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Canopy cover and forest management shape vertebrate scavenger assembly but not carrion removal rates

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A R T I C L E I N F O

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A B S T R A C T

Carrion decomposition is a key process in nutrient cycling and ecosystem functioning, driven by microorganisms, necrophagous insects, and vertebrate scavengers. The rate of decomposition is influenced by various factors, including environmental conditions, carcass characteristics, and scavenger assembly. In forests, canopy cover and structure shape microclimatic conditions and habitat features, yet little is known about how these characteristics affect carrion decomposition by vertebrate scavengers. As forest disturbances increasingly open up canopies, understanding the impact of canopy cover on carrion decomposition becomes essential. We investigated removal rates of small carrion at paired gap and closed-forest plots along a gradient of forest-management intensity in three regions in Germany, using camera traps to monitor vertebrate scavengers. Of 89 rat carcasses, 67 were removed by vertebrates. Initial removal rates were higher in gaps than in closed forests and at plots with higher forest-management intensity. However, over the full exposure time, removal rates were similar across all treatments. Differences in temporal patterns of carrion removal were linked to shifts in scavenger dominance, with red kite (*Milvus milvus*) prevalent in gaps and red fox (*Vulpes vulpes*) in closed forest. Our findings indicate that forest management and changes in canopy cover, such as those caused by disturbances, have little impact on carrion removal rates. Vertebrate scavenger assembly however differed between open and closed forests, which suggests functional redundancy among scavengers but that it is important that carrion resources are available for scavengers both in gaps and closed forests to promote overall biodiversity and maintain their ecosystem functions.

1. Introduction

Decomposition of carrion, i.e., dead animals, is an important process across ecosystems. Compared to plant necromass, the magnitude at which carrion is present in ecosystems is smaller, but carrion has a higher nutrient value due to low C:N ratios (Benbow et al., 2019). Decomposition of carrion is typically faster than of many types of plant necromass and more strongly driven by invertebrate decomposers and vertebrate scavengers (Barton et al., 2013). Among those, many necrophagous invertebrates are specialized on carrion, while most vertebrate scavengers, except vultures, are opportunistic and carrion is only part of their diet (DeVault et al., 2002). Most carrion studies have focused on larger carcasses, such as ungulates, studying for example scavenger communities in different ecosystems (Inagaki et al., 2022; Mateo-Tomás et al., 2015; Selva et al., 2005), competition of vertebrate scavengers with invertebrates (Ray et al., 2014; Sawyer et al., 2022) or changes in carrion availability after reestablishment of large predators (Wikenros et al., 2013; Wilmers et al., 2003). Carrion decomposition rates differ between carrion of different sizes (Selva et al., 2005; Wierer et al., 2024) and larger carcasses usually support more scavenger species over longer time periods (Stiegler et al., 2020; Turner et al., 2017). In contrast, smaller carcasses, for example of rodents or lagomorphs, are

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consumed quickly or even at once by vertebrate scavengers (Mctee et al., 2019).

Carrion decomposition rates are generally influenced by abiotic factors, such as temperature and precipitation (Turner et al., 2017), and decomposer communities (Barton et al., 2013). In forests, canopy cover is a major driver of microclimatic conditions (Thom et al., 2020), cover of understory vegetation (Zellweger et al., 2020) and of biodiversity across taxonomic and trophic groups (Penone et al., 2019). Thus, canopy cover could also affect carrion decomposition and involved decomposer communities (Bartel et al., 2024). Higher temperatures in canopy gaps might lead to higher microbial and invertebrate activity (Barton and Bump, 2019; Englmeier et al., 2023) and could lead to stronger odor development which promotes olfactory searching scavengers (Kane et al., 2017). By contrast, removal rates of visually searching scavengers could be reduced in gaps when covered by a dense herb and shrub layer which reduce visibility (Guiden and Orrock, 2017). Scavenger communities differ between human-impacted grasslands and forest patches, and may thus differ between open and closed forests (Stiegler et al., 2020; Turner et al., 2017). However, it remains unknown whether gaps in forests affect carrion removal rates. Considering that increasing forest disturbance rates lead to more canopy openings (Senf et al., 2020), a better understanding is needed of how canopy openness affects carrion decomposition, including the removal by vertebrate scavengers.

