

1                   **Carrion decomposition in a subtropical forest biodiversity experiment**

2     Running title: Carrion decomposition in BEF-China

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26    **Abstract**

- 27    (1) Tree species richness promotes the diversity of higher trophic levels and ecosystem  
28    functioning. Tree species richness may thus also affect communities of insect  
29    decomposers, and through this, accelerate the decomposition of animal carrion.  
30    However, these effects might be masked by other factors driving decomposition, such  
31    as forest structure, topography, and competition between different decomposer groups.
- 32    (2) We placed 1719 dead mice and observed their decomposition for up to seven days, and  
33    captured carrion decomposers with mouse-baited traps across 96 plots in the  
34    worldwide largest forest biodiversity experiment (BEF-China) in subtropical China in  
35    May 2023 and July 2024.
- 36    (3) We sampled 30,975 decomposer invertebrates from at least 65 species of nine orders.  
37    The abundance, species richness, and composition of decomposer groups (flies, ants,  
38    other arthropods) was related to sampling year, canopy cover and slope steepness, but  
39    not to tree species richness. Flies (Calliphoridae, Sarcophagidae and Muscidae) were  
40    nine times more abundant and were more often the primary decomposer of carrion in  
41    2023 than in 2024, especially in closed forests. In contrast, when flies were rare in  
42    2024, ants primarily decomposed carrion, especially in areas with more ants or fewer  
43    flies, independently of environmental factors or tree species richness.
- 44    (4) Carrion decomposition was accelerated in 2023 compared to 2024, in closed forests  
45    and partially on steeper slopes, but was not influenced by tree species richness.  
46    Carrion decomposition was faster when flies instead of ants were the primary  
47    decomposers. When both insect groups co-occurred on carrion, ants typically  
48    outcompeted flies, resulting in slower decomposition.
- 49    (5) This study shows that carrion decomposers were largely unaffected by tree species  
50    richness, and consequently, carrion decomposition also appeared to be insensitive to

51 bottom-up effects of tree species richness. Instead, our results highlight the interactive  
52 effects of temporal and environmental factors on decomposer communities of small  
53 vertebrate carrion, the competitive interactions between decomposer groups, and  
54 decomposition rates. Our findings thus challenge the general expectation that tree  
55 diversity promotes higher-trophic diversity and ecosystem functioning.

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

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62    **Introduction**

63    Tree diversity can enhance ecosystem functioning through mechanisms such as niche  
64    partitioning, facilitation, and multitrophic interactions, which improve the efficiency of  
65    resource use and promote the stability of ecological functions (Trogisch et al., 2021). For  
66    example, biodiversity-ecosystem functioning (BEF-)experiments have shown that mixtures of  
67    tree species, in particular those with complementary traits, can increase forest productivity  
68    and carbon sequestration (Bongers et al., 2021; Depauw et al., 2024; Huang et al., 2018; Liu  
69    et al., 2018), and promote the diversity of other organisms (Chen et al., 2023; Fornoff et al.,  
70    2019; Schultdt et al., 2019) and their functions (Beugnon et al., 2023; Fornoff et al., 2019;  
71    Plath et al., 2012; Schnabel et al., 2025; Vehviläinen & Koricheva, 2006). This has made  
72    BEF-research a key contributor to forest restoration strategies (Baeten et al., 2019) and has  
73    helped justifying biodiversity conservation to society and policymakers beyond purely ethical  
74    and aesthetic arguments (Messier et al., 2022). Yet despite these insights, many ecological  
75    functions, particularly those not centered on trees, remain understudied in BEF-experiments  
76    (Grossman et al., 2018). One such example is animal carrion decomposition, a key process in  
77    nutrient cycling and food web dynamics.

78    When an animal dies, its body becomes a concentrated, ephemeral and spatially unpredictable  
79    source of energy and nutrients, which is attractive to a diverse community of decomposers  
80    and scavengers throughout the food web (Carter et al., 2006; Wilson & Wolkovich, 2011).  
81    Among them, arthropods are central to carrion decomposition (Amendt et al., 2004; Büchner  
82    et al., 2024; Paula et al., 2016; Payne, 1965; Wierer et al., 2024), and this role has been  
83    amplified by the decline of vertebrate scavengers in many regions (Oaks et al., 2004;  
84    Sonawane et al., 2025). Flies, especially blow and flesh flies, lay eggs in natural openings,  
85    from which larvae emerge and rapidly consume the tissue. As they feed, the larvae secrete  
86    digestive enzymes that break down proteins and fats, causing the carrion to soften, liquefy,

87 and essentially ‘melt’ into the ground (Fig. 1). Ants and beetles also feed on the carrion and  
88 preying on fly larvae as they compete for dominance. When ants act as primary decomposers,  
89 they often cover the carrion with soil or suppress other decomposers, which can result in a  
90 drying and eventual mummification of the carrion (Fig. 1). Interspecific competition and  
91 predation among decomposers can therefore influence both the rate of decomposition and the  
92 community structure of arthropods present on carrion (de Jong et al., 2021; Wei et al., 2023).

93 Although animal carrion represents a relatively small portion of the total detritus pool in  
94 forest ecosystems (Barton et al., 2019), it is a local hotspot of arthropod activity and exerts a  
95 disproportionately large influence on the diversity of consumers and nutrient cycling (Carter  
96 et al., 2006; Johnson-Bice et al., 2023), ultimately enhancing the functioning of forests.

97 Tree diversity positively affects arthropod diversity through increased habitat complexity and  
98 resource availability (Schuldt et al., 2019; Wang et al., 2025), but the strength of this effect  
99 likely depends on mobility and habitat use of arthropods (Guo et al., 2021; Staab et al., 2014)  
100 and may weaken with increasing trophic levels (Scherber et al., 2010; Schuldt et al., 2019).

101 Because animal carrion decomposition is related to the diversity and community composition  
102 of arthropods in forest ecosystems (Barton & Evans, 2017; Farwig et al., 2014; Marschalek &  
103 Deutschman, 2022), positive tree diversity effects on arthropod decomposers may indirectly  
104 accelerate the decomposition of carrion in diverse forests. However, testing effects of tree  
105 diversity on animal carrion decomposition in forests is challenging because other abiotic and  
106 biotic factors may interact with tree diversity in complex ways.

107 Microclimatic conditions, shaped by canopy structure (Schnabel et al., 2025), may play a  
108 particularly important role in carrion decomposition. In open forests, higher temperatures may  
109 attract a more diverse arthropod community, and thus, could accelerate decomposition rates  
110 directly and indirectly (Achury et al., 2023). In contrast, drying (or ‘mummification’) of  
111 carrion may limit microbial activity and access for some decomposers, potentially slowing the

112 process (Finaughty & Morris, 2019). In closed forests, cooler and moister conditions may  
113 either reduce decomposer activity or, by preserving moisture, make carrion more accessible to  
114 arthropods and hence promote decomposition. The direction and magnitude of microclimatic  
115 effects on decomposition may therefore depend on interactions between the forest  
116 environment, the arthropod community and seasons (de Carvalho & Linhares, 2001; Farwig et  
117 al., 2014; Finaughty & Morris, 2019; Paula et al., 2016).

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

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

134 The BEF-China experiment (Bruelheide et al., 2014), with its experimental manipulations of  
135 tree species richness and topography, provides an ideal setting to address these questions  
136 combined. In this study, we investigated how the forest environment, particularly tree species

137 richness, influences decomposer communities and animal carrion decomposition. We  
138 analyzed the relative importance of tree diversity effects in comparison to other factors,  
139 including canopy cover, forest slope steepness, and the role of primary decomposers.  
140 Furthermore, we explored how environmental effects on carrion decomposition were  
141 mediated by their effects on the decomposer community. We hypothesized that (i) tree species  
142 richness increases the diversity of carrion decomposers, either by providing a wider range of  
143 resources and habitats, or by altering forest structure and microclimate, and thereby,  
144 accelerate the decomposition of animal carrion; (ii) canopy cover influences decomposer  
145 diversity and carrion decomposition rates, with the direction of this effect being dependent on  
146 season, arthropod communities, or their interaction; (iii) slope steepness affects  
147 decomposition directly by increasing carrion fragmentation and aeration and indirectly via  
148 impacts on microclimatic conditions or the decomposer communities; and (iv) carrion  
149 decomposition strongly depends on the main decomposer groups, especially ants, whose  
150 effects could be either negative (through competition with other decomposers) or positive  
151 (through direct consumption), depending on local context and time.

152 **Material and methods**

153 **Study area**

154 This study took place in the BEF-China experiment, which is located in a hilly region near  
155 Xingangshan, Jiangxi Province, China ( $117^{\circ}54' E$ ,  $29^{\circ}07' N$ ) between 28 May – 5 June 2023  
156 and 30 June – 25 July 2024. The mean annual temperature and precipitation are  $16.7^{\circ}C$  and  
157 1800 mm. The natural vegetation of this region is a subtropical broad-leaved forest with  
158 evergreen tree species being predominant. BEF-China encompasses two study sites which  
159 were established in 2009 (site A) and 2010 (site B), are 4 km apart from each other and  
160 together occupy 50 ha. This makes BEF-China the worldwide largest tree diversity  
161 experiment ([www.treedivnet.ugent.be](http://www.treedivnet.ugent.be)) (Paquette et al., 2018). A total of 566 study plots of

162 25.8 m × 25.8 m were set up with 400 tree seedlings in a 20 × 20 grid with a spacing of 1.29  
163 m between each seedling (i.e. a density of 0.6 trees per m<sup>2</sup>). The gradient of tree species  
164 richness comprises 1, 2, 4, 8, 16, and 24 tree species per plot, obtained from a pool of 40 tree  
165 species. Each site has a pool of 24 broad-leaved native tree species, with eight tree species  
166 shared between sites. All trees are represented in monocultures and all higher diversity  
167 mixtures represent randomly assigned mixtures of tree species according to a broken-stick  
168 design. The position of individual trees within plots, as well as the different levels of tree  
169 species richness among plots were randomly assigned. All plots were initially weeded twice a  
170 year to reduce growth of competing forbs between trees. Site A ranges in altitude from 105 m  
171 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°  
172 (site A = 25°, site B = 30°). An extended description of the BEF-China experiment is provided  
173 in Bruelheide et al. (2014). In our study, we used a subset of 96 plots (48 plots for site A, 48  
174 plots for site B), with tree species richness levels represented as follows: 32 monocultures, 16  
175 two-species mixtures, 16 four-species mixtures, 16 eight-species mixtures, 10 sixteen-species  
176 mixtures, and all 6 available twenty-four-species mixtures. This ensured a balanced  
177 representation of each tree species level across the gradient.

