of dissimilarity between samples (Bray & Curtis 1957). To account for the nested structure of the design, arthropod samples were permuted within study sites, with 9999 permutations used to calculate a quasi-F statistic. Differences among arthropod samples from traps were visualized using nonmetric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity, using two dimensions. Plots where traps were knocked over in one of the two years were excluded in the analysis.

Table S3: PERMANOVA summary on the relationship between arthropod decomposer and tree species richness, canopy cover and slope steepness in the BEF-China experiment.

Community (Year)	**Predictor**	**Df**	**SS**	**R²**	**F**	**p**
Flies in 2023	Tree species richness	1	0.04	0.004	0.38	0.888
	Canopy cover	1	1.27	0.109	11.12	**<0.001**
	Slope	1	0.11	0.010	1.00	0.359
	Residual	87	9.94	0.853		
Flies in 2024	Tree species richness	1	0.27	0.022	1.80	0.242
	Canopy cover	1	0.76	0.060	5.03	0.094
	Slope	1	0.17	0.013	1.10	0.312
	Residual	76	11.56	0.906		
Ants in 2024	Tree species richness	1	0.43	0.015	1.33	0.451
	Canopy cover	1	1.31	0.046	4.08	0.092
	Slope	1	0.90	0.032	2.80	**0.001**
	Residual	80	25.75	0.903		
Other decomposers in 2024	Tree species richness	1	0.08	0.006	0.39	0.972
	Canopy cover	1	0.95	0.064	4.39	0.175
	Slope	1	0.28	0.019	1.28	0.215
	Residual	62	13.46	0.902		

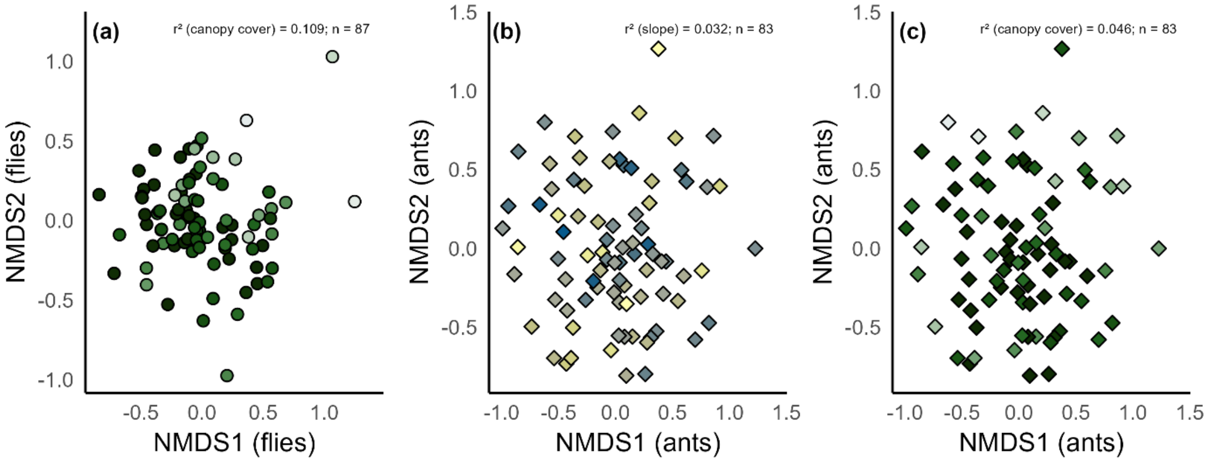

Figure S12: Nonmetric multidimensional scaling (NMDS) ordination of arthropod decomposer abundances based on Bray-Curtis dissimilarities in mice carrion-bated traps in BEF-China. The dissimilarity of (a) fly communities between open and closed forests in 2023, and (b, c) the dissimilarity of ant communities between forests (c) with shallow and steep slopes and (d) between open and closed forests in 2024.

Table S3: Mixed-model analyses of variance of the effects of tree species richness, canopy cover, slope steepness, fly and ant abundance on the proportion of mice carrion primarily decomposed by flies (in 2023) and by ants (in 2024) in the BEF-China experiment. Bold Wald-χ^2 values indicate significant effects ($p < 0.05$).

Predictors	**Decomposition by flies in 2023**	**Decomposition by ants in 2024**
	Chisq	**Chisq**
Initial mass	0.18	0.15
Tree richness	1.65	2.44
Canopy cover	**24.08***	0.39
Slope steepness	0.99	0.10
Number of flies	0.64	**6.42***
Number of ants	0.56	**11.02***

Table S4: Mixed-model analyses of variance of the effects of initial mass of mice carrion, tree species richness, canopy cover, slope steepness, the primary decomposer (ants vs. flies vs. both vs. NA), year and their interactions on the relative mass of carrion remaining after two days (i.e. decomposition rate) in the subtropical forest of BEF-China in 2023 and 2024.

Predictors	% remaining mass		
	DF	Chisq	p
Initial mass	1	1.61	**0.205**
Tree species richness	1	2.59	0.108
Canopy cover	1	21.42	**< 0.001**
Slope steepness	1	0.12	0.728
Primary decomposer	3	112.63	**< 0.001**
Year	1	19.09	**< 0.001**
Year × initial mass	1	1.82	0.177
Year × tree species richness	1	9.90	**0.002**
Year × canopy cover	1	33.09	**< 0.001**
Year × slope steepness	1	9.59	**0.002**
Year × primary decomposer	3	4.19	0.241

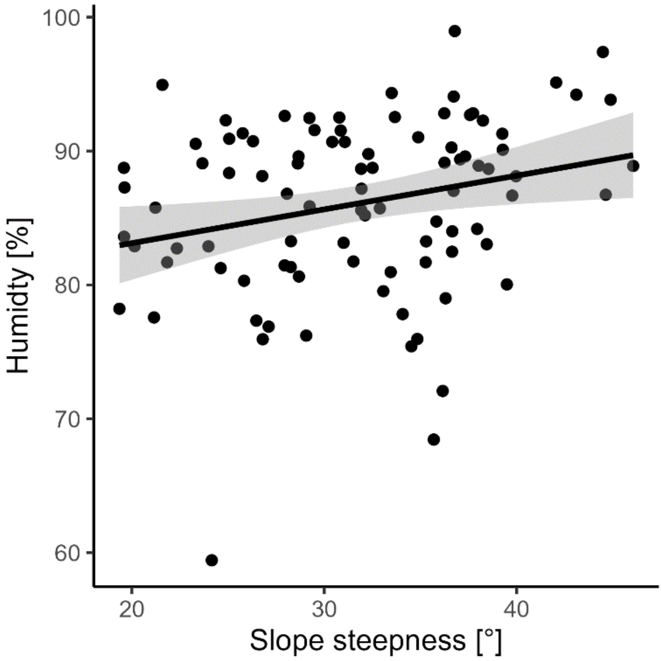

Figure S13: Humidity during the experiment in relation to the slope steepness in BEF-China.