In this study we focused on the removal of carrion by vertebrate scavengers that is not only affected by canopy openness, but also by other forest structures or tree species composition which are altered by forest management. Invertebrate decomposer communities, for example, differ between differently managed forests (von Hoermann et al., 2020; Weithmann et al., 2020). Higher forest-management intensity is linked to less structural diversity and resources such as deadwood which has negative effects on biodiversity (Brockerhoff et al., 2017; Hämäläinen et al., 2014). Stiegler et al. (2020) observed that heterogeneous surrounding habitats are associated with vertebrate scavenger species richness, which may suggest that vertebrate scavengers could be affected by higher forest-management intensity. However, dominant vertebrate scavengers in Central Europe are often habitat generalists, such as red fox *Vulpes vulpes,* and might therefore be less affected by forest management than invertebrates. In a German national park, for example, carrion removal was not affected by the distance to the next managed forest (De Pelsmaeker et al., 2024), while scavenging lynx (*Lynx lynx*) were more likely to be observed with increasing distance to the next trail (Stiegler et al., 2020). These contrasting results indicate that it is still unclear, whether forest-management intensity has an effect on the removal of carrion by vertebrate scavengers.

To contribute to a better understanding how scavenger assemblies and carrion removal rates differ between forests comprising different stand properties due to differences in management intensity, we measured removal rates of rats at forest sites with paired plots with closed canopy and gaps along a gradient of forest-management intensity in three regions of Germany. We recorded removal by vertebrate scavengers using camera traps during the summer months of two consecutive years. Specifically, we ask the following questions:

(i) What is the effect of canopy openness (closed vs. gap) and forest-management intensity on carrion removal rates?
(ii) Does the scavenger assembly differ between canopy gaps and closed canopy in forests and between forest management intensities?

2. Methods

2.1. Study area

As part of the *Biodiversity Exploratories* research platform (www.biodiversity-exploratories.de), this experiment took place at 26 forest sites in three regions of Germany including the north-eastern Schorfheide-Chorin (n = 9), the central Hainich-Dün (n = 9) and the south-western Swabian Alb (n = 8) (Fischer et al., 2010). Within each region, the sites are located within one to 20 km distance from each other. The experimental sites cover a gradient of forest-management intensity from unmanaged beech forests to extensively managed beech forests to mixed stands of beech and conifer to intensively managed conifer forest stands. The natural tree species composition in all three regions is dominated by European beech (*Fagus sylvatica*), while intensively managed forests are dominated by conifers (Scots pine, *Pinus* sylvestris, in Schorfheide-Chorin or Norway spruce, *Picea abies*, in Swabian Alb). Thereby, forest-management intensity (Schall et al., 2023) is quantified as (a) the proportion of harvested tree volume, (b) the proportion of tree species that are not part of the natural forest community and (c) the proportion of dead wood showing signs of saw cuts (Kahl and Bauhus, 2014) based on a forest inventory conducted between 2014 and 2016 (Schall et al., 2018).

In early 2020, a canopy gap experiment was implemented (for details, see 2.2. Forest experiment, Staab et al., 2022) by felling and removing trees within an approximately circular area with a 25 – 37 m diameter. Gap sizes differ in relation to stand height to ensure comparable conditions in relative terms. Gaps were created next (min. 100 m distance) to an untreated control plot with closed canopy in stands with similar tree species composition and structure as the control plots resulting in paired plots (closed canopy vs. gap) at each site (Fig. 1).

