Removal and decomposition of fruit respond in opposite ways to canopy cover in a biodiversity experiment

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Abstract.

Trees often produce more fruits than frugivores consume. As a result, many fruits fall to the ground, where they are either secondarily removed by vertebrates, potentially leading to seed dispersal, or they are decomposed by arthropods. Although often neglected, fallen fruits are an important component of forests and contribute to their functioning via these two distinct pathways. While fruit removal is well studied, the environmental drivers of fruit decomposition remain poorly understood. We tested the effects of tree species richness and the association with canopy cover on fruit removal and fruit decomposition in a forest biodiversity experiment in subtropical China (BEF-China). We placed 1005 plums across 95 plots, spanning from monoculture to 24 tree species mixtures, in autumn 2025. After four days, 27.2% of fruit were removed while the remaining fruit lost 55.7% of their mass (95% CI: 14.6-84.3%) due to decomposition. Fruit removal varied markedly across plots and decreased by 23% with canopy cover, whereas mass loss increased with canopy cover by 29%. Tree species richness had no detectable effect on either process. Accordingly, removal and decomposition of fruits were only weakly coupled across the forest, with higher overall fruit turnover in open forests. These results suggest that canopy cover, rather than tree species richness, drives fruit turnover by decoupling the pathways of removal and decomposition in young subtropical forests. Fruit decomposition experiments, such as the one used in this study, provide a rapid and simple proxy for assessing forest functioning and contribute to advancing necromass ecology.

Keywords: biodiversity-ecosystem functioning, frugivores, fruit turnover, litter, nutrient cycling, rapid ecosystem function assessment, seed dispersal mutualism, tree species richness, trophic interactions, BEF-China

1 Introduction

Globally, about half of all terrestrial plant species produce nutritious fruits that animals consume (Aslan et al., 2013; Jordano, 2014). By doing so, animals move seeds away from the parent plant and increase the probability of seedling establishment and the growth of plant populations (Beckman and Sullivan, 2023; Howe and Smallwood, 1982). Because both partners benefit, the consumption of fruits by animals and the associated seed dispersal is considered a mutualism (Bronstein, 2009; Guimarães, 2020). This interaction is important for the functioning of forests (Rehling et al., 2023; Wenny and Levey, 1998). However, frugivores have declined across the world, and many forests now contain fewer and often smaller frugivores (Dirzo et al., 2014; Fricke et al., 2022; Rogers et al., 2021a). As a result, fewer fruits are consumed and fewer seeds are moved away from the parent plant (Fricke et al., 2022). This effect is especially strong for plants with large fruits, which often lack animals that can consume them (Pires et al., 2018). Even in intact communities, frugivores do not remove all available fruit because plants compete for dispersers, and foraging decisions depend on resource availability and detectability (Albrecht et al., 2015; Smith and McWilliams, 2014). For these reasons, plants often produce more fruit than are ultimately consumed (Hampe, 2008).

When fruits are not or only partly eaten, they fall to the ground and follow two main pathways. Some are removed by ground-dwelling vertebrates (Jansen et al., 2012; Li et al., 2023a; Mittelman et al., 2020), which may disperse but also often predate seeds, thereby undermining the mutualism (Rehling et al., 2024; Van Leeuwen et al., 2022). Second, fruits remain on the forest floor. There, arthropods and microorganisms break them down and return nutrients to the soil (Winston, 1956). The seeds from those fruits, however, barely recruit to seedlings (Rogers et al., 2021b). Although seed dispersal ecology has a long tradition, studies of fruits on the ground have mostly focused on plant recruitment, with the Janzen Connell framework as the most prominent example (Comita et al., 2014; Connell, 1971; Janzen, 1970). The fate of uneaten fruits and their role in decomposition have received much less attention, despite their importance for forest functioning (van Klinken and Walter, 1996; Łukasik and Johnson, 2007), especially under global change, as shifts in animal communities increase the proportion of fruits that decompose rather than being dispersed.