## 178 Carrion decomposition experiment

179 To measure decomposition of vertebrate carrion, we purchased frozen carriions of white *Mus*  
180 *musculus* (house mouse) through an online retailer in China. We stored the frozen mice in a  
181 deep freezer (-18°C), and weighed them before the experiment. Initial mass of frozen mice  
182 was on average 34.6 g, with 95% of values ranging from 24.5 g to 50.8 g. Mice used for the  
183 experiment in 2023 were c. 15% heavier than those used in 2024 (37.2 g vs 32.1 g;  
184 Supplementary Figure S1).

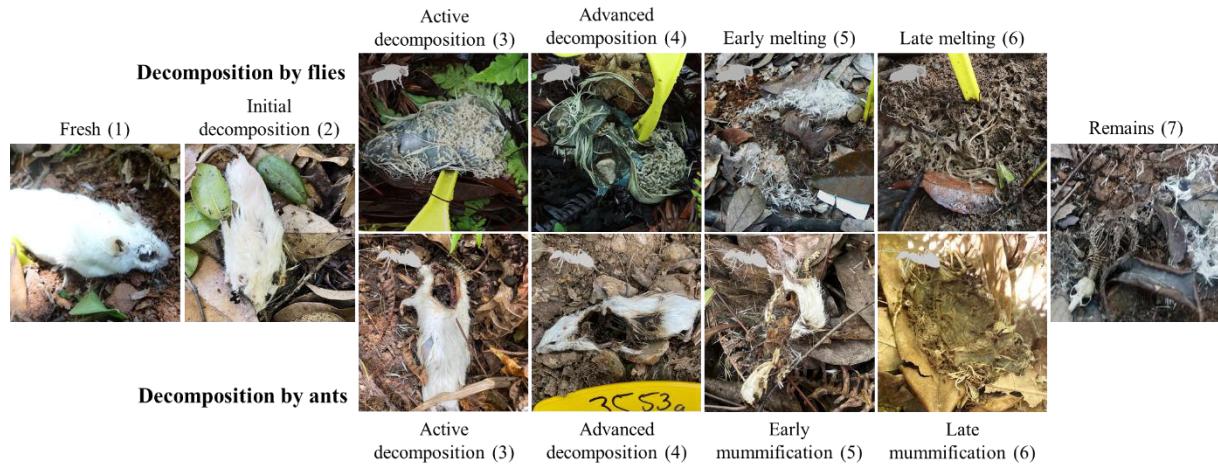
185 To study carrion decomposition along the experimental tree diversity gradient, we laid out three  
186 mouse carrion around each of three trees in a plot (n = 9 carrion per plot). The location of trees

187 around which the carrion was placed was assigned randomly in the field, avoiding the  
188 intensively studied centres of the plots to reduce spatial overlap with other experiments in BEF-  
189 China (Fig. S2). In 2023, the decomposition experiment spanned nine days (28 May–5 June)  
190 and was completed quickly with assistance from local helpers. In 2024, the experiment was  
191 conducted over 27 days (30 June–25 July), and initiated on eleven separate days, covering an  
192 average of nine plots per session (range: 6–17 plots). The extended time frame in 2024 resulted  
193 from the experiment being conducted by a single researcher without additional support.

194 In total, we laid out 1719 carriions (3 mice × 3 trees × 96 plots across the two sites × 2 years;  
195 one plot was omitted in 2023). The carrion was not protected from scavenging by vertebrates.  
196 During the experiment, a total 102 mice (12.3%) in 2023 and 291 mice (34.4%) in 2024 were  
197 lost. Complete loss of all nine carriion occurred at one plot in 2023 and at eight plots in 2024.  
198 To monitor carriion decomposition, we took photos of decomposing carriion twice during the  
199 experiment; one photo was taken usually two days after deployment ( $\pm 1$  d, mean  $\pm 95\%$  CI,  
200 but see ‘Statistical methods), and a second photo after 4.5 days ( $\pm 1$  d). Time intervals for photos  
201 were based on the observation of a pilot study in 2023 indicating that many carriions were fully  
202 decomposed after 7 days.

### 203 **Decomposition scores and relative mass loss**

204 Based on the appearance of carriion in photos, four observers (for photos taken in 2023) or two  
205 observers (for photos taken in 2024) assigned a decomposition score from 1 (fresh) to 7 (only  
206 remains) to each photo (Fig. 1). This scoring system followed the general structure of previously  
207 established carriion decomposition stages (Farwig et al., 2014; Payne, 1965), but adapted to  
208 seven stages. In addition to assigning scores of decomposition, we noted the dominant  
209 decomposer for each photo: flies were assigned when carriion showed signs of liquefaction  
210 (‘melting’, Fig. 1) or maggots were visible in the photographs; ants were assigned when signs  
211 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. Although these pathways are typically distinct, decomposition by flies can also lead to mummification of a carrion under dry conditions (e.g., in open forest habitats). Images by Finn Rehling and Marc Nagel; icons of the fly and ant from Phylopic ([www.phylopic.org](http://www.phylopic.org)).

212 were observed on photos, we recorded both as decomposers. More detailed information on  
 213 characteristics of each state of the decomposition succession is provided in electronic  
 214 supplementary material (Fig. 1, Table S1, Supplementary text S1).

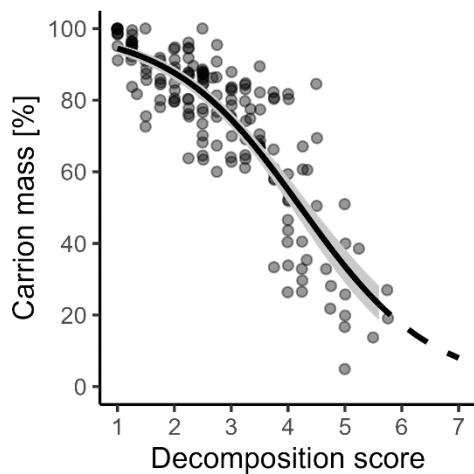
215 Observers were trained on test photos to harmonize criteria before scoring all images  
 216 independently. Agreement among observers was near-perfect across years and sites  
 217 (Cronbach's  $\alpha = 0.97$ ,  $n = 2669$ ). In 2023, when photo quality was occasionally compromised  
 218 (Text S1), we only averaged scores if at least two observers rated the same photo (96.3% of  
 219 cases), excluding the remainder.

220 In 2023, we freshly weighed a subset of 176 carrion samples (site A:  $n = 75$ , site B:  $n = 101$ )  
 221 from 25 plots after two days. Relative (fresh) mass loss was strongly correlated with photo-  
 222 based decomposition scores (GLMM with betabinomial log link:  $R^2 = 0.965$ ,  $\chi^2 = 290.7$ ,  $p <$   
 223 0.001; Fig. 2), confirming the validity of the scoring approach. We converted ordinal scores (x)  
 224 into a continuous measure of relative carrion mass using the GLMM parameters (Fig. 2):

225

$$\text{relative carrion mass } (x) = \frac{1}{1 + e^{-(3.7183 - 0.8801*x)}} \quad (1)$$

226 More detailed information on the decomposition scores and the calculation of relative mass  
 227 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  $\pm$  95% CI.

228

229 **Sampling and identification of arthropod decomposers**

230 In the week after we completed the decomposition experiment, we exposed one trap baited with  
 231 mouse carrion at the center of each plot to sample carrion-associated arthropod communities  
 232 (Fig. S4, Fig. S5). The trap consisted of a large plastic container (5 L) and a small plastic bottle  
 233 (0.5 L). The barrel was cut at the lower middle to allow arthropods access to the carrion, and  
 234 the small bottle had a hole in the bottom, allowing it to be placed on top of the large barrel to  
 235 capture flying arthropods. The carrion was placed on a mesh wire in 2023, and in plastic cups  
 236 in 2024 inside the large bottle (Fig. S4). The traps were partially buried in the soil to protect  
 237 them from vertebrate scavengers, and the bottles were filled with salt-soap water, with detergent  
 238 added to break surface tension. After two days, we emptied the bottles and removed the  
 239 remaining carrion. For both years, we collected all arthropods from the traps, cleaned the

240 specimens with 100% ethanol and stored them in 100% ethanol (changed after the first 24 and  
241 72 hours) in a deep freezer until species identification.

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

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

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

### 273 **Canopy cover**

274 Canopy cover was estimated for each plot using elevation-normalized LiDAR point clouds  
275 collected in 2023. We acquired drone-based LiDAR data during the leaf-on season of  
276 September 2023 using a Hesai Pandar40P laser scanner (LiAir 220N system, GreenValley  
277 International). The drone flew at an average altitude of 100 m above the ground and at a velocity  
278 of 8 m/s, resulting in an average point density  $> 164.6$  points  $m^{-2}$ . Most flight lines overlapped  
279  $> 50\%$  and the maximum scan angle was  $\pm 15^\circ$ . The LiDAR data were pre-processed using  
280 LiDAR360 software (GreenValley International, Beijing, China) following a standardized  
281 workflow (Liu et al., 2024). Canopy cover was approximately the inverse of the gap fraction  
282 and estimated as the proportion of the ground covered by forest canopy (above 2 m) in  
283 percentage.

### 284 **Statistical analysis**

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

288 *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., no traps for flies in 2023, 8 traps for flies in 2024, 4 traps for ants in 2024, and 9 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*

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

322           *Carrion decomposition analysis*

323 There were two important caveats in the analysis of carrion decomposition. Firstly, carrion  
324 decomposed much more quickly in 2023 compared to 2024 (see Results). As a consequence,  
325 approximately 40% of mice were already fully decomposed by the time the second photo (after  
326 4-5 days) was taken in 2023 (see Fig. S8). This posed a problem for the analysis because the  
327 high proportion of fully decomposed mice led to right-skewed censoring and a loss of variation.  
328 This loss of variation may have affected the results qualitatively, as the effect sizes of the tested  
329 variables (canopy cover, steepness of forest slope, tree species richness) were smaller in models  
330 that included interaction effects with year and experiment duration of carrion decomposition  
331 (Fig. S9). To avoid potential problems associated with a partial right censoring of the data, we  
332 decided to analyze only the decomposition of mice after two days.

333 Second, when we took photos of a decomposing mouse for the first time, we photographed the  
334 decomposing mice after one ( $n = 117$ ), two ( $n = 1098$ ) or three days ( $n = 99$ ) in 2023, whereas  
335 we always photographed the decomposing mice on the second day in 2024 (except for one plot  
336 where we took photos on the fourth day). The number of days until the first photo was taken  
337 had a strong influence on the score of decomposition of the mouse in 2023, with later photos  
338 corresponding to more advanced decomposition (GLMM, Wald- $\chi^2 = 55.7$ ,  $p < 0.001$ ). To

339 account for this, based on this model, we adjusted the scores of decomposition for differences  
340 in the number of days so that all scores reflected the expected state for photos taken on the  
341 second day. Scores from the one plot in 2024, where we took photos only on the fourth day,  
342 were divided by two (Fig. S10).