2.2. Experimental setup

As a standardized small carrion, we purchased frozen rats (*Rattus norvegicus*, 350–450 g, n = 104) from a pet food supplier (XCLUSIVE SNAKES, Reilingen, Germany). The fur colour of the rats varied to some extent from mostly white to completely brown, but (Sawyer et al., 2022) found no effect of fur colour on removal rates. The rats were defrosted 24 h before the setup of the experiment and handled with disposable gloves as little as possible to avoid human scent on them. One rat was placed at each plot (52 paired plots of gaps with open canopy and closed forests at 26 sites).

A camera trap (Browning, Model BTC-8E, Utah, USA) was placed at a 2.5–3.5 m distance from the rat, either on a tree or a post. The camera was positioned at roughly 0.6 m height and angled downwards so that the carrion was in the center of the photo. When triggered, the camera took a series of eight rapid photos with a minimal delay of one second between sequences. In 2023, the installation of the experiments took place between May and June and started in the Schorfheide, two weeks later in the Hainich and another two weeks later in the Swabian Alb. In 2024, installation of the experiment started in the Swabian Alb in May and in Hainich-Dün and Schorfheide-Chorin in June. Camera traps monitored the plots for at least four weeks.

2.3. Data processing

To organize and classify photos taken by the camera traps, the digital platform www.agouti.eu (WUR and INBO, 2025) was used. The starting time of the experiment, i.e. when the small carrion was placed, was marked as the starting point of the exposure time. Observed animals were classified to species level and interactions with the small carrion were classified by different behavioral categories: If an animal took, ate or carried away the small carrion, it was classified as *removal.* If no removal was observed, the last time the carrion was visible on the camera was classified as *last seen.* The time between setup and removal or last seen was calculated as *removal time.*

2.4. Statistical analyses

Further data processing and analyses were conducted in R 4.4.2. (R Core Team, 2023) using the packages *tidyverse* (Wickham et al., 2019), *lubridate* (Grolemund and Wickham, 2011), *survival* (Therneau, 2024),