Fruit turnover depends on the activity of vertebrate consumers and invertebrate decomposers, both of which are influenced by forest structure and composition. Within biodiversity–ecosystem functioning (BEF) research, tree species richness has been identified as an important driver of ecosystem functioning (Liu et al., 2026). Higher tree species richness can increase stand productivity (Huang et al., 2018), resource availability (Beugnon et al., 2023), and structural complexity (Dadda et al., 2025; Deng et al., 2025; Perles-Garcia et al., 2021), and, through this, modify forest microclimate (Schnabel et al., 2025). These changes are known to affect the diversity and activity of consumer and decomposer communities in forest ecosystems (Beugnon et al., 2023; Schuldt et al., 2019). As a result, tree species richness can also be expected to enhance both ground fruit removal by vertebrates and fruit decomposition by arthropods and microorganisms, although this has not yet been explicitly tested.

In addition to tree species richness, organisms involved in fruit turnover may be affected by canopy cover through its influence on light availability and microclimate at the forest floor. For ground-dwelling vertebrates, canopy cover mainly affects habitat openness and foraging conditions. Open canopies increase visibility and movement efficiency, which may facilitate fruit detection and removal, whereas closed canopies may reduce these processes (Chen et al., 2022; Perea et al., 2011; Taneja et al., 2022). For arthropods and microorganisms, canopy cover primarily acts through microclimatic regulation. Higher canopy cover increases humidity and buffers temperature fluctuations, creating more favourable conditions for decomposition and potentially accelerating fruit decomposition on the forest floor (Rehling et al., 2025; Staab et al., 2022).

Beyond the limited attention given to fruit decomposition (Hoefle et al., 2026), it remains unclear how tree species richness and canopy cover jointly shape fruit fate through their effects on ground fruit removal and fruit decomposition. In particular, it is not well understood whether fruit removal and decomposition respond similarly or are decoupled from these forest attributes.

In this study, we investigate how the forest environment influences the turnover of fruit on the forest floor (removal and decomposition), while disentangling effects of tree species richness and canopy cover. We focus on two key dimensions of forest variation that shape multi-trophic interactions within the BEF-China experiment, the largest forest biodiversity experiment worldwide (Bruelheide et al., 2014; Klein et al., 2026). We test three hypotheses. First, tree species richness accelerates fruit removal and fruit decomposition by enhancing habitat complexity and resource availability for consumer and decomposer communities. Canopy cover is expected to decouple these processes by, second, reducing fruit removal (through lower foraging efficiency, movement, and visibility of terrestrial vertebrates in closed forests) and, third, increasing fruit decomposition (through more humid conditions).

2 Material and methods

2.1 Study area

This study was conducted in the BEF-China experiment in a hilly region near Xingangshan, Jiangxi Province, China (117°54′ E, 29°07′ N). The region experiences a subtropical monsoon climate, with a mean annual temperature of 16.7 °C and annual precipitation of approximately 1800 mm. Natural vegetation is dominated by subtropical evergreen broad-leaved forest.

The BEF-China experiment consists of two sites established in 2009 (site A) and 2010 (site B), located about 4 km apart and covering a total area of 50 ha. In total, 566 experimental plots (25.8 m × 25.8 m) were established. Each plot contains 400 tree individuals planted in a regular 20 × 20 grid with 1.29 m spacing between trees. Tree species richness follows a gradient of 1, 2, 4, 8, 16, and 24 species per plot, drawn from a pool of 40 native broad-leaved tree species according to a broken-stick design. A detailed description of the BEF-China experiment is provided by Bruelheide et al. (2014). For this study, we selected 95 plots (47 at site A, 48 at site B), ensuring a mostly balanced number of replicates across the full tree species richness gradient. The sampling included 29 monocultures, 16 two-species mixtures, 17 four-species mixtures, 16 eight-species mixtures, 13 sixteen-species mixtures, and 4 twenty-four-species mixtures.