343 After converting the scores into values of relative mass loss using Eq. (1), we used a generalized  
344 linear mixed model to investigate the relationship between the proportion of carrion mass lost  
345 after two days and initial carrion mass, log2-transformed tree species richness, canopy cover,  
346 slope steepness and the identity of primary decomposer, each in interaction with year to account  
347 for temporal variation. We used a beta-binomial error distribution with a logit link to account  
348 for normality and homoscedasticity of variances. We included plots nested within sites (i.e., A  
349 or B), and the tree species around which the carrion was placed as orthogonal random intercept.  
350 Dispersion was modelled as a function of year, canopy cover and primary decomposer to  
351 account for heterogeneity in variability. All continuous predictors were z-transformed (to mean  
352 = 0 and SD = 1) before analysis.

353 All statistical analyses were done with R program version 4.4.1 (R Core Team, 2021).  
354 Generalized linear mixed models were constructed using the R-package ‘glmmTMB’ version  
355 1.1.10 (Brooks et al., 2017). Multicollinearity among predictor variables was assessed using  
356 ‘performance’ version 0.12.4 (Lüdecke et al., 2021). Significance values were obtained using  
357 Wald- $\chi^2$ -tests in the package ‘car’ version 3.1.2 (Fox & Weisberg, 2019). Model performance  
358 was evaluated using the R-package ‘DHARMa’ version 0.4.7 (Hartig, 2021). Species richness  
359 estimation and sample coverage calculations were performed using the R-package ‘iNEXT’  
360 version 3.0.1 (Hsieh et al., 2016). The multivariate analysis was conducted using the R-  
361 packages ‘vegan’ version 2.6.6.1 (Oksanen et al., 2020), with ‘RVAideMemoire’ version  
362 0.9.83.7 (Hervé, 2022) used for type II PERMANOVA tests and permutation-based procedures.

363 **Results**

364 ***Decomposer diversity***

365 We collected a total of 25,027 flies, representing 16 species (including three morphospecies),  
366 from 9 genera and 5 families, with 192 carrion-baited traps in BEF-China in 2023 and 2024.  
367 The five most abundant species were *Chrysomya megacephala* (46.0%), *Lucilia porphyrina*  
368 (31.4%), *Hemipyrellia ligurriens* (6.9%), *Sarcophaga peregrina* (6.5%), and *Chrysomya*  
369 *pinguis* (5.0%). Other carrion-associated flies constituted ~1.5% or fewer individuals (see  
370 Supplementary table S2). Flies of the family Calliphoridae (n = 22,709) were an order of  
371 magnitude more frequent than those of Sarcophagidae (n = 1,643) or Muscidae (n = 617).

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

381 We collected a total of 4,946 ants, representing 13 species from 11 genera and four  
382 subfamilies, in BEF-China in 2024. The five most abundant species were *Crematogaster cf.*  
383 *rogenhoferi* (26.2%), *Pheidole nodus* (17.3%), *Polyrhachis illaudata* (sensu lato, 14.7%),  
384 *Polyrhachis dives* (10.2%), and *Lepisiota* sp. (7.6%). Other carrion-associated ants each  
385 accounted for less than 7% of the total (see Supplementary Table S2). The abundance of ants  
386 in carrion-baited traps did not change with tree species richness or canopy cover, but

387 increased with slope steepness of forests (Table 1, Fig. 3 d-f). Species richness of ants was  
388 strongly associated with their abundance at plot-level, and slightly increased with canopy  
389 cover (Fig. S11 e-h). The community composition of ants was related to slope steepness and  
390 canopy cover (Table S3, Fig. S12).

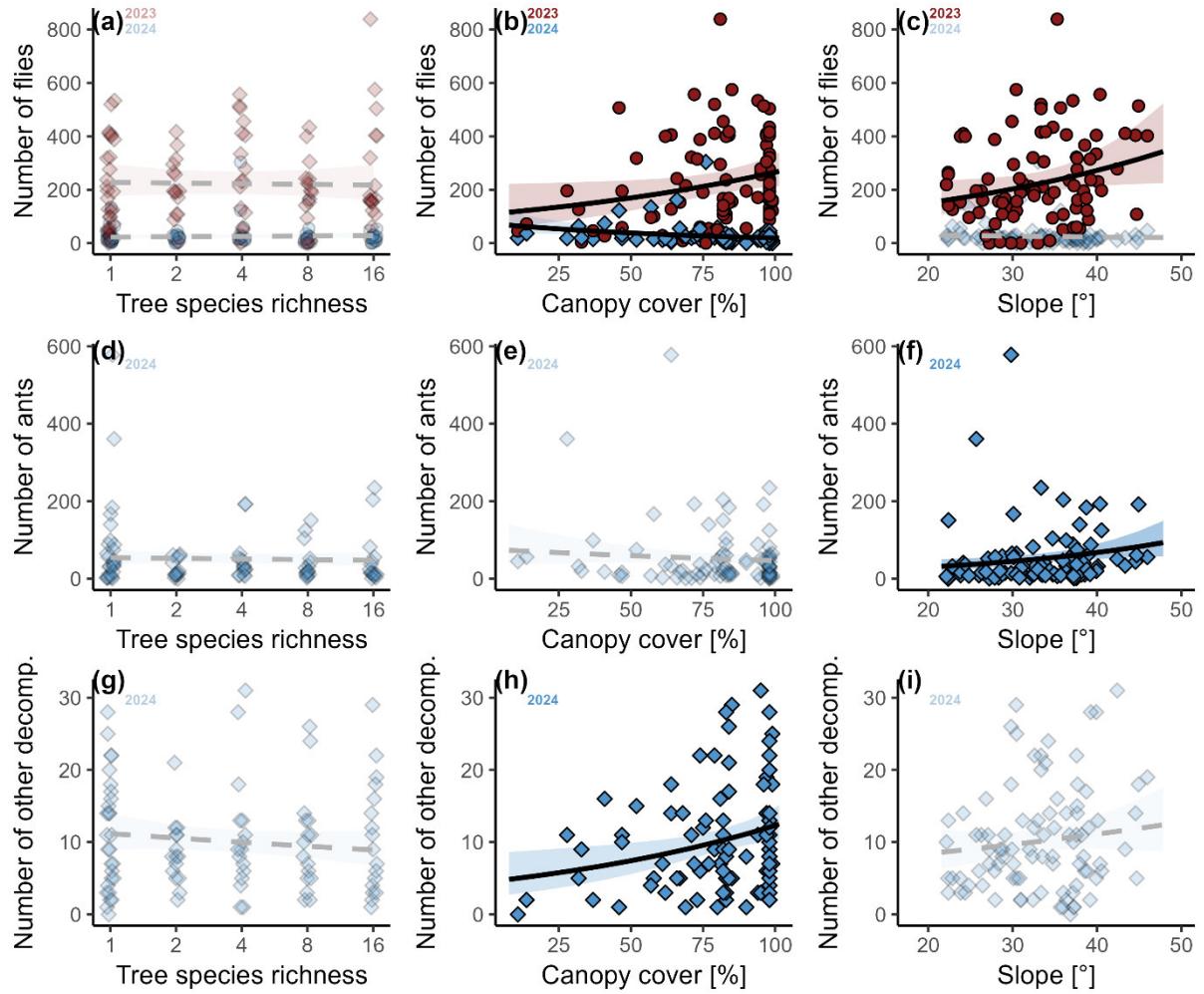
391 In addition to flies and ants, we collected a total of other 1,002 invertebrates in 2024 from  
392 carrion-baited traps in BEF-China, spanning at least 36 taxa across 10 insect orders and one  
393 centipede family. The majority belonged to Coleoptera (67.2%), Lepidoptera (14.7%), and  
394 Orthoptera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

406

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

Predictors	Flies		Ants		Other decomposers	
	Abundance	Richness	Abundance	Richness	Abundance	Richness
	Chisq	Chisq	Chisq	Chisq	Chisq	Chisq
Tree richness (log)	0.04	0.93	0.31	0.42	1.37	0.19
Canopy cover	<b>4.57*</b>	1.08	1.27	3.26	<b>7.27*</b>	0.85
Slope steepness	<b>4.23*</b>	0.05	<b>6.67*</b>	0.02	1.46	3.66
Abundance (log)		<b>5.27*</b>		<b>4.01*</b>		<b>17.76*</b>
Year	<b>244.09*</b>	<b>8.39*</b>				
Year × Tree richness	0.63	0.03				
Year × Canopy cover	<b>15.27*</b>	3.60				
Year × Slope steepness	<b>4.10*</b>	0.19				
Year × Abundance		<b>9.83*</b>				

412

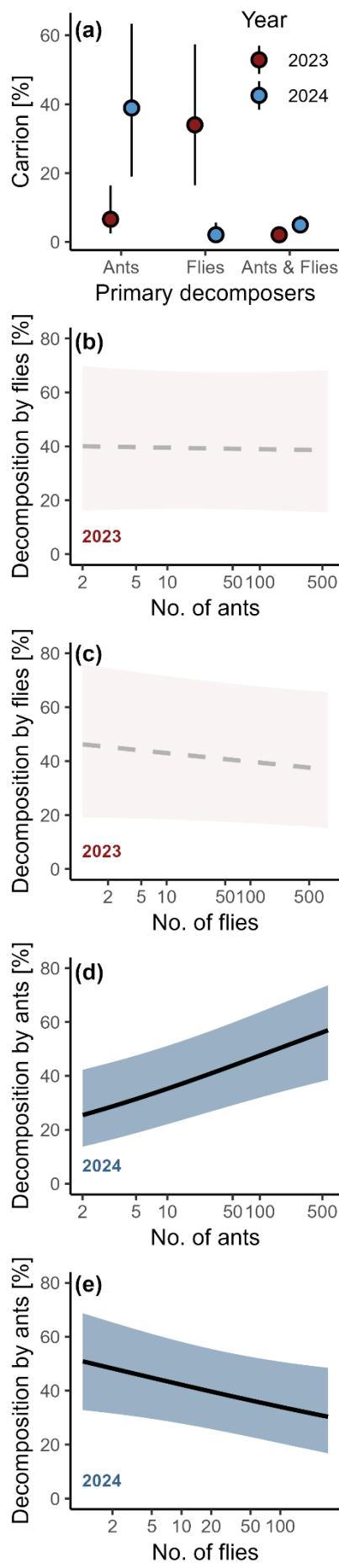


**Figure 3:** Relationship between the abundance of (a-c) flies, (d-f) ants and (g-i) other decomposer in carrion-baited traps after two days in the subtropical forest of BEF-China in 2023 (red circles) and 2024 (blue diamonds) and forest environmental factors: (a, d, g) tree species richness (log2-transformed), (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  $\pm$  95% CI).

414    ***Primary decomposer of mouse carrion***

415    We identified ants as the primary decomposers in 827 carrion samples, flies in 731 samples,  
416    and both flies and ants together in 135 samples. For 944 carrion samples, the primary  
417    decomposer could not be determined from photographs or decomposition succession (Fig. 1).  
418    In 2023, carrion was primarily decomposed by flies (39.4%), while in 2024 ants were the  
419    main decomposers (41.0%; Fig. 4a).