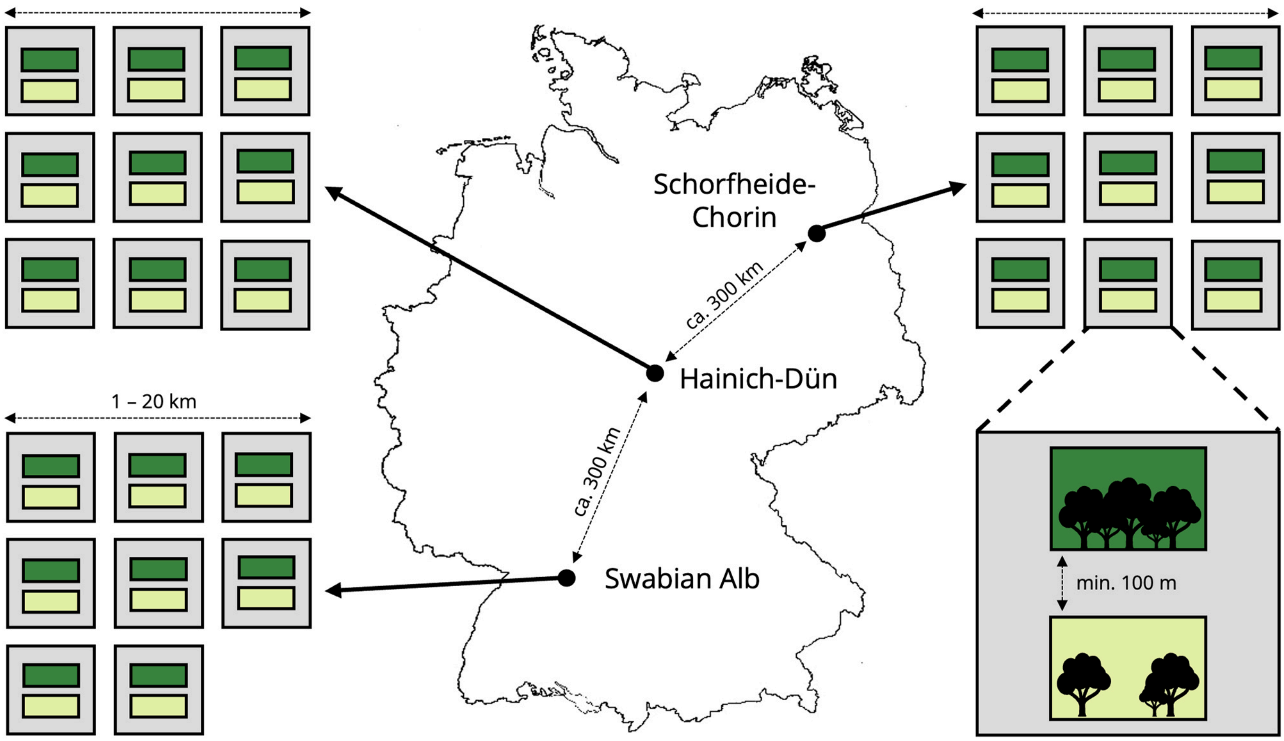

Fig. 1. Overview showing the distribution of the 26 sites representing forest management-intensity gradients in three regions of Germany. Each site consisted of a pair of plots, one with a closed canopy and with a gap created three to four years before this study.

lme4 (Bates et al., 2015), *ggsurvfit* (Sjoberg et al., 2024), *ggplot2* (Wickham, 2016) and *gridExtra* (Auguie, 2017). To analyze which factors influence the removal rates we used Cox Proportional Hazard Regression models (function: coxph()). Thereby, the removal time until the removal event was used (in hours) as response variable and closed forest or gap with open canopy (binary), forest-management intensity (continuous: range = 0–3), the region (factorial: Schorfheide, Hainich-Dün or Swabian Alb) and the year (factorial: 2023 or 2024) as predictor variables. Site was used as random effect variable (factorial, n = 26). Small carrion is regularly consumed at once by vertebrate species and thus, early detection is essential for scavengers. Since we visually noticed a difference in removal rates for the overall exposure time (42 days) and the first five days, we fitted two separate models, one for the overall exposure time and one for the first five days only.

The number of observed removal events varied among scavenger species. Therefore, we analyzed the removal of the three most abundant scavenger species (*Buteo buteo*, *Milvus milvus* and *Vulpes vulpes*) in relation to canopy cover (closed forest versus caps) and forest-management intensity. We used a logistic regression model for each species separately, binary removal by a given species (presence or absence) as the response variable and, forest-management intensity (continuous: range = 0–3) and canopy (binary) as predictor variables.

3. Results

In total, 104 rats were placed. For 89 cases, data was available to calculate the duration (in minutes) from the placement to removal (n = 69) or until last seen with the camera (n = 20). In 15 cases, not sufficient data was available to be included in the analyses, possibly due to technical failure of the camera. The highest number of rates was removed by red fox *Vulpes vulpes* (26), followed by red kite *Milvus milvus* (21) and common buzzard *Buteo buteo* (20); one rat each was removed by wild boar *Sus scrofa* and European badger *Meles meles* (Fig. 2).

3.1. Removal

The time until half of all carrion was removed was shorter in gaps (2.7 days) than in closed forests (4.5 days), but over the full exposure time the percentage of rats removed was similar (Fig. 3). Our Cox Proportional Hazard model considering the full exposure time showed that

Fig. 2. Camera trap picture of a red fox removing a rat in a closed forest (A, left) and of a red kite removing a rat in a gap with open canopy (B, right).

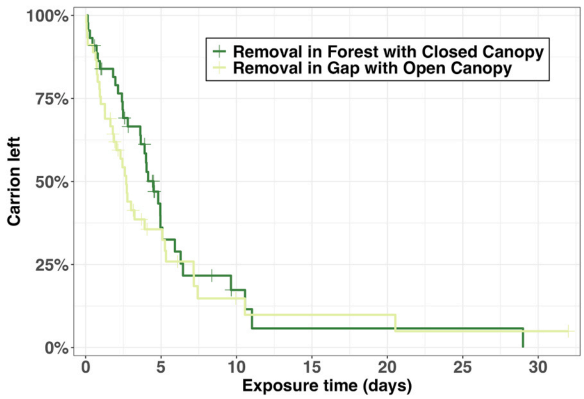

Fig. 3. Kaplan-Meier survival curves for carrion removal over the full exposure time (in days) for forests with closed canopy and gaps with open canopy.

