Tree species richness and forest structure influence vertebrate scavenging

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Abstract

Tree species richness can alter forest structure and resource availability, often enhancing ecosystem functioning. However, biodiversity–ecosystem functioning research has largely focused on plant-mediated processes, leaving it unclear whether vertebrate-mediated functions such as carrion scavenging respond similarly to tree species richness.

We investigated how tree species richness, canopy cover, and slope steepness influence vertebrate scavenging by quantifying the removal of 2,392 mouse carcasses across 96 plots between 2023 and 2025 in a subtropical forest biodiversity experiment in south-eastern China.

Carcass removal was substantially higher in summer 2024 (25.1%) than in spring 2023 (10.5%) and autumn 2025 (10.9%). Across years, carcass removal increased significantly from 7.2% to 15.8% with tree species richness. More carcasses were removed in plots with lower canopy cover in one of the three years. Slope steepness had negligible effects on carcass removal.

Overall, these findings underscore the role of forest structure and temporal variation, rather than topography, in shaping the vertebrate scavenging of small carcasses. They further demonstrate that the effects of tree diversity can extend to higher trophic functions not directly linked to primary productivity.

Keywords: biodiversity-ecosystem functioning, BEF-China, cadaver, canopy cover, carrion, dead organic matter, mouse decomposition, necromass turnover, nutrient cycling, scavenging, slope steepness, topography.

Introduction

Following death, animal carcasses provide a nutrient-rich resource for vertebrates, invertebrates, and decomposers (Janzen 1977, Carter et al. 2006). Although they constitute only a small fraction of the detrital pool in forest ecosystems, carcasses create localized hotspots of biological activity and are consumed predominantly by vertebrate scavengers in many terrestrial ecosystems (Beasley et al. 2019, Johnson-Bice et al. 2023). Through carcass consumption, vertebrate scavengers contribute to ecosystem functioning by redistributing nutrients, influencing food-web dynamics, and affecting pathogen transmission (Parmenter and MacMahon 2009, Wilson and Wolkovich 2011, Vicente and VerCauteren 2019).

Forest biodiversity–ecosystem functioning (BEF) experiments have shown that higher tree species richness generally enhances ecosystem processes and services, including productivity and multi-trophic diversity (Verheyen et al. 2016, Liu et al. 2026). These positive effects are often driven by increased resource heterogeneity and structural complexity, which can propagate bottom-up through food webs (Eisenhauer et al. 2019, Li et al. 2024, Martini et al. 2026). However, most studies focus on plants and invertebrates (Grossman et al. 2018, Klein et al. 2026), partly because bottom-up effects of tree species richness are expected to weaken with increasing trophic level (Scherber et al. 2010). Nonetheless, birds and mammals also respond to tree species richness (Milligan and Koricheva 2013, Cook-Patton et al. 2014, Muiruri et al. 2016, Nell et al. 2018, May-Uc et al. 2020, but see Rehling et al. 2026). This may be driven by increased structural complexity and resource availability in more diverse forests, which in turn can influence scavenger behavior and carcass detectability (Pardo-Barquín et al. 2019). Despite these indications, effects on vertebrates and associated ecosystem functions, such as carcass removal, remain poorly understood.

In addition to tree species richness, canopy cover can also influence vertebrate scavenging. Canopy cover can reduce the abundance and diversity of vertebrate scavengers (Pardo-Barquín et al. 2019), while its effects on carcass consumption appear less consistent (Naves-Alegre et al. 2021, Wenting et al. 2024). These patterns may reflect changes in carcass detectability and microclimate along gradients of canopy cover, with visually oriented scavengers (e.g., birds of prey) potentially experiencing reduced detection efficiency in denser vegetation, while ground-dwelling, olfactory-oriented scavengers (e.g., mammals and some reptiles) may be less constrained and benefit from faster decomposition and increased odor production in warmer, more open forests (DeVault and Rhodes 2002; Inagaki et al. 2022). Moreover, topographic features, such as slope steepness, may influence carcass removal by limiting the movement of terrestrial vertebrates, but how canopy cover and slope affect carcass removal remains unclear.