2.2 Experiment on removal and decomposition of fruit

Fruit exposure took place from 15 September to 31 October 2025. We used ripe fruit of Chinese plum (*Prunus salicina*) as experimental material. A pilot experiment under subtropical conditions showed that plum fruit decompose at intermediate rates, with approximately 50% mass loss after four days. We purchased plums locally at a supermarket in Xingangshan shortly before the experiment. We visually inspected and weighed all undamaged fruit before deployment (initial mass: 24.2 ± 3.0 g; Appendix A).

In each plot, we placed nine fruit on the forest floor around three randomly selected trees (three fruit per tree; Appendix B). We ran the experiment in multiple rounds across plots over the study period, resulting in a total duration of 42 days. We placed fruit directly on the soil surface without protection to allow vertebrates and invertebrates to access them. After approximately 4 days of exposure (90–101 h; Appendix A), we retrieved and reweighed all remaining fruit to quantify proportional mass loss. In 17 plots, at least seven fruit were removed before the end of the exposure period. We therefore repeated the setup in these 17 plots to obtain additional data for the decomposition of fruit. However, in five of these plots, all fruit were removed in both trials, so we could not quantify rates of fruit decomposition. We excluded these cases from analyses of fruit decomposition and turnover (n plots = 90). We forgot to lay out fruit around one tree in one plot. In total, we deployed 1,005 fruit across the two trials ((95 + 17) plots × 3 trees × 3 fruit – 3 fruit).

For fruit turnover, we calculated turnover at the plot level as the total initial fruit mass minus the remaining fruit mass, divided by the total initial mass. We treated removed fruit as complete mass loss (100%), while non-removed fruit contributed their observed proportional mass loss due to decomposition.

2.3 Canopy cover

We estimated canopy cover for each plot using elevation-normalized LiDAR point clouds collected in 2023. We collected additional LiDAR data during the leaf-on season in September 2024 using a LiAir 220N system (GreenValley International) equipped with a Hesai Pandar40P laser scanner mounted on a drone. We flew the drone at an average height of 100 m and at a speed of about 8 m s^{-1}. This flight design produced a high point density of more than 164 points m^{-2}. Flight lines overlapped by more than 50%, and we limited the scan angle to ±15° to improve data quality. We pre-processed all LiDAR data using LiDAR360 software (GreenValley International, Beijing, China) following a standard workflow (Liu et al., 2024). We calculated canopy cover as the proportion of the ground area above 2 m that was covered by vegetation. This measure corresponds approximately to the inverse of canopy gap fraction.

2.4 Statistical analysis

We analyzed the effects of tree species richness ($\log_2$-transformed) and canopy cover on fruit removal, fruit decomposition, and fruit turnover using generalized linear mixed models (type III sums of square). Because tree species richness and canopy cover are partially correlated in this system (df = 93, r = 0.366, $p < 0.001$), we fitted two complementary model sets: (i) models including tree species richness only, capturing the total effect of the experimental manipulation, and (ii) models including both tree species richness and canopy cover, allowing us to separate diversity effects from those associated with forest structure. We included initial fruit mass and experimental duration as covariates to account for variation in fruit condition and exposure time. Across all models, we used the geomorphological type (i.e. hollow, ridge, slope, spur, valley) of a plot as a random effect. We standardized all continuous predictors (mean = 0, SD = 1) before the analysis.

For fruit removal, we modelled the number of removed fruit per plot as a binomial response, with removed fruit as successes and non-removed fruit as failures. We fitted models with a beta-binomial error distribution and a logit link to account for overdispersion. Because the plot represented the unit of replication, we included site (A or B) as a random effect. In this analysis, we only used data from the first experimental run, because the experiment was repeated only in a subset of plots where all fruit had been removed. Including these repeated observations would have led to a non-random subset of plots and biased estimates of fruit removal.