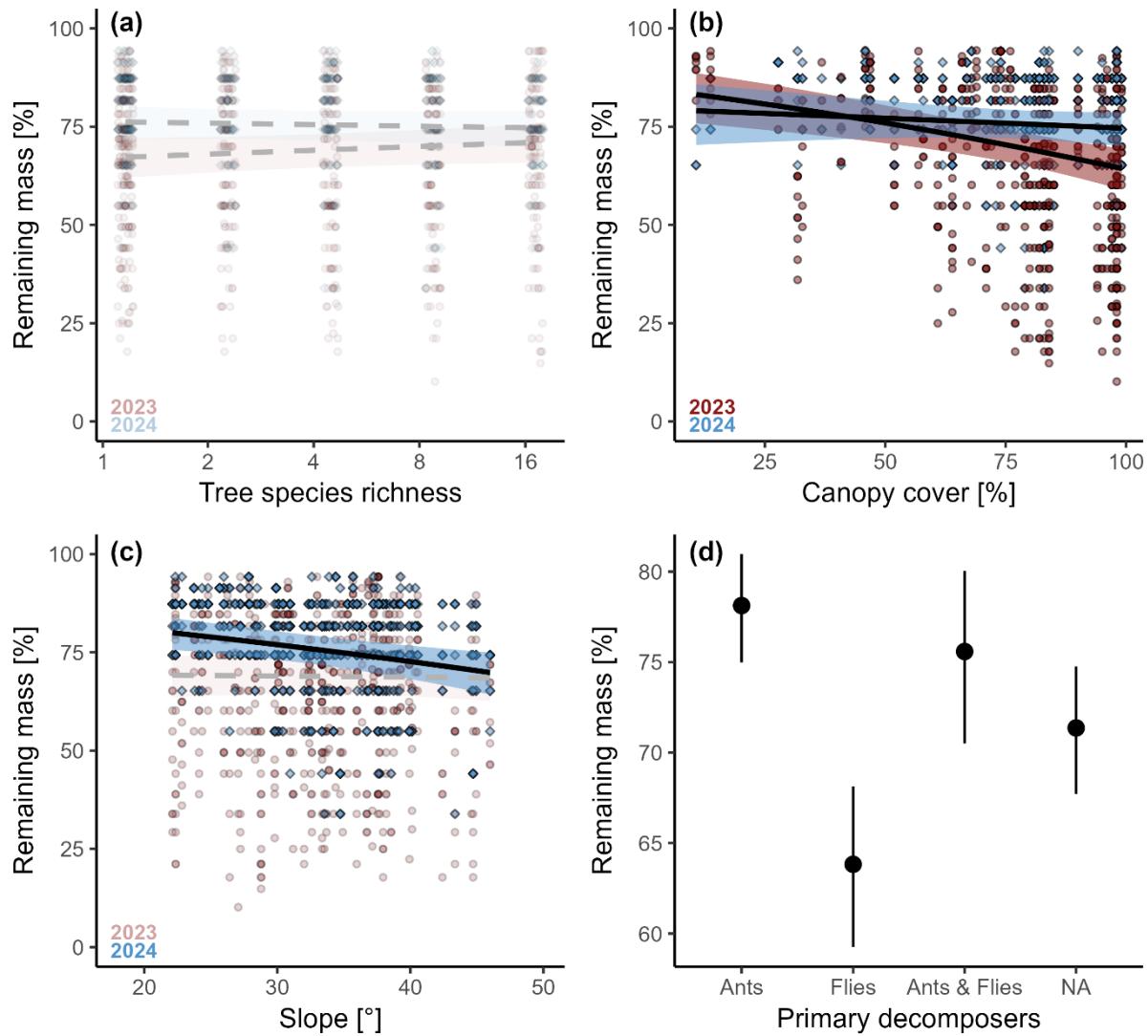
420    The proportion of carrion decomposed by flies in 2023 was not influenced by tree species  
421    richness ( $\text{Wald-}\chi^2 = 1.18$ ,  $p > 0.05$ , Table S3) and was not related to the abundance of ants  
422    ( $\text{Wald-}\chi^2 = 0.03$ ,  $p > 0.05$ , Fig. 4b), the abundance of flies ( $\text{Wald-}\chi^2 = 1.00$ ,  $p > 0.05$ , Fig. 4c)  
423    or slope steepness ( $\text{Wald-}\chi^2 = 0.13$ ,  $p > 0.05$ ). However, the proportion of carrion decomposed  
424    by flies was positively associated with canopy cover ( $\text{Wald-}\chi^2 = 15.84$ ,  $p < 0.001$ , Table S3).  
425    In 2024, the proportion of carrion decomposed by ants was strongly related to the abundance  
426    of ants ( $\text{Wald-}\chi^2 = 10.95$ ,  $p < 0.001$ , Fig. 4d) and flies ( $\text{Wald-}\chi^2 = 4.31$ ,  $p = 0.038$ , Fig. 4e) at  
427    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. Ants were not considered in 2023; therefore, 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  $\pm$  95% confidence intervals.

429    ***Carriion decomposition***

430    The relative mass of carriion lost after two days in the subtropical forest of BEF-China was  
431    strongly influenced by the initial mass, study year, forest variables, and their interactions  
432    (Table S4, Fig. 5). Overall, carriion was 6.7% more decomposed after two days in 2023 than in  
433    2024. Tree species richness did not have a significant effect on carriion decomposition in  
434    either year ( $\text{Wald-}\chi^2 = 2.09$ ,  $p = 0.148$ ). The relationship between tree species richness and  
435    decomposition differed significantly between years, but the slopes did not differ from zero in  
436    both years ( $\text{Wald-}\chi^2 = 7.30$ ,  $p = 0.007$ ; Fig. 5a). Carriion decomposition was accelerated in  
437    closed forests, particularly in 2023 (year  $\times$  canopy cover interaction:  $\text{Wald-}\chi^2 = 19.32$ ,  $p <$   
438    0.001; Fig. 5b), and increased on steep slopes in 2024 (year  $\times$  slope interaction:  $\text{Wald-}\chi^2 =$   
439    14.15,  $p < 0.001$ ; Fig. 5c). Carriion decomposition was strongly dependent on the primary  
440    decomposer. In our study, ants buried carriion with soil in about 3.3% of all cases (10.3% of  
441    cases dominated by ants), and in 88% of these instances, the burial of carriion effectively  
442    excluded flies. Regardless of the year, carriion decomposed by ants were 9.2% less  
443    decomposed after two days than carriion decomposed by flies (Fig. 5d). When ants and flies  
444    co-occurred on carriion, the decomposition rate was similar to that of carriion dominated by  
445    ants.



446

**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.

447 **Discussion**

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

456 **Lack of effect of tree species richness**

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

462 We found no effect of tree species richness on the decomposer community, competitive  
463 interactions, or the rate of carrion decomposition. This result contrasts with many BEF-  
464 studies, which commonly report positive effects of tree diversity on the diversity of higher  
465 trophic levels and their associated ecosystem functions. For instance, tree diversity has been  
466 shown to enhance arthropod diversity by increasing habitat complexity and resource  
467 heterogeneity (Schuldt et al., 2019; Wang et al., 2025). However, recent work highlights that  
468 BEF relationships are context-dependent: diversity effects differ between ecosystem functions  
469 (Tang et al., 2022), can vary over space and time (Amyntas et al., 2023; Bongers et al., 2021;  
470 Trogisch et al., 2021), and may be overridden by abiotic conditions or biotic interactions (Li

471 et al., 2023). As a result, BEF-relationships may weaken or vanish at certain ecological scales,  
472 which challenges the application of BEF-principles in real-world ecosystems (Manning et al.,  
473 2019).

474 Mobility and habitat use may explain the lack of a tree diversity effect on decomposers. While  
475 most BEF effects are related to effects at the local scale (REF), multitrophic interactions often  
476 operate at broader scales (Fichtner et al., 2018; Yu et al., 2024). For instance, carrion flies are  
477 known to move between 100 m and 2 km per day, especially species that rely on carrion for  
478 oviposition (Braack & Retief, 1986; Smith & Wall, 1998; Spradbery et al., 1995). Because  
479 flies need to find carrion over large areas, they probably respond to signals from larger  
480 distances, rather than to local tree neighborhoods (Johnson-Bice et al., 2023). This mismatch  
481 in spatial scale potentially explains the absence of localized effects of tree species richness on  
482 fly diversity and decomposition. Similar scale mismatches might also influence other  
483 ecosystem functions carried out by highly mobile organisms, such as pollination, seed  
484 dispersal or predation (Jordano et al., 2007; Pasquet et al., 2008; Tucker et al., 2018).

485 Ants, the second most important group of decomposers, are less mobile and more locally  
486 bound. Canopy and litter ant richness often increases with tree diversity (Skarbek et al.,  
487 2020), yet this pattern is weaker or absent for ground-dwelling, omnivorous ants, which often  
488 remain diverse even in disturbed forests (Staab et al., 2014). Their broad diets and flexible  
489 nesting behavior (Blüthgen & Feldhaar, 2009) likely reduce the dependence of omnivorous  
490 ants on the resources (e.g. leaf litter) provided by specific tree species.

491 Tree diversity also did not show any effect on other decomposers, although grouping these  
492 taxa may have masked more nuanced, taxon-specific relationships (e.g. in Lepidoptera,  
493 Coleoptera or Orthoptera). Nonetheless, any subtle positive effects were likely too weak to  
494 lead to changes in carrion decomposition. Moreover, flies or ants may have further  
495 outcompeted other decomposers or suppressed their activity (Trumbo & Bloch, 2000). Finally,

496 tree species richness also did not influence carrion decomposition indirectly via microclimatic  
497 buffering, such as temperature or moisture moderation (Schnabel et al., 2025). Taken together,  
498 our findings suggest that tree species richness neither supports decomposer diversity nor  
499 enhances carrion decomposition, directly or indirectly. This challenges the widespread  
500 assumption that tree diversity generally promotes diversity of higher trophic levels and  
501 ecosystem functioning.

502 **Competition between flies and ants for carrion**

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

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

515 In contrast, ants dominated carrion decomposition in summer 2024. This period marks the  
516 early wet season, when monsoonal conditions intensify. The period experienced increased  
517 rainfall, persistently high humidity, slightly elevated temperatures, and more cloud cover than  
518 in 2023. These conditions may reduce fly activity and abundances (Arnaldos et al., 2001; de  
519 Carvalho & Linhares, 2001; Shi et al., 2009). For instance, we sampled nine times fewer flies

520 in summer 2024 than in spring 2023 ( $n = 21,242$  vs.  $n = 2,402$ ), indicating a decline in fly  
521 abundance and dominance. Although slightly different trap designs were used in the second  
522 year (Supplementary text S2), the large differences in fly abundance between spring 2023 and  
523 summer 2024 are unlikely to be explained by trap design alone. In contrast, it has been often  
524 demonstrated that ant abundance in (sub-)tropical forests increases during the wet season  
525 (Kass et al., 2023; Levings, 1983; Queiroz et al., 2023; Suwabe et al., 2009). The combination  
526 of reduced fly activity (and abundance) and increased ant abundance may have contributed to  
527 the observed shift in decomposer dominance between spring 2023 and summer 2024.