The BEF-China experiment, currently the largest BEF experiment in the world, with gradients in tree species richness and topography, offers a unique opportunity to test how forest structure and topography affect vertebrate scavenging (Bruelheide et al. 2014). Here, we analyzed the relationships between tree species richness, canopy cover, and slope steepness with carcass removal by vertebrate scavengers. We hypothesized that more carcasses will be removed by vertebrate scavengers (H1) in forests with high tree species richness via improved structural complexity and overall resource availability, (H2) in forest plots with low canopy cover, due to increased carcass visibility and odor production, and (H3) in forest plots with shallower slopes, due to improved access and movement.

Materials and methods

Study area

The experiment was conducted in the BEF-China platform near Xingangshan, Jiangxi Province, China (117°54′ E, 29°07′ N), a subtropical region dominated by evergreen broad-leaved forests with a mean annual temperature of 16.7 °C and mean annual precipitation of 1800 mm. The experimental platform comprises two sites 4 km apart (site A established in 2009 and site B in 2010), spanning 566 plots (25.8 × 25.8 m; total area 50 ha) distributed across elevations of 105–

275 m a.s.l. (site A) and 105–190 m a.s.l. (site B), with slopes ranging from 0° to 46° (mean slope: 27.5° and 31°, respectively). Each plot contains 400 regularly planted seedlings arranged in a 20 × 20 grid at 1.29 m spacing, forming a tree species richness gradient of 1–24 species from a pool of 40 native broad-leaved tree species, with monocultures and mixtures assigned in a randomized broken-stick design. A detailed description of the experimental design is provided in Bruelheide et al. (2014). The final dataset comprised 96 plots in total: 30 monocultures, 16 two-species, 17 four-species, 16 eight-species, and 11 sixteen-species mixtures, with four originally 24-species plots reassigned to the 16-species level due to species loss.

Carcass experiment

Frozen *Mus musculus* carcasses were purchased from an online animal supplier, stored at −18°C, and weighed prior to deployment (mean ± SD: 32.1 ± 6.0 g in 2024, 37.6 ± 8.7 g in 2023, and 40.5 ± 7.8 g in 2025; Fig. S1). Carcasses were deployed across three consecutive study periods (28 May–05 June 2023, 30 June–25 July 2024, and 28 September–25 October 2025), with nine carcasses placed per plot around three randomly selected trees, resulting in 2592 deployments across 96 plots (i.e., 9 mice per plot × 48 plots × 2 sites × 3 years). Due to known rapid removal within two days (Rehling et al. 2025), carcass presence was assessed after two days. Carcass absence was interpreted as vertebrate scavenging; after excluding 200 carcasses with missing or delayed checks (7.7%), the final dataset comprised 2392 carcasses, with 17 plots replicated only twice, and at two plots only once over the three study periods.

Canopy cover

Canopy cover was quantified for each plot using elevation-normalized drone-based LiDAR point cloud data collected during the leaf-on period (September 2021–2024). Surveys were conducted with a LiAir 220N system equipped with a Hesai Pandar 40P laser scanner. The LiDAR data were preprocessed following a standardized workflow, which included outlier removal, noise filtering, classification, and normalization (Deng et al. 2025). Canopy cover was measured estimated as the proportion of the ground covered by forest canopy in percentage.

Statistical analyses

Carcass removal was analyzed using generalized linear mixed-effects models (GLMMs), with a binomial error distribution and a logit link. Carcass removal (the number of removed carcasses versus the number of non-removed carcasses per plot) was used as a binomial denominator response variable. Predictors included tree species richness, forest canopy cover, and slope steepness, each interacting with year to analyze temporal variation. Additionally, mouse fresh mass at the beginning of the experiment was included as a covariate to control for potential mass-related differences in carcass removal. The experimental site (i.e., A or B) was included as a random effect in the model. Tree species richness was log2-transformed, and all predictors (mouse fresh mass, canopy cover, slope and log2-transformed tree species richness) were z-transformed (to mean = 0 and SD = 1) before the analysis. Multicollinearity among predictors was checked visually and with variance inflation factors.

All analyses were performed with R program version 4.5.1 (Team 2020). Multicollinearity was assessed with the R-package "performance", version 0.15.3 (Lüdecke et al. 2021). Significance of model terms was evaluated using Type III Wald $\chi 2$ tests implemented in the package "car", version 3.1.5 (Fox and Weisberg 2019). Generalized linear mixed-effects models were computed using the package "glmmTMB", version 1.1.13. (Brooks et al. 2017). Model performance was analysed using the package "DHARMa", version 0.4.7 (Hartig 2021). Statistical significance was assessed at a level of $\alpha = 0.05$.