probability of removal did not differ between closed forest and gaps and were not affected by management intensity applied to the surrounding forest, but the probability of removal was higher in the second year (Table 1). When considering only the first five days, the probability of removal was significantly higher in gaps compared to closed forests and in forests with higher management intensity. The probability of removal did not differ between the three regions in either model.

3.2. Scavenger species

The number of rats removed by the three most common scavenger species in gaps and closed forest were 17: 4 for red kite, 9: 11 for common buzzard and 10: 16 for red fox (Fig. 4a). Logistic regression models indicated that removals by red kite were significantly higher in gaps (GLM, t = 2.134, $P = 0.002$) and significantly higher at higher forest-management intensity (GLM, t = 1.925, $P = 0.002$; Fig. 4b). The removal probability by common buzzard and red fox were not significantly affected by canopy cover or forest-management intensity (Table S1).

3.3. Further observations

We further observed Wild boar piglets, Eurasian jays (*Garrulus glandarius*), Great tits (*Parus major*), Great spotted woodpeckers (*Dendrocopos major*) and Blackbirds (*Turdulus merula*) close to the carrion, or the place where the carrion was located, feeding on insects, but they never removed that rat. Common ravens (*Corvus corax*) were detected in two locations at the Swabian Alb cautiously examining the carrion, but never removing it or feeding on it.

Table 1
Overview of test statistics of the Cox Proportional Hazard regression model testing effects of canopy cover, forest-management intensity (ForMI), region and study year on the probability of removal of rats for the full exposure time (left) and the first five days (right). Regions are HAI (Hainich), SCH (Schorfheide) and ALB (Swabian Alb). Significant effects are highlighted by bold typesetting ($P < 0.05$).

	Full exposure time (n = 89)			First five days only (n = 68)		
	Coefficient ± SE	χ^2	P	Coefficient ± SE	χ^2	P
Canopy: gap - closed	0.248 ± 0.252	0.97	0.320	**1.068 ± 0.354**	**9.09**	**0.003**
ForMI	0.514 ± 0.328	2.51	0.110	**0.833 ± 0.399**	**4.36**	**0.037**
Region: HAI - ALB	- 0.005 ± 0.377	0.00	0.990	0.831 ± 0.474	3.08	0.079
Region: SCH - ALB	- 0.515 ± 0.368	1.97	0.160	0.346 ± 0.482	0.51	0.470
Year	**0.813 ± 0.283**	**8.21**	**0.004**	0.263 ± 0.310	0.72	0.400

Note: SE indicates the Standard Error, P indicates the p-value.

4. Discussion

We investigated whether the removal rates of small carrion by vertebrate scavengers differ between gaps and closed forest and along a gradient in forest-management intensity. Earlier removal was more likely in gaps than in closed forest and in plots with higher forest-management intensity, but over the full exposure time, removal rates across all plots were equal. We found a link between fast removal by red kite in gaps and plots with higher forest-management intensity indicating that differences in the temporal patterns of carrion removal were associated with differences between the dominant scavenger species in open and closed forest. Our observed removal rates (50 % removal time in gaps with open canopy and forests with closed canopy: 2.7 vs 4.5 days, respectively) are within the range of comparable studies (DeVault et al., 2002; Schwegmann et al., 2023) as is the number of observed vertebrate scavenger species (Sawyer et al., 2022; Turner et al., 2017).