For fruit decomposition, we modelled the proportion of fresh mass loss after four days at the level of individual fruit. We used a beta error distribution with a logit link. Because fruit were nested within plots, we included plot nested within site as a random effect, as well as the identity of tree species under which the fruits were placed. To ensure model convergence, we grouped tree species with five or fewer observations into a single category.

We analyzed effects on fruit turnover using a beta error distribution with a logit link. We subtracted 0.01 from values of 1 to allow fitting a beta distribution. In this analysis, we only used data from the first experimental run, because the experiment was repeated only in a subset of plots where all fruit had been removed. Including these repeated observations would have led to a non-random subset of plots and biased estimates of fruit removal. Finally, we assessed the association between fruit removal and fruit decomposition across plots using a Spearman rank correlation.

All statistical analyses were done with R program version 4.4.1 (R Core Team, 2021). Generalized linear mixed models were constructed using the R-package ‘glmmTMB’ version 1.1.10 (Brooks et al., 2017). Multicollinearity among predictor variables was assessed using ‘performance’ version 0.12.4 (Lüdecke et al., 2021). Significance values were obtained using Wald-χ^2-tests in the package ‘car’ version 3.1.2 (Fox and Weisberg, 2019). Model performance was evaluated using the R-package ‘DHARMa’ version 0.4.7 (Hartig, 2021).

3 Results

Across all plots, 27.2% of fruit plum were removed after four days, with strong variation and overdispersion among sites (Fig. 1, median = 11.1%, range 0–100%). Fruit removal was weakly (-13%) but significantly associated with tree species richness in the model excluding canopy cover, but this effect was not apparent when canopy cover was included (Fig. 1a, Table 1). In the full model, fruit removal was not significantly associated with canopy cover (Fig. 1d), although more fruit were removed in open forests (45%) than in closed forests (22%). Initial fruit mass was positively associated with fruit removal, but did not change with the duration of the experiment (Table 1).