Results

Across the 96 plots and three study periods, 15.8% (378 of 2392) of carcasses were removed within two days. Removal rates varied among years (Wald $\chi^2 = 27.47$, $p < 0.001$, Figure 1, Table 1), reaching 25.1% in 2024 compared to 10.5% in 2023 and 10.9% in 2025. Tree species richness increased carcass removal across years (Wald $\chi^2 = 4.84$, $p = 0.028$, Fig. 1) from 7.2% in monocultures to 15.8% in plots with 16 tree species, but this effect varied among years and was strongest in 2024 (interaction of tree species richness × year, Wald $\chi^2 = 11.05$, $p = 0.004$, Fig. 1). Canopy cover had no overall effect on carcass removal (Wald $\chi^2 = 0.33$, $p = 0.564$), although its effect differed among years and was most strongly negative in 2024 (canopy cover × year: Wald $\chi^2 = 6.29$, $p = 0.043$). Neither slope steepness (Wald $\chi^2 = 0.29$, $p = 0.592$) nor carcass mass (Wald $\chi^2 = 2.39$, $p = 0.122$) influenced carcass removal, and the effect of slope did not vary among years (slope × year: Wald $\chi^2 = 2.32$, $p = 0.314$).

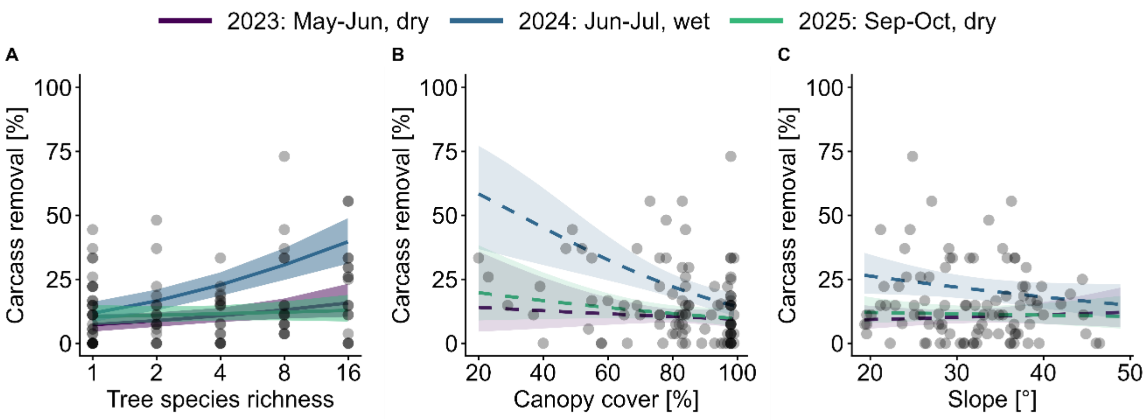

Figure 1: Associations between the removal of mouse carcasses and tree species richness (log2-transformed), canopy cover and slope (A, B, C). Colors represent different seasons/years in which carcass removal was studied. Points represent the arithmetic mean of observed carcass removal across the three study years. Solid colored lines indicate significant main effects (Type III Wald χ^2 tests, $p < 0.05$), while dashed lines indicate non-significant main effects. Polygons indicate the 95% CI.

Discussion

This study examined how tree species richness, canopy cover and slope steepness influence carcass removal during different seasons in three subsequent years (2023-2025) in a subtropical forest. Carcass removal varied substantially between years, with, on average, 16% of carcasses being removed within two days. Tree species richness generally increased carcass removal. Canopy cover decreased carcass removal in one of the three years, and slope steepness had no influence. These results highlight the importance of forest structure and temporal variation over topographical effects on the removal of carcasses by vertebrate scavengers.

The positive effect of tree species richness on the removal of small vertebrate carcasses corroborates previous findings of positive tree diversity–vertebrate relationships (Nell et al. 2018; May-Uc et al. 2020, but see Rehling et al. 2026). In this study, however, carcass mass was standardized across plots, minimizing variation in resource availability as a driver of scavenger responses. The observed patterns therefore likely reflect general foraging activity of common ground-dwelling scavengers in the system (e.g. *Sus scrofa*, snakes). This is consistent with evidence that fine-scale vegetation structure can outweigh the broader landscape context in shaping the activity of scavenger communities (Pardo-Barquín et al. 2019).