Over the full exposure time, there were no differences in the removal rates between forest-management intensity and in gaps and forests with closed canopy, as well as between the different regions with their different forest types (uneven-aged beech forests to pine or spruce forests). This is in line with other studies, which found that carrion removal was not affected by the cover of trees (Wenting et al., 2022, 2024) or forest patch size and the connectivity between forests (Olson et al., 2016). In addition, McKee et al. (2024) found that the reduction of mesomammalian populations (due to an invasive predator) did not affect scavenging efficiency, but they did observe a change in the scavenger community composition. This demonstrates functional redundancy of the scavenger species, although it does not exclude the possibility of indirect consequences for ecosystem processes. Overall, this indicates that the removal of small carrion is relatively stable across forest regions, such as our three regions, and across forests with different canopy cover and management intensity. The contribution of the different dominant vertebrate scavengers to carrion removal, however, was affected by forest management and particularly by canopy cover. We suggest that the dominant vertebrate scavengers in Central European forests are functionally similar, leading to comparable carrion removal rates despite differences in scavenger assemblies. The three dominant scavenger species in our study are versatile, inhabiting diverse environments, and as facultative scavengers they do not exclusively rely on carrion (BirdLife International, 2020; Castañeda et al., 2022; Cieśluk et al., 2024).

Despite similar overall removal rates, we did observe removal differences in the first days after placement. Carrion is a nutrient-rich resource and there is a strong competition to be the first one to arrive at a carcass (Selva and Fortuna, 2007) in particular, when the carcass can be consumed at once. While many bird species rather rely on visual cues (Sawyer et al., 2022), mammalian scavengers tend to rely more on olfactory cues to locate carrion (Inagaki et al., 2020; Schwegmann et al., 2023; Turner et al., 2017). Whereas odor may become stronger over time due to microbial and bacterial activity (Barton and Bump, 2019; Englmeier et al., 2023), visual cues are present throughout or may become weaker over time. We observed earlier removal by red kites and common buzzards and later removal by red foxes. Since both bird species use visual cues for foraging (Caves et al., 2024), while foxes also use olfactory cues (DeVault et al., 2002; Ruzicka and Conover, 2012), faster removal by red kite and common buzzard than by red fox can be likely explained by different cues used for scavenging as well as the higher motion capacity of these birds.

In forests with dense vegetation structure, olfactory cues emitted by carrion may be more important for predators and scavengers to find food than visual cues (Moleón et al., 2019; Seibold et al., 2013). Carrion removal rates of the different scavenger species can differ between open land and closed forests (Arrondo et al., 2019). Moreover, forest