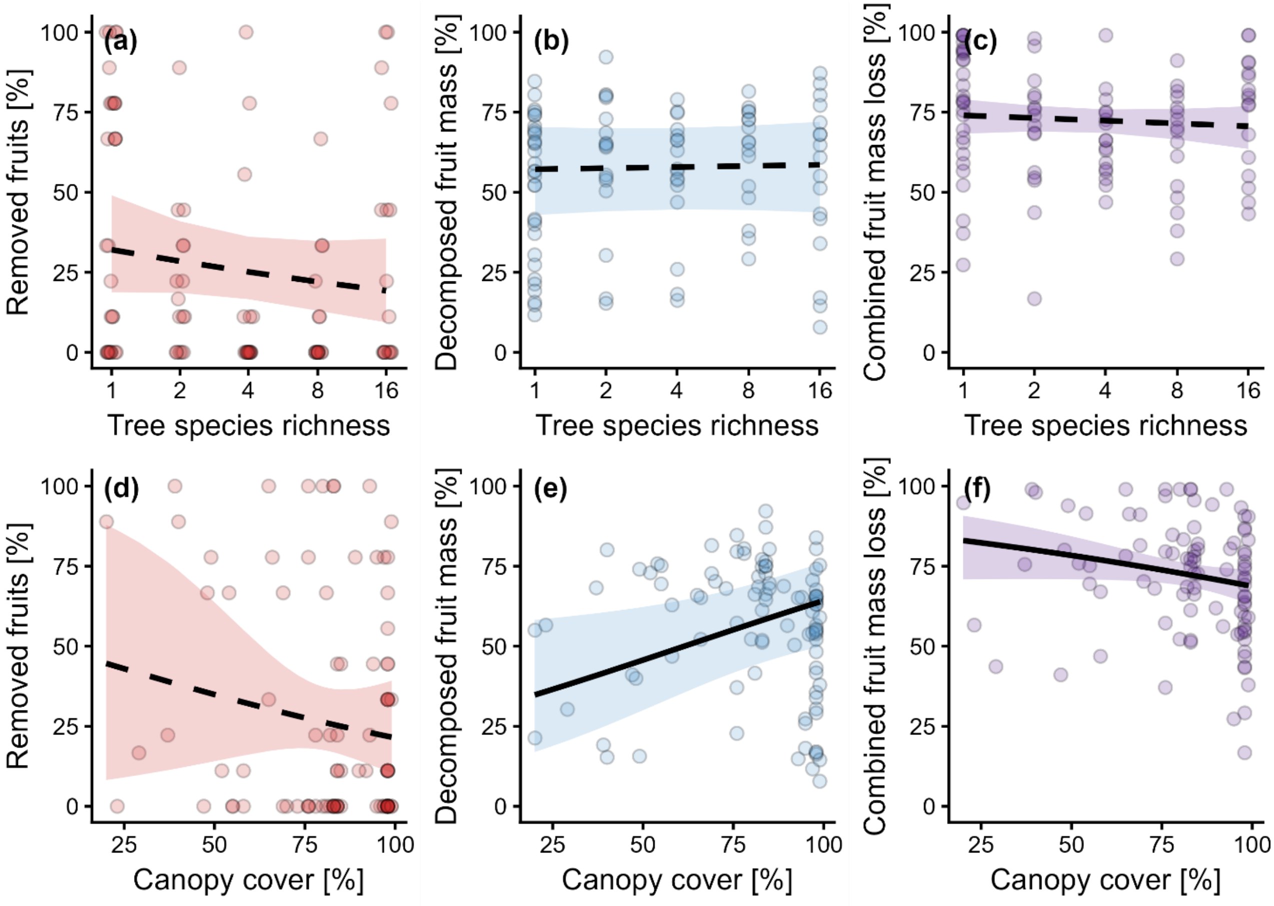


Figure 1: The effect of tree species richness (a-c) and canopy cover (d-f) on removal, decomposition and turnover (i.e., the combined rates of removal and decomposition) of plum (*Prunus salicina*). Each point represents one plot. Solid lines indicate statistically significant relationships with 95% CI as shaded polygons, while grey dashed lines represent non-significant relationships.

The remaining fruit were on average decomposed by 55.7% (median = 62.9%) after four days, with 95% of values ranging between 14.6% and 84.3%. Decomposition was significantly associated with canopy cover (Table 1) and increased from 35% in open forests to 64% in closed forests (Fig. 1e). Tree species richness had no detectable effect on fruit decomposition in the models (Table 1), and decomposition was unrelated to the initial mass of fruit and experimental duration.

When both processes were combined, mean fruit mass loss was 71.4% across plots after four days. Turnover was unaffected by tree species richness but slightly decreased with canopy cover (Table 1), from approximately 83% in open forests to 69% in closed forests. It was also positively associated with initial fruit mass and experimental duration (Table 1). Fruit removal and decomposition were weakly and negatively correlated across plots (Spearman $\rho = -0.19$, $p = 0.069$).

Table 1: Mixed model analyses of variance of the effects of tree species richness and canopy cover on removal (% removed fruit), decomposition (% mass loss) and turnover (% turnover) of plum (*Prunus salicina*).

		% removed fruit		% mass loss		% turnover	
		χ^2	p	χ^2	p	χ^2	p
Fruit mass	*1*	*3.86*	***0.049***	*0.02*	*0.900*	*3.38*	***0.066***
Experimental duration	*1*	*0.41*	*0.525*	*1.98*	*0.160*	*9.38*	***0.002***
Tree species richness	1	4.01	**0.044**	2.51	0.114	2.22	0.137
Residual	88 / 680						
Fruit mass	*1*	*2.91*	***0.089***	*< 0,01*	*0.981*	*3.88*	***0.049***
Experimental duration	*1*	*0.42*	*0.515*	*2.35*	*0.125*	*6.70*	***0.010***
Tree species richness	1	1.35	0.244	0.05	0.822	0.49	0.486
Canopy cover	1	0.57	0.451	5.32	**0.021**	3.36	**0.067**
Residual	87 / 679						

Random effects: sites (n = 2), plots (n = 90 or n = 95), tree species (n = 38), geomorphological type of the plot (n = 5). Statistically significant values are in bold face.