528 In addition, when flies were abundant and species-rich, as in spring 2023, neither fly nor ant  
529 abundance was related to their dominance on carrion. Under such conditions, a single carcass  
530 may host between 100 and 1,000 flies. Ovipositing sarcophagids and calliphorids typically  
531 produce ~20–40 live larvae per cycle (Knippling, 1936), which could result in comparably high  
532 numbers of larvae per mouse carrion (Archer & Elgar, 2003). Such saturation likely makes  
533 resource control less sensitive to small changes in fly or ant abundance. In contrast, when flies  
534 were relatively rare, ant dominance on carrion was strongly associated with the abundance of  
535 both ants and flies at the plot level. Together, these results indicate that decomposer  
536 interactions are shaped by local densities when flies are rare, but when flies are super-  
537 abundant, fly dominance is less dependent on local competition between decomposer groups  
538 and potentially more influenced by factors such as early arrival or environmental conditions  
539 that promote fly activity (Brundage et al., 2014; Dawson et al., 2022; Michaud & Moreau,  
540 2017). These findings highlight that decomposer interactions are strongly abundance-driven  
541 and shaped by seasonal and environmental filters (Farwig et al., 2014; Hernández-Ortiz et al.,  
542 2022). However, because ant sampling was limited in the first year, further replicated studies  
543 are needed to better understand how seasonal dynamics and environmental conditions

544 influence decomposer competition and decomposition rates in subtropical forests (Barton et  
545 al., 2013; Eubanks et al., 2019; Kishimoto-Yamada & Itioka, 2015).

546 Ants used a range of physical and behavioral strategies  
547 to interfere with flies. In our study, ants buried carrion  
548 with soil in about 3.3% of all cases (10.3% of cases  
549 dominated by ants), and in 88% of these instances (Fig.  
550 6), the burial of carrion effectively excluded flies  
551 (Cornaby, 1974; Lindgren et al., 2011). When carrion  
552 remained uncovered, we observed ants attacking adult  
553 flies, likely reducing oviposition and larval development  
554 (Stoker et al., 1995). Ants also preyed on fly larvae from  
555 carrion, as previously reported (Barton & Evans, 2017; de Jong & Hoback, 2006; Early &  
556 Goff, 1986; Stoker et al., 1995). These behaviors influenced the decomposition process, and  
557 likely depend on ant species and on their ability to discover a carrion early. Carrion dominated  
558 by ants decomposed more slowly than carrion dominated by flies, allowing ants to exploit the  
559 resource over a longer period. Even when both groups co-occurred, decomposition rates  
560 resembled those of ant-dominated carrion, suggesting strong suppression of fly activity by  
561 ants. This study is among the first to show that interspecific competition among decomposers  
562 is strongly related to their abundances and can shape carrion decomposition across  
563 environmental gradients (Barton & Evans, 2017; Fernandes et al., 2024). This aligns well with  
564 broader ecosystem functioning research where key processes have also been shown to be  
565 strongly abundance-dependent (Gaston et al., 2018; Houadria & Menzel, 2017; Rehling et al.,  
566 2023; Winfree et al., 2015).



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

567 In addition, our results on the decomposition by ants are consistent with studies showing that  
568 ants mostly slow down carrion decomposition by disrupting necrophagous communities

569 (Barton & Evans, 2017; de Jong & Hoback, 2006; Lin et al., 2022; Pereira et al., 2017; Wei et  
570 al., 2023), while only a few studies point out positive effects of ants on carrion decomposition  
571 through facilitating decomposition (Meyer et al., 2020). However, different ant species  
572 employ different ecological strategies (Nooten et al., 2022), highlighting the need for further  
573 research into tri-trophic interactions among ants, flies, and other carrion-associated arthropods  
574 (Alvarado-Montero et al., 2021). Such studies are essential to understand when and how ants  
575 influence decomposition, and its effects on ecosystem functioning (Fornoff et al., 2019; Tiede  
576 et al., 2017). Our findings emphasize the role of ants in decomposer interactions and carrion  
577 decomposition, particularly in tropical and subtropical forests (Amendt et al., 2004; Paula et  
578 al., 2016; Stoker et al., 1995).

579 **The role of forest structure**

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

589 Beyond flies, canopy cover also influenced the community composition of ants and beetles, in  
590 line with previous findings that these groups differ in their associations between forests and  
591 grasslands (Barton & Evans, 2017). Seasonal variation further modulated these patterns. For  
592 example, fly abundance on carrion was generally higher in spring 2023 than in summer 2024,  
593 but canopy effects differed between the two time periods. While Barton & Evans (2017)

594 observed no canopy effect on fly community composition, we found clear compositional  
595 shifts, suggesting environmental filtering may vary in strength across seasons or years  
596 (Farwig et al., 2014) and systems. Overall, our results align with previous evidence that  
597 decomposition proceeds more rapidly in closed compared to open forests (Alvarado-Montero  
598 et al., 2021; de Carvalho & Linhares, 2001). Nonetheless, very few studies have directly  
599 linked decomposer diversity, forest structure, and decomposition outcomes. The results of this  
600 study highlight the complex and context-specific role of forest structure in controlling  
601 decomposer interactions and carrion decomposition.

602 **The role of topography**

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

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

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

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

### 631 Conclusion

632 Our study has provided comprehensive insights into carrion decomposition in subtropical  
633 forests. We found that tree species richness had little influence on decomposer diversity, their  
634 interactions, or carrion decomposition. This lack of effect may stem (i) from the weak  
635 dependence of carrion decomposers on trees, and/or (ii) from a mismatch in spatial scale  
636 between local tree neighborhoods and the scales at which decomposer communities respond  
637 to environmental variation. In contrast, carrion decomposition was primarily related to the  
638 abundance-dependent interactions between flies and ants, with their competition modulated  
639 by seasonal and environmental variability. Forest structure and topography influenced  
640 decomposer communities and their interactions. Future research could investigate whether  
641 other animal groups and ecosystem functions exhibit similar scale mismatches, and whether

642 some functions remain sensitive to local tree diversity despite the broad movement ranges of  
643 the organisms involved. Studies could also test whether different necromass types respond  
644 similarly to tree species richness, forest conditions, topography, and decomposer competition  
645 (Barton et al., 2024; Benbow et al., 2019). These insights will help predict and preserve key  
646 ecosystem functions of multi-trophic communities in forests.

647 **Author Contributions**

648 **Finn Rehling:** conceptualization (lead), data curation, formal analysis (lead), investigation  
649 (equal), methodology (equal), formal analysis (lead), visualization (lead), writing - original  
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667 **Declaration of generative AI and AI-assisted technologies in the writing process**

668 During the preparation of this work, the authors used large language models to assist with  
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671 **Conflict of interest statement**

672 The authors declare that they have no conflict of interest.

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692 **Data availability statement**

693 All data generated or analyzed during this study, as well as the code used for analysis, is  
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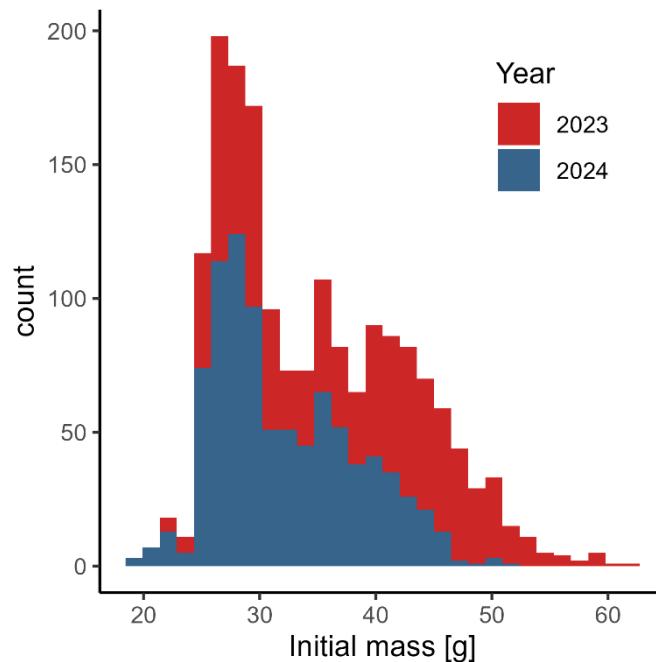
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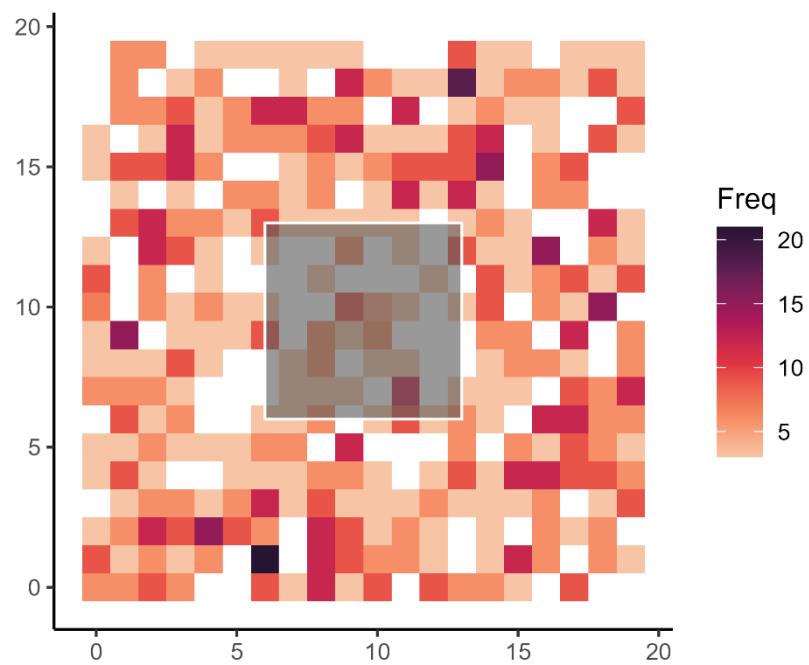
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## **Supplementary Material: Carrion decomposition in a subtropical forest biodiversity experiment**

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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 ~15% more than mice in 2024 ( $\chi^2 = 233.0$ ,  $p < 0.001$ ).