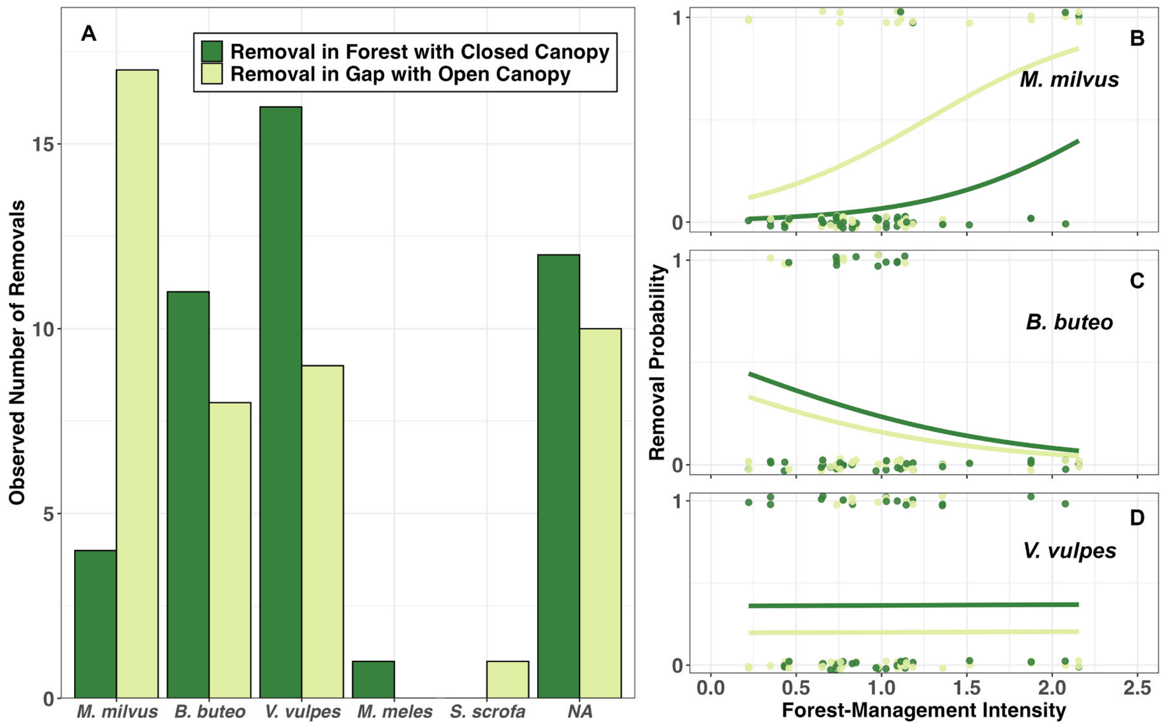

Fig. 4. A: Frequency of carrion removal by different scavenger species in forests and gaps, Fig. 4.B-D: Predicted carrion removal probability by the three most common scavengers based on forest-management intensity and canopy. The removal of the three most abundant scavenger species (*Buteo buteo*, *Milvus milvus* and *Vulpes vulpes*) between forests with closed canopy and gaps and for the forest-management intensity was tested with a logistic regression model for each species separately: As response variable the binary removal by a given species (presence or absence) was used, with forest-management intensity and canopy cover and their interaction effect as explanatory variables. Effects of canopy and forest management intensity were significant only for M. milvus.

management affects canopy cover, but also other structural characteristics and tree species composition (Schall et al., 2018) and could thus further influence carrion removal. Although we found no effects of canopy cover and forest management on carrion removal rates over the full exposure time, we found significantly higher removal rates in gaps compared to closed forest and an increase with increasing forest-management intensity when focusing on the first days after placement. These effects can be linked to differences in scavenger assemblies and particularly the contribution of red kites, as removal rates by red kite differed significantly between gaps and closed forest and were significantly higher in intensively managed forest. Here, all four removal events by red kite in closed forest plots took place in either Scots pine or Norway spruce dominated forests in Swabian Alb or Schorfheide-Chorin, which is in line with the red kite's habitat preference for a mixture of forests and open land (BirdLife International, 2020). Similarly, complementary studies found high carrion removal rates for scavenging birds along roads, which are a major source of carrion due to frequent wildlife-vehicle collisions (Morant et al., 2023). This pattern is likely driven by increased visibility along roadways (Dhiab et al., 2023), yet other road-kill studies could not confirm these results, suggesting that scavenger foraging behavior may be highly species-specific (Lambertucci et al., 2009). For removals by common buzzard and red fox, differences were not significant but red fox showed a tendency to more removals in closed forest. These differences may be explained by different foraging behavior (Montenegro et al., 2025; Pardo-Barquín et al., 2019). Red kite has a larger wingspan than common buzzard (Svensson et al., 2023) which could make it more difficult to maneuver in closed forest and is thus typically found to forage more in open habitats (BirdLife International, 2020), whereas common buzzard is known to forage also under closed canopies, preying even on animals breeding in woodpecker cavities (Zahner et al., 2017). In contrast, red foxes have a lower movement capacity than birds of prey and their foraging strategy relies primarily on olfactory cues. As a highly opportunistic species red foxes show little preference for a certain habitat type or diets as they occur globally and have a very flexible diet (Castañeda et al., 2022), which likely makes them less sensitive to variations in forest-management intensity. In our study, the gradient in forest-management intensity is strongly linked to differences in tree species from European beech to Norway spruce or Scots pine, the two latter typically have a more open canopy structure and harvesting intensity, which have typically a more open canopy structure, and harvesting intensity leading also to higher canopy openness in more intensively managed forests (Schall et al., 2018). However, since management includes either shelterwood or selection cutting, canopy openings in managed forests in our study regions are rather small and create a weaker contrast than our experimental gaps. This may explain why the effects of canopy treatments were stronger than the effects of forest-management intensity.