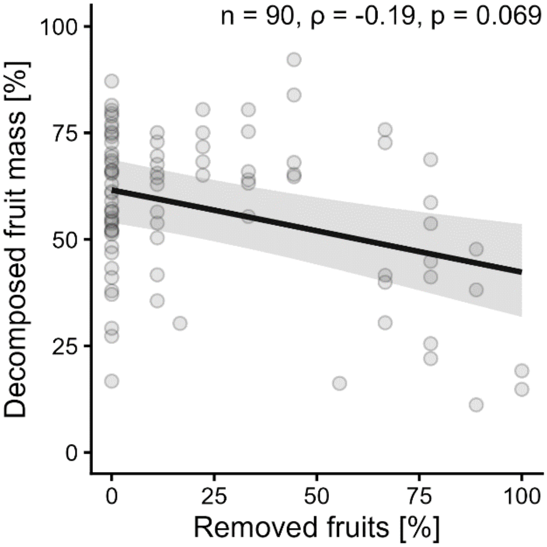


Figure 2: Spearman rank correlation between removal and decomposition (i.e., the two components of turnover) of plum (*Prunus salicina*) after four days. Each point represents one plot. Mean ± 95% CI.

4 Discussion

This study examined how tree species richness and canopy structure influence the fate of fruit in a subtropical forest. Contrary to our expectations, tree species richness showed a weak and inconsistent association with fruit removal, decomposition, and overall fruit turnover across models. Instead, canopy cover emerged as the more important driver, with decoupling effects on the two processes of fruit turnover: fruit removal tended to be higher in more open plots, whereas decomposition enhanced in more closed forests. These results indicate that the fate of fallen fruit is governed by two partly decoupled pathways, likely driven by different functional animal groups and environmental conditions, rather than by tree diversity per se.

4.1 Removal of fruit

Fruit removal was higher in monocultures, but this relationship was not independent of canopy cover in the full models, and no effect of tree species richness was detected within closed forests (i.e. >70% canopy closure, $\chi^2 = 0.66$, $p = 0.416$). Many ground-dwelling animals move across large areas and do not restrict their foraging to single plots (Pires et al., 2018). As a result, fruit removal on the forest floor may depend more on forest structure and resource distribution at larger spatial scales than on local variation in tree species richness (Yu et al., 2024). This is consistent with the general expectation that bottom-up effects of tree diversity attenuate with increasing trophic level (Li et al., 2023b; Scherber et al., 2010). Nonetheless, both our results and those of others (Milligan and Koricheva, 2013) suggest that tree diversity effects on vertebrate foraging can emerge when it generates strong local contrasts in resource availability or habitat structure that alter foraging decisions.

In our experiment, fruit were placed randomly under trees in constant amounts and not originate from trees within the plots. This design prevented animals from responding to variation in fruit availability in the plots, as may normally occur in natural forests over longer time periods (Landim et al., 2025; Schnurr et al., 2004). The observed patterns therefore likely reflect the general foraging activities of the most common ground-dwelling vertebrates (e.g., *Muntiacus reevesi*, *Sus scrofa*) rather than active fruit-tracking behaviour. Tree diversity effects on fruit removal may be stronger in systems where fruiting trees are embedded within species mixtures, where resource availability and habitat structure vary together and shape foraging decisions. In addition, our study was conducted in a relatively young forest, where plant–frugivore interactions may still be developing (Landim et al., 2025). As the forest matures, increasing interaction frequency may strengthen tree diversity effects on fruit removal.