**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  $20 \times 20$  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	<ul style="list-style-type: none"><li>- Eyes decomposed</li><li>- Fur intact</li></ul> 
Initial decomposition – Score 2:	<ul style="list-style-type: none"><li>- Fur starts to get loose</li><li>- Body often bloated</li><li>- With few, small (&lt; = 2) holes</li></ul> 

Active decomposition – Score 3:

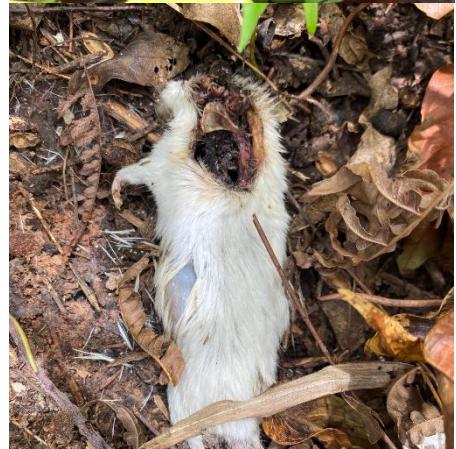
Decomposition by flies:

- 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 carriion 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 liquefaction ('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:

$$\text{relative carrion mass } (x) = \frac{1}{1 + e^{-(3.7183 - 0.8801*x)}} \quad (1)$$

## Supplementary text S2: Trap nest design and associated issues



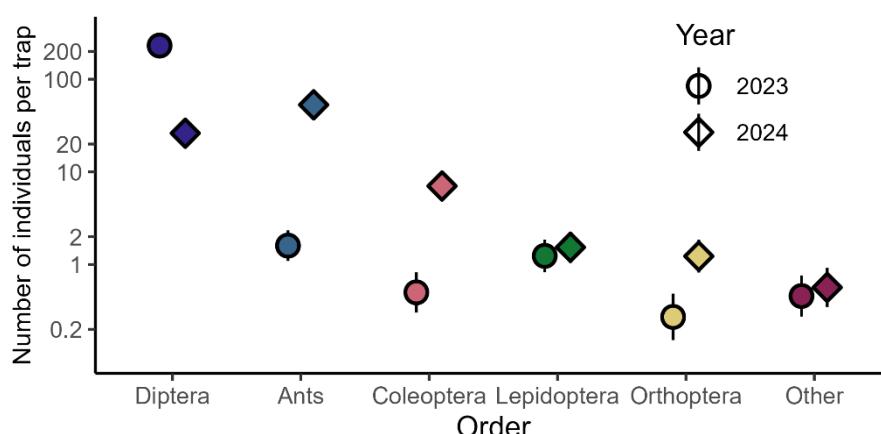
**Figure S4:** Photograph of a baited trap used to sample carrion-associated arthropods in 2023 (left) and 2024 (right). The trap consisted of a large (5 L) and a small plastic bottle (0.5 L). Small openings at ground level allowed arthropods to access the carrion, while the small bottle at the top of 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

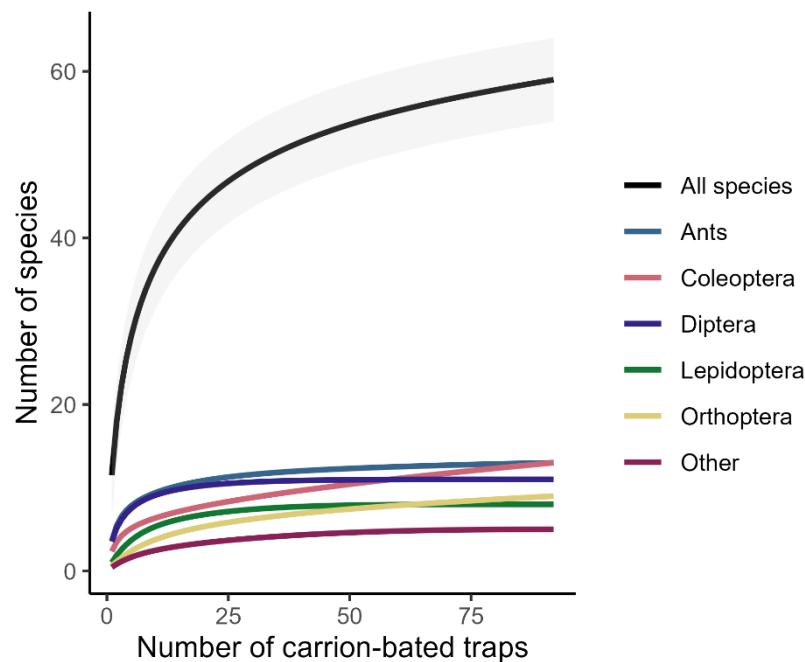
mice during sampling and facilitated arthropod collection with a filter as no carrion remains could leak into the preservation fluid. For both years, we collected all arthropods from the trap and brought them to the laboratory at the field station, where we cleaned the specimens with tap water and stored 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 *Vespa 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.

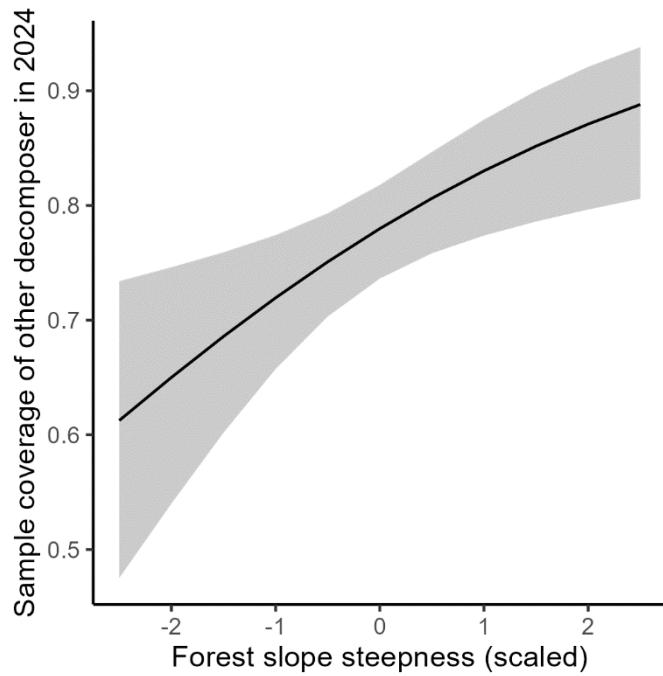


**Figure S5:** Number of individuals for mice carrion-feeding arthropods; here orders of diptera, ants (Hymenoptera), coleoptera, lepidoptera, orthoptera and other arthropods in baited traps with carrion in 2023 and 2024. Predicted mean  $\pm$  95%-CI. Note that the y-axis is on a log-scale.

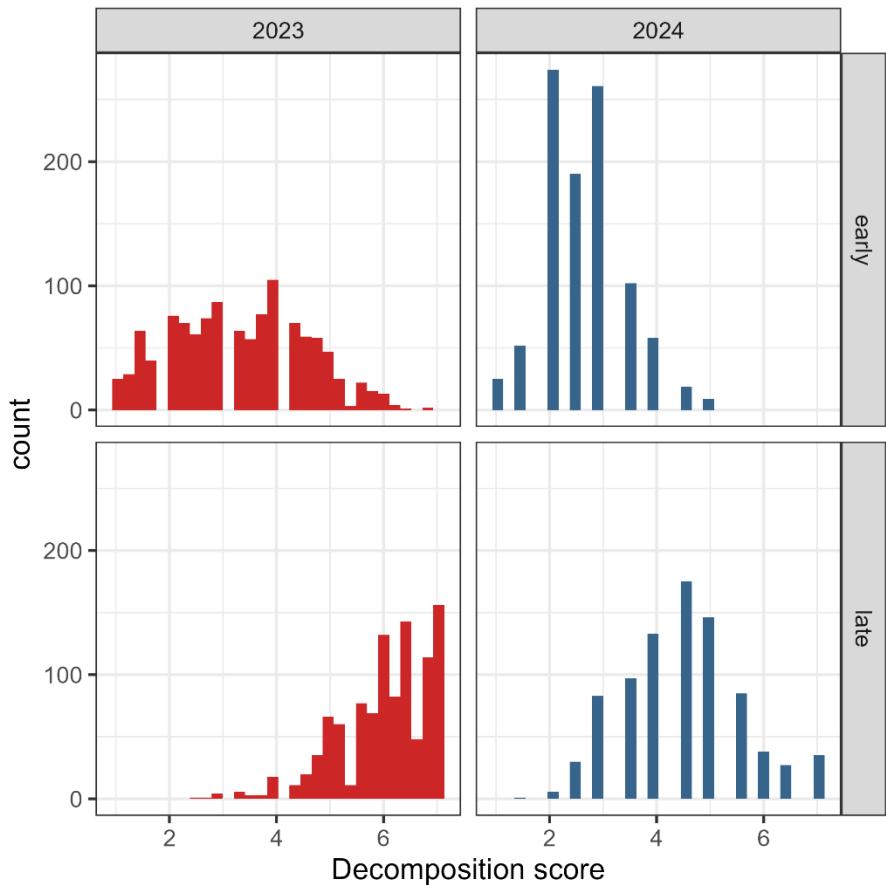
The carrion-baited traps captured nearly complete necrophagous communities of flies and ants, while other decomposers were somewhat underrepresented, particularly at shallow forest slopes (Table S2, Fig. 6-7). Mean sample coverage was 98.2% for flies in 2023, 96.3% for flies in 2024, 96.0% for ants in 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).