Vertebrate species compete with invertebrates and microbes for (small) carrion (Devault et al., 2003). The methods we applied did not allow to quantify the impact of invertebrates on small carrion removal. In 33 % of the cases, we did not observe a removal event, which is comparable to studies in urban ecosystems (Inger et al., 2016; Welti et al., 2020) as well as in other forest ecosystems (Schwegmann et al., 2023). Possibly due to technical failures, we were not able to trace all placed rats. However, some camera trap photos indicated that these rats were buried by carrion beetles which may reduce availability to vertebrate scavengers. As we focused on vertebrate scavengers and did not want to disturb the study sites too much, we did not check whether invertebrates buried the small carrion when we did not observe a removal by vertebrates. In our study, the fastest scavengers were red kites mainly removing carrion placed in gaps. Therefore, less carrion was available in gaps compared to forests with closed canopy during later stages which may have led to an underestimation of the removal probability by the other species in gaps during later stages. Carrion removal rates of red foxes and common buzzards did not differ significantly between closed forests and gaps, but whether this is due to foraging habitat preferences or due to the availability of carrion remains unclear. Nevertheless, the observed patterns are in line with the rather generalist foraging behavior of red foxes and common buzzards. The effect of early removals on later removals could have been avoided by replacing removed rats. However, the main goal of our study was to evaluate the effects of canopy cover and forest-management intensity on overall removal rates of carrion. In the analysis for the overall exposure time, we found significantly higher removal in the second year than in the first year. This indicates that long-term studies are needed to identify the drivers of interannual variation in carrion removal. Notably, we observed no carrion removal by corvids, although they were regularly observed to feed on carrion in other studies (e.g. Gomo et al., 2017; Mctee et al., 2019; Schwartz et al., 2018). Common ravens, carrion crows (*Corvus corone*) as well as other corvid species occur in our study regions, but we only observed common ravens cautiously looking at the carrion at two locations without removing it. Most likely, ravens avoided the plots with the experimental installations due to their high neophobia and cautious behavior (Heinrich et al., 1995) or their preference for larger carcasses (Selva et al., 2005). Finally, some of the used rats had a white fur or mixed white and grey or brown fur which could have increased the chance of removal by visually operating predators, however, previous studies found no effect of fur color (Sawyer et al., 2022) which is why we did not account for fur colour in our analysis.

4.1. Recommendations

Overall, our results indicate that removal of small-sized carrion by vertebrate scavengers was not affected by forest-management intensity and canopy cover and was similar across three regions in Germany. However, carrion removal was initially faster in gaps with open canopy and at sites with higher forest-management intensity, which was associated with the occurrence of red kite, a scavenger species that rather relies on visual cues, preferring open habitat for foraging. This suggests that the dominant vertebrate scavenger species in forests in Germany are functionally similar, leading to comparable overall carrion removal rates in gaps and closed forest and differently managed forest when longer time spans are considered. Nevertheless, even if our results suggest that carrion removal is overall not strongly affected by forest management decisions, the increasing opening of forests due to natural disturbances enforced by climate change (Senf et al., 2020) could lead to faster carrion removal, if vertebrate scavengers relying on visual cues are abundant. This could have effects on vertebrate scavengers as well as invertebrate and microbial decomposers using carrion during later stages of decomposition and potentially lower resource availability. Vertebrate scavenger assembly differed between open and closed forests, which suggests that it is important that carrion resources are available for scavengers both in gaps and closed forests to promote overall biodiversity and maintain their ecosystem functions.

CRediT authorship contribution statement

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

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122920.

Data availability

All data used for analyses 365 are publicly available from the Biodiversity Exploratories Information System 366 (https://doi.org/10.17616/R32P9Q) at https://www.bexis.uni-jena.de/PublicData/.

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