As expected, fruit removal tended to be higher in open forests. Open forests increase visibility and reduce physical barriers on the forest floor which can improve detection and access to fruit. Similar effects of canopy cover on frugivore activity have been reported in other systems as well (Taneja et al., 2022). However, responses to canopy cover are not consistent. Higher removal rates have also been observed in closed forests (Diaz et al., 1999), and effects of canopy cover can weaken when fruit availability is low or spatially heterogenous (Donoso et al., 2017). Nonetheless, fruit removal varied strongly across the canopy cover gradient, and the approximately 20% difference between open and closed forests was not statistically significant. This suggests that fruit removal is strongly influenced by stochastic encounters between fruits and animals, resulting in high spatial variation that may limit the detectability of habitat effects, even in well-replicated experiments.

4.2 Decomposition of fruit

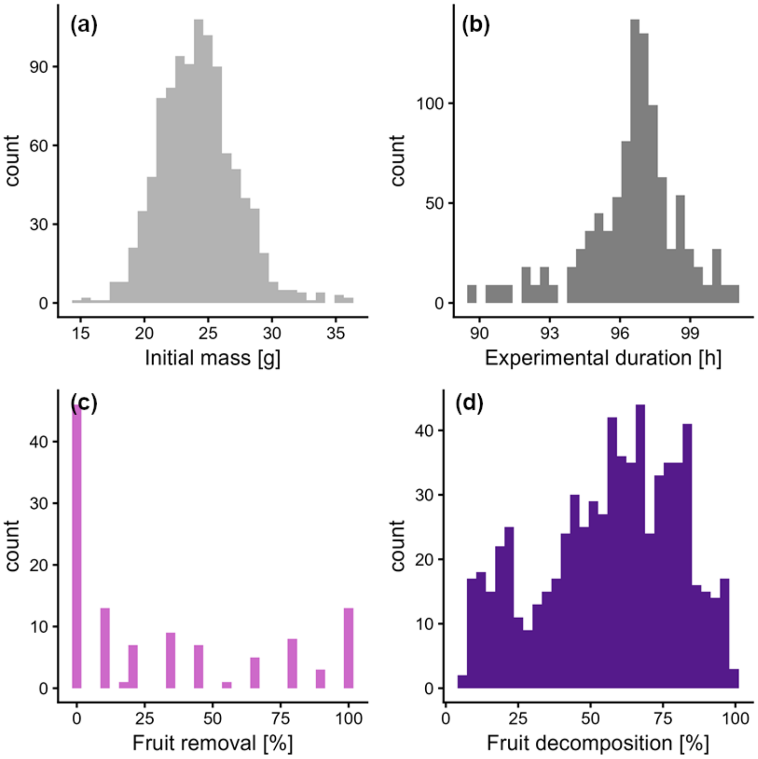
Tree diversity did not influence the velocity of fruit decomposition on the forest floor. This result contrasts with expectations from biodiversity-ecosystem functioning theory, which often links higher tree diversity to enhanced ecosystem functioning. For example, leaf litter decomposition typically accelerates with tree diversity as more diverse forests produce more litter (i.e., mass effect) and trait complementarity among leaf types (i.e. diversity effect) (Beugnon et al., 2023; Sonkoly et al., 2019). However, only 18 of the 42 tree species in the experiment produce fleshy fruits, and not all are currently reproductive, so fruit decomposition is only indirectly related to tree composition. Effects of tree diversity through litter inputs are thus likely limited for this process and primarily channeled through leaf litter. Notably, leaves and fruits differ in chemical composition and decomposition pathways: the sugar- and moisture-rich fruits break down rapidly (days to weeks) through bacteria and yeasts, whereas the tough, lignin- and cellulose-laden leaves decompose slowly (months to years) via specialized fungi. Because of these differences, effects of tree species richness on leaf litter cannot be directly transferred to fruit decomposition, even when one litter type might affect the decomposition of the other (De Paz et al., 2018).
A similar lack of tree diversity effects on decomposition has been observed for other necromass types. No effect of tree species richness on wood decomposition has been found in this system (Eichenberg et al., 2017; Pietsch et al., 2019). Comparable weak responses have also been reported for carrion decomposition (Rehling et al., 2025). Across these necromass types, decomposition is often driven by a small number of generalist invertebrates such as ants or termites. These taxa are present in almost all plots, including monocultures (Spitz et al. in review), and can rapidly exploit nutrient-rich resources. Because they are highly competitive, they may dominate decomposition processes and may mask effects of tree diversity on decomposition rates (Rehling et al., 2025).