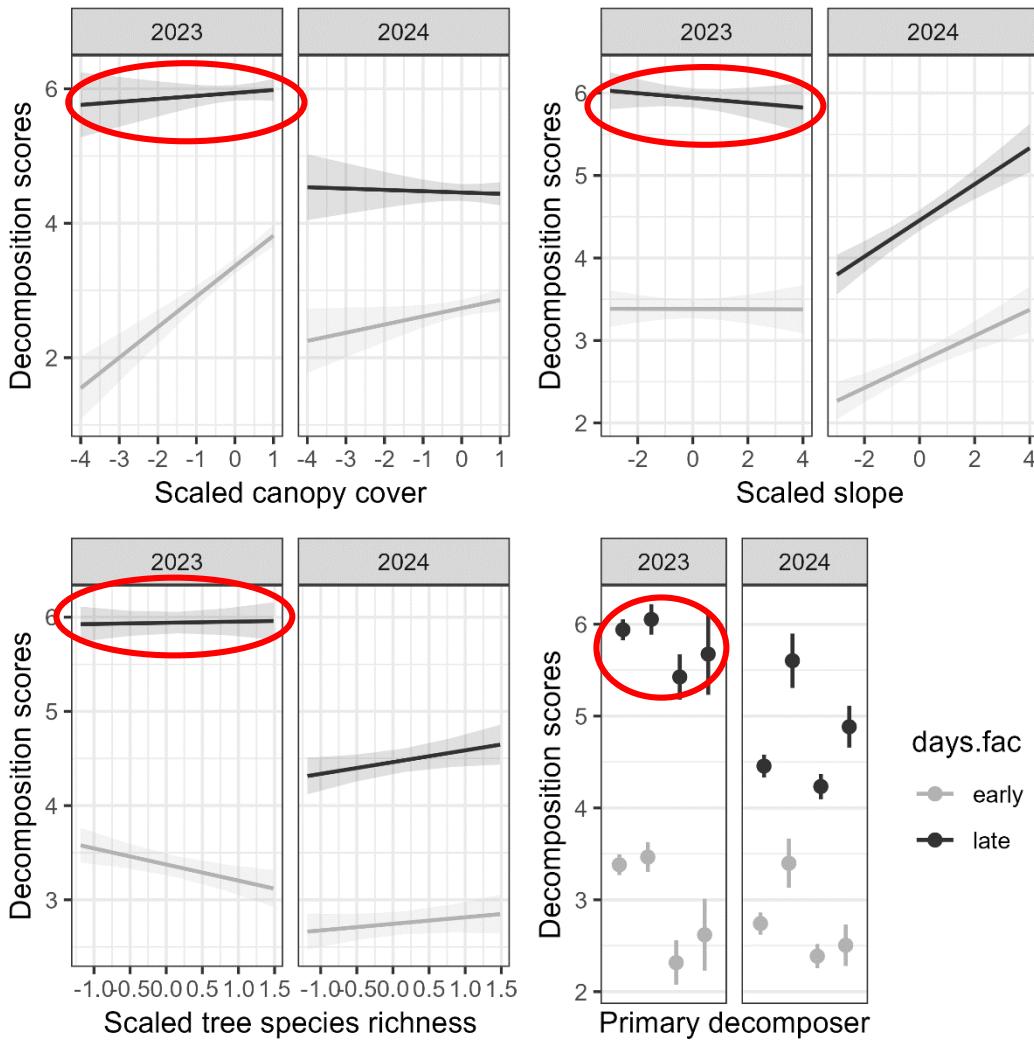
**Figure S6:** Rarefaction curves showing species richness of different groups of decomposers in relation to the number of carrion-baited traps, after two days of trap presence in the forest in 2023 and 2024 in BEF-China. Predicted mean  $\pm$  95% CI.



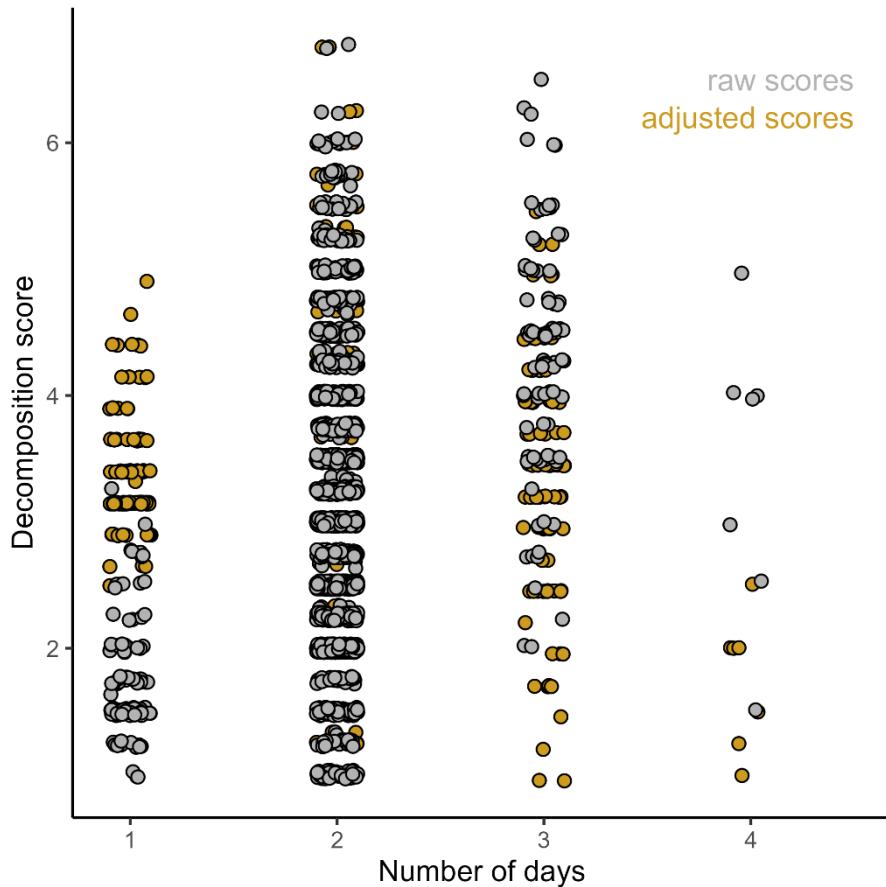
**Figure S7:** Sample coverage of other decomposers in mice carrion-baited traps along the forest slope gradient in BEF-China in 2024. Predicted mean  $\pm$  95% CI.



**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  $\geq 6.5$ ).



**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  $\pm$  95%CI.



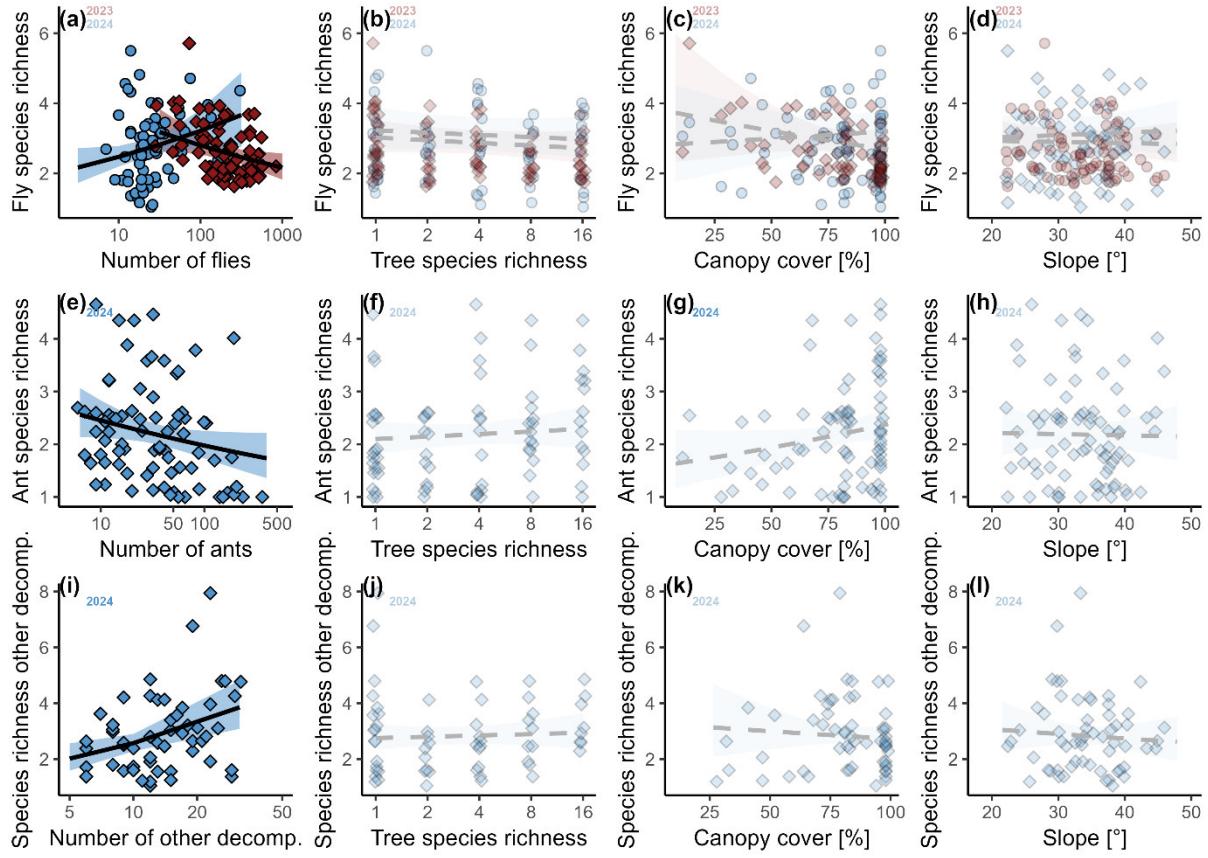
**Figure S10:** The effect of number of days until a photo was taken on the decomposition stage (i.e. the score) of mice carriions on photos. There was a strong positive relationship between the number of days until a photo of was taken and the decomposition score of a mouse (Wald- $\chi^2 = 55.7$ ,  $p < 0.001$ ). 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
<b>Flies</b>					
Diptera	Calliphoridae	Chrysomya	<i>Chrysomya megacephala</i>	10825	676
Diptera	Calliphoridae	Lucilia	<i>Lucilia porphyrina</i>	7672	177
Diptera	Calliphoridae	Hemipyrellia	<i>Hemipyrellia ligurriens</i>	1008	725
Diptera	Sarcophagidae	Sarcophaga	<i>Sarcophaga peregrina</i>	619	1024
Diptera	Calliphoridae	Chrysomya	<i>Chrysomya pinguis</i>	1213	55
Diptera	Muscidae	Dichaetomyia	<i>Dichaetomyia</i> sp.	340	47
Diptera	Calliphoridae	Lucilia	<i>Lucilia bazini</i>	252	106
Diptera	Muscidae	Hydrotaea	<i>Hydrotaea chalcogaster</i>	6	106
Diptera	Muscidae	Atherigona	<i>Atherigona</i> sp.	40	11
Diptera	-	-	Morphospecies #3	51	0
Diptera	Muscidae	Dichaetomyia	<i>Dichaetomyia bibax</i>	4	21
Diptera	Muscidae	Dichaetomyia	<i>Dichaetomyia</i> sp.	21	0
Diptera	-	-	Morphospecies #1	11	0
Diptera	-	-	Morphospecies #2	7	0
Diptera	Stratiomyidae	Ptecticus	<i>Ptecticus aurifer</i>	3	4
Diptera	Limoniidae		Limoniidae	3	0
<b>Ants</b>					
Hymenoptera	Formicidae	Crematogaster	<i>Crematogaster cf. rogenhoferi</i>	sampled	1294
Hymenoptera	Formicidae	Pheidole	<i>Pheidole nodus</i>	sampled	857
Hymenoptera	Formicidae	Polyrhachis	<i>Polyrhachis illaudata</i> (sensu lato)	sampled	729
Hymenoptera	Formicidae	Polyrhachis	<i>Polyrhachis dives</i>	sampled	503
Hymenoptera	Formicidae	Lepisiota	<i>Lepisiota</i> sp. (potentially <i>xichangensis</i> )	sampled	375
Hymenoptera	Formicidae	Camponotus	<i>Camponotus pseudorritans</i>	sampled	342
Hymenoptera	Formicidae	Pheidole	<i>Pheidole pieli</i>	-	342
Hymenoptera	Formicidae	Ectomomyrmex	<i>Ectomomyrmex astutus</i>	sampled	211
Hymenoptera	Formicidae	Aphaenogaster	<i>Aphaenogaster</i> sp.	-	199
Hymenoptera	Formicidae	Tetramorium	<i>Tetramorium wroughtonii</i>	-	69
Hymenoptera	Formicidae	Leptogenys	<i>Leptogenys kitteli</i>	-	12
Hymenoptera	Formicidae	Odonthomachus	<i>Odonthomachus monticola</i>	-	11
Hymenoptera	Formicidae	Anochetus	<i>Anochetus risii</i>	-	2
<b>Other decomposer</b>					
Blattodae	Blattidae	Periplaneta	<i>Periplaneta fuliginosa</i>	-	3
Blattodae	Blaberidae	Pseudoglomeris	<i>Pseudoglomeris</i> sp.	-	3
Coleoptera	Staphylinidae	Aleochara	<i>Aleochara postica</i>	sampled	111
Coleoptera	Carabidae	Brachinus	<i>Brachinus</i> sp.	-	1
Coleoptera	Scarabaeidae	Copris	<i>Copris</i> sp. 1	-	8
Coleoptera	Scarabaeidae	Copris	<i>Copris</i> sp. 2	-	93
Coleoptera	Passalidae	Diamesus	<i>Diamesus osculans</i>	-	1
Coleoptera	Silphidae	Necrophila	<i>Necrophila cyaniventris</i>	sampled	-
Coleoptera	Silphidae	Necrophila	<i>Necrophila jakowlewi</i>	-	1
Coleoptera	Silphidae	Nicrophorus	<i>Nicrophorus nepalensis</i>	sampled	-
Coleoptera	Scarabaeidae	Onthophagus	<i>Onthophagus</i> sp. 1	-	364
Coleoptera	Scarabaeidae	Onthophagus	<i>Onthophagus</i> sp. 2	-	48
Coleoptera	Scarabaeidae	Paragymnopleurus	<i>Paragymnopleurus</i> sp.	sampled	19
Coleoptera	Curculionidae	Phytoscaphus	<i>Phytoscaphus</i> sp.	-	4
Coleoptera	Staphylinidae	Platydracus	<i>Platydracus brevicornis</i>	sampled	2
Coleoptera	Scarabaeidae	Sophrops	<i>Sophrops</i> sp.	-	1
Coleoptera	Carabidae	Trigonotoma	<i>Trigonotoma lewisi</i>	-	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
<b>Other decomposer</b>					
Dermaptera	Anisolabididae	Gonolabis	<i>Gonolabis</i> sp.	-	14
Hemiptera	Rhyparochromidae	Metochus	<i>Metochus</i> sp.	sampled	30
Lepidoptera	Geometridae	Amblychia	<i>Amblychia angeronaria</i>	-	8
Lepidoptera	Crambidae	Glyphodes	<i>Glyphodes</i> sp.	-	34
Lepidoptera	Nymphalidae	Lethe	<i>Lethe syrcis</i>	3	-
Lepidoptera	Geometridae	-	Morphospecies #4	45	46
Lepidoptera	-	-	Morphospecies #5	9	17
Lepidoptera	Nymphalidae	Mycalesis	<i>Mycalesis mineus</i>	4	5
Lepidoptera	Geometridae	Ophthalmitis	<i>Ophthalmitis</i> sp. 1	3	7
Lepidoptera	Nymphalidae	Panthema	<i>Panthema adelma</i>	18	4
Lepidoptera	Geometridae	Parapercnia	<i>Parapercnia giraffata</i>	1	-
Lepidoptera	Geometridae	Plagodis	<i>Plagodis</i> sp.	17	-
Lepidoptera	Erebidae	Spirama	<i>Spirama retorta</i>	7	-
Lepidoptera	Erebidae	Synoides	<i>Synoides fumosa</i>	10	22
Orthoptera	Tettigoniidae	Atlanticus	<i>Atlanticus fengyangensis</i>	sampled	10
Orthoptera	Acrididae	Ceracris	<i>Ceracris kiangsu</i>	-	6
Orthoptera	Tettigoniidae	China	<i>China mantispoides</i>	-	1
Orthoptera	Rhaphidophoridae	Diestramima	<i>Diestramima excavata</i>	-	33
Orthoptera	Acrididae	Hieroglyphus	<i>Hieroglyphus annulicornis</i>	-	4
Orthoptera	Tettigoniidae	Mecopoda	<i>Mecopoda niponensis</i>	-	1
Orthoptera	Tettigoniidae	Meloimorpha	<i>Meloimorpha japonica</i>	-	9
Orthoptera	-	-	Morphospecies #6	-	1
Orthoptera	Gryllidae	Xenogryllus	<i>Xenogryllus marmoratus</i>	-	59
Scutigeromorpha	Scutigeridae	-	Morphospecies #7	-	2