In line with this, we also found a negative relationship between canopy cover and carcass removal, but only in one of the three years. Open forests likely facilitate carcass detection and access for avian scavengers (Pardo-Barquín et al. 2019, Arrondo et al. 2019, Hertlein et al. 2025), a pattern also observed for ground fruit removal at the same sites (Rehling et al. 2026). However, the absence of a consistent canopy effect may reflect a weak response of ground-dwelling scavengers to canopy variation or context-dependent detectability effects associated with the understory structure (Naves-Alegre et al. 2021, Wenting et al. 2024). Slope steepness showed no detectable effect, possibly because vertebrates (especially snakes) can access steep plots by following contour lines. Only very steep slopes (>40°) are likely to constrain movement, particularly that of larger-bodied species (Kie et al. 2005, LeBlanc et al. 2018).

Due to local restrictions on camera trapping, we could not identify the local scavenger community. Consequently, the mechanisms underlying the observed effects of tree species richness and partially canopy cover, as well as the contribution of different scavenger groups, remain unresolved. Given that carcass removal rates also vary substantially between years and seasons (which are confounded in this study), future work could address seasonal and inter-annual variation in vertebrate-mediated ecosystem functions across gradients of the forest environment, including potential shifts in functional group contributions. Overall, this study highlights the role of forest biodiversity and structural complexity in shaping vertebrate-mediated ecosystem functions, including those not closely linked to stand productivity, while also revealing strong variation in BEF relationships across seasons and years.

Data and Code archiving statement

Data and code will be made accessible via GitHub (https://github.com/nature-rehling/) and the BEF-China data portal.

Conflict of interest statement

The authors declare no conflict of interest.

Ethics statement

No specific permits were required for this study. All experimental procedures complied with applicable institutional and national guidelines. No live animals were handled or harmed in this experiment.

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CRediT statement

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Supplementary Material

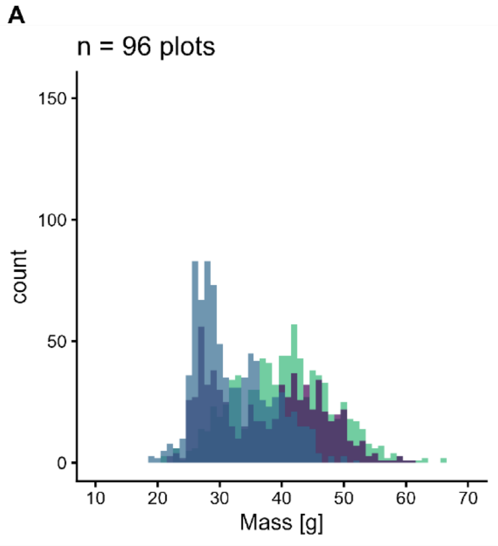

Figure S1: Histogram showing the distribution of masses of mice used in the BEF-China experiment for the years 2023 (purple), 2024 (blue), and 2025 (green) distributed across 96 plots (A).

Figure S2: To investigate the removal of carcasses by vertebrate scavengers, three frozen mice were placed around three randomly selected trees on each plot. Carcass removal was checked two days after deployment.

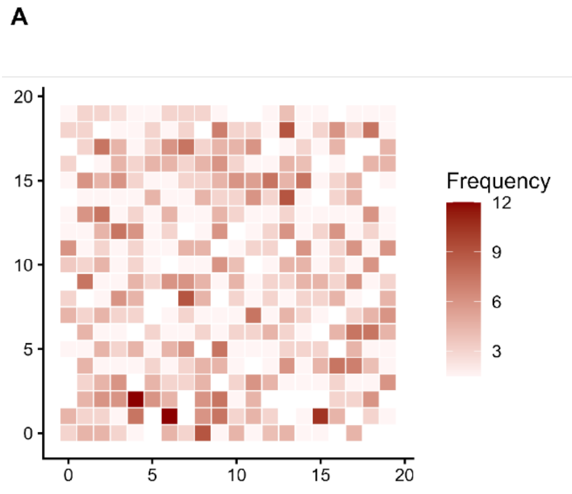

Figure S3: Frequency of the random locations where mouse carcasses were placed around trees across the 96 plots sampled in 2023-2025. Each plot contains a 20 × 20 tree grid, i.e. each cell depicts the location of carcasses around trees.