Most immediate effects can be attributed to canopy cover. Canopy cover influenced how fast fruit decomposed on the forest floor, with higher decomposition rates in closed forests. Canopy cover affects temperature and moisture, which regulate microbial activity and decay. Closed forests are cooler and more humid, which can support decomposition and reduce drying. In open forests, hot and dry conditions in subtropical systems may limit microbial and decomposer activity. Similar microclimatic effects are known for leaf litter, wood, and carrion (Beugnon et al., 2023; Eichenberg et al., 2017; Pietsch et al., 2019; Rehling et al., 2025). Direct evidence for fruit decomposition remains scarce.

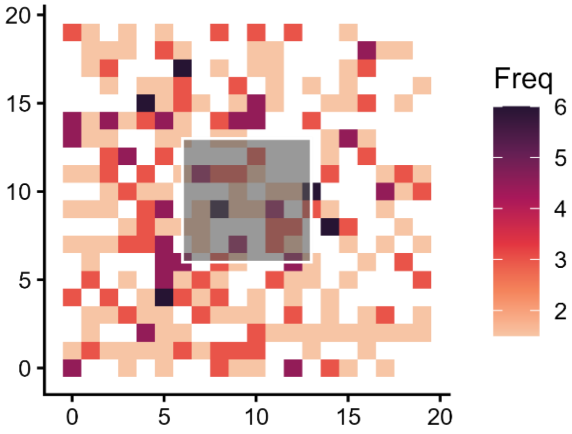
5 Conclusion

Tree species richness was not consistently associated with fruit turnover, whereas canopy cover showed contrasting effects on its component processes. Consequently, seed dispersal (via secondary fruit removal) and nutrient cycling (via fruit decomposition) are partially decoupled by the forest environment. The extent as to which this can be attributed to still young forest developmental stages needs to be studied in further approaches to better understand the role of fruit decomposition and its ecological drivers in ecosystem functioning. More broadly, this study highlights that fruit decomposition remains a relatively understudied component of necromass ecology (Benbow et al., 2019).

6 Appendices



Appendix A: Distribution of (a) the mass of fruit [g] used in the experiment before start, (b) experimental duration [h], (c) fruit removal [%], and (d) mass loss [%] of fruit after four days in BEF-China.



Appendix B: The frequency of locations (i.e. where fruit were placed around trees) at the 95 plots of BEF-China. Each plot consists of a grid of 20 × 20 planted trees, and three mice were laid out around each of three trees. The grey shaded area represents the intensively investigated center of the plots.

Code and data availability

Data and code can be accessed via GitHub (https://github.com/nature-rehling/). A permanent option will be created upon acceptance.

Author contributions

Finn Rehling: conceptualization (lead), data curation, formal analysis (lead), visualization, writing - original draft preparation (lead). **Luisa Martha Senger**: conceptualization (support), investigation (equal), methodology (equal), writing – original draft preparation (support), writing – review & editing (equal). **Franz Tillmann Niedernhoefer**: investigation (equal), methodology (equal), writing – review & editing (equal). **Nora Anderson**: investigation (equal), methodology (equal), writing – review & editing (equal). **Tim Diekötter**: validation (equal), writing - review & editing (equal). **Alexandra Erfmeier**: validation (equal), writing - review & editing (equal). **Yi Li**: conceptualization (support), formal analysis (support), writing – review & editing (equal). **Alexandra-Maria Klein**: funding acquisition (equal), project administration (equal), supervision (equal), writing - review & editing (equal).

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Competing interests

The authors declare that they have no conflict of interest.

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