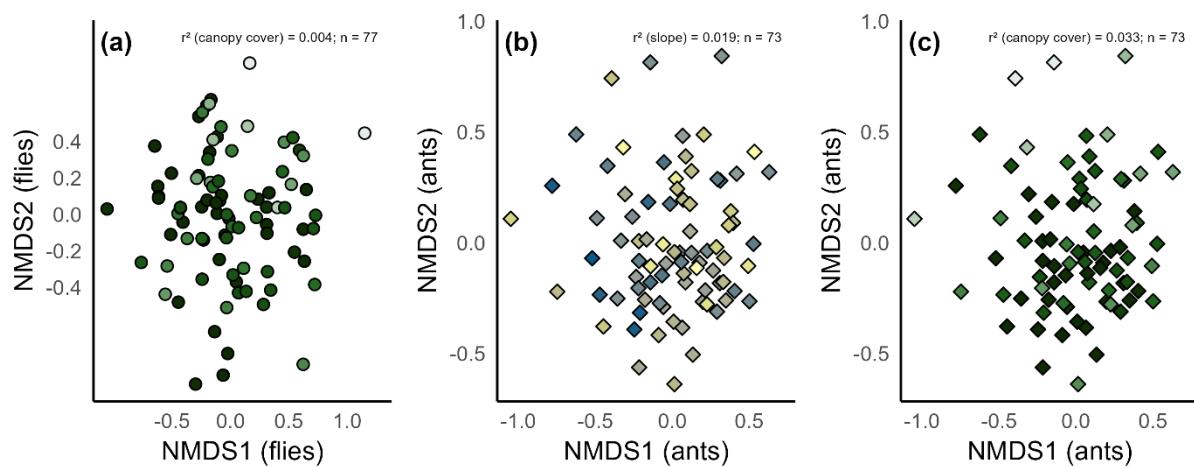
**Figure S11:** Relationship between the expected richness of species (i.e. species richness corrected for differences in sampling coverage) of (a-d) flies, (e-h) ants, (i-l) and other decomposers in mice carrion-baited traps after two days in the BEF-China experiment in 2023 (red circles) and 2024 (blue 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  $\pm$  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	R <sup>2</sup>	F	p
Flies in 2023	Tree species richness	1	0.04	0.004	0.35	0.917
	Canopy cover	1	1.15	0.109	10.57	<b>0.001</b>
	Slope	1	0.12	0.011	1.10	0.303
	Residual	83	9.57	0.856		
Flies in 2024	Tree species richness	1	0.25	0.022	1.75	0.300
	Canopy cover	1	0.76	0.065	5.26	0.108
	Slope	1	0.14	0.012	0.98	0.390
	Residual	73	10.58	0.904		
Ants in 2024	Tree species richness	1	0.42	0.015	1.32	0.408
	Canopy cover	1	1.28	0.047	4.04	0.095
	Slope	1	0.91	0.033	2.86	<b>0.002</b>
	Residual	77	24.51	0.900		
Other decomposers in 2024	Tree species richness	1	0.08	0.006	0.36	0.977
	Canopy cover	1	0.82	0.055	3.88	0.151
	Slope	1	0.30	0.021	1.42	0.182
	Residual	60	13.67	0.910		



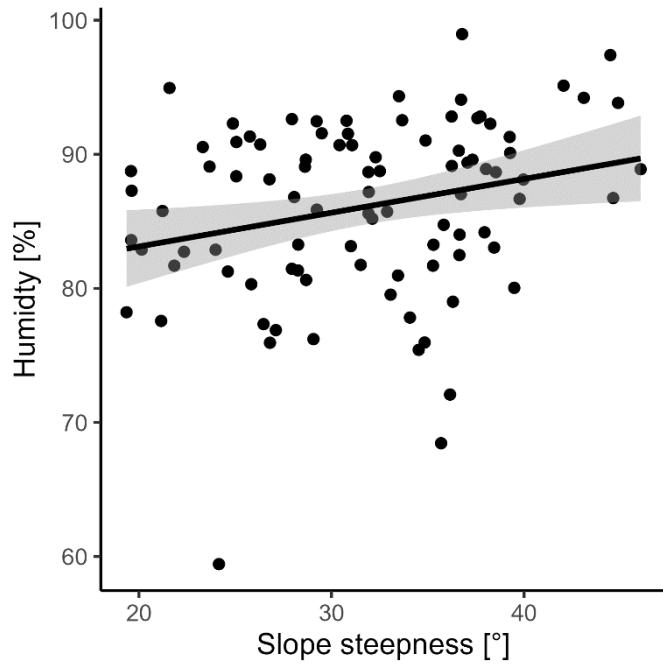
**Figure S12:** Nonmetric multidimensional scaling (NMDS) ordination of arthropod decomposer abundances based on Bray-Curtis dissimilarities in mice carrion-baited traps in BEF-China. The dissimilarity of (a) fly communities between open and closed forests in 2023, and (b, c) the dissimilarity of ant 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- $\chi^2$  values indicate significant effects ( $p < 0.05$ ).

Predictors	Decomposition by flies in 2023		Decomposition by ants in 2024
	Chisq	Chisq	Chisq
Tree richness	1.18		2.21
Canopy cover	<b>15.84*</b>		0.14
Slope steepness	0.13		0.01
Number of flies	1.00		<b>4.31*</b>
Number of ants	0.03		<b>10.95*</b>

**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	4.09	<b>0.043</b>
Tree species richness	1	2.09	0.148
Canopy cover	1	14.47	< 0.001
Slope steepness	1	0.03	0.855
Primary decomposer	3	105.44	< 0.001
Year	1	21.83	< 0.001
Year × initial mass	1	4.85	<b>0.028</b>
Year × tree species richness	1	7.30	<b>0.007</b>
Year × canopy cover	1	19.32	< 0.001
Year × slope steepness	1	14.15	< 0.001
Year × primary decomposer	3	5.14	0.162



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