


# Diverse Effects of Climate, Land Use, and Insects on Dung and Carrion Decomposition

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## ABSTRACT

Land-use intensification and climate change threaten ecosystem functions. A fundamental, yet often overlooked, function is decomposition of necromass. The direct and indirect anthropogenic effects on decomposition, however, are poorly understood. We measured decomposition of two contrasting types of necromass, rat carrion and bi-

son dung, on 179 study sites in Central Europe across an elevational climate gradient of 168–1122 m a.s.l. and within both local and regional land uses. Local land-use types included forest, grassland, arable fields, and settlements and were embedded in three regional land-use types (near-natural, agricultural, and urban). The effects of insects on decomposition were quantified by experimental exclusion, while controlling for removal by vertebrates. We used generalized additive mixed models to evaluate dung weight loss and carrion decay rate along elevation and across regional and local land-use types. We observed a unimodal relationship of dung decomposition with elevation, where greatest weight loss occurred between 600 and 700 m, but no effects of local temperature, land use, or insects. In contrast to dung, carrion decomposition was continuously faster with both increasing elevation and local tempera-

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ture. Carrion reached the final decomposition stage six days earlier when insect access was allowed, and this did not depend on land-use effect. Our experiment identified different major drivers of decomposition on each necromass form. The results show that dung and carrion decomposition are rather robust to local and regional land use, but future climate change and decline of insects could alter decomposition processes and the self-regulation of ecosystems.

**Key words:** decay; ecosystem function; global change; land-use intensification; necrobiome; urbanization.

## HIGHLIGHTS

- Local and regional land-use intensity does not impact dung and carrion decomposition.
- Carrion decomposition strongly responds to local temperature, elevation, and insect access.
- Dung decomposition has a unimodal relationship with the elevation.

## INTRODUCTION

The decomposition of organic matter (detritus or necromass) is a crucial process for nutrient cycling (Cardinale and others 2012), influences trophic networks, and stabilizes ecosystem structure and function (Moore and others 2004; Nichols and others 2008). The functioning of an ecosystem, in turn, depends on the diversity of functional and taxonomic groups (Millennium Ecosystem Assessment 2005). However, the interaction of stressors, that is, climate change and intensified land use, exacerbates the risk of biodiversity loss (Jetz and others 2007; Mantyka-Pringle and others 2015; Sala and others 2000; Visconti and others 2016), including those associated with necromass decomposition, and potentially affects the functioning of ecosystems and their associated services.

Necromass is a very nutrient-rich but ephemeral resource; it provides shelter and habitat for a wide variety of detritivorous organisms, like microbes and insects, that extensively contribute to decomposition (Benbow and others 2015, 2019; Hanski and Cambefort 1991; Moore and others 2004). Over the past several decades, however, there have been documented reductions in terrestrial insect biomass by more than two-thirds in Germany

(Hallmann and others 2017; Seibold and others 2019), and negative effects of anthropogenic activities on the functional and taxonomic diversity of copro- and necrophagous insects (Sánchez-Bayo and Wyckhuys 2019; von Hoermann and others 2018). Insect decline is a general threat to both ecosystem services and economics. For instance, a reduction in functional diversity of dung beetles results in lower decomposition rates (Beynon and others 2012). Without the ecosystem service provided by dung beetles, however, slowly decomposing cattle feces would lead to fouling of rangeland (for example, in Australia) and attract pest species, which in turn lead to drastic economic losses (Castle and MacDaid 1972; Losey and Vaughan 2006).

Global warming, as one of the major threats to biodiversity, applies physical stress in terms of heat to species, and by changing their phenology, geographical distribution, community structure, and ecosystem functions (Angilletta Jr. 2009; Barton and Bump 2019; Graham and Grimm 1990; Warren and others 2013). Higher temperatures, however, also enhance metabolic activities of insects and microbes (Barton and Bump 2019) and are related to higher abundances of carrion and dung beetles (Gebert and others 2020; von Hoermann and others 2018; 2020), and soil-inhabiting fungi in temperate regions, whereas soil-inhabiting bacterial abundance decreases with increasing temperatures (Castro and others 2010). Higher microbial respiration rates were also observed at higher elevations despite cooler temperatures, suggesting moisture as another important determinant of microbial activity (Murphy and others 1998). Yet, high microbial species richness, for example, in deadwood, can also negatively correlate with decay rate due to competition among saprophytic species (Fukami and others 2010; Hagge and others 2019).

Land-use intensification leads to changes in soil properties, habitat loss, and habitat fragmentation (Dudley and Alexander 2017; Lauber and others 2008). Decomposer communities and services provided by them respond independently to different land-use types, and higher soil-fauna richness and abundances are not necessarily linked to higher decomposition rates (Yang and others 2018). For dung beetles, Frank and others (2017) found clear habitat preferences among species and distinct dung removal rates across habitat types. The sprawl of agricultural areas, however, and the transformation from primary to secondary plantation forests reduce dung beetle abundance (Gardner and others 2008; Sánchez-Bayo and Wyckhuys

2019). Similarly, carrion-feeding insects are influenced by forest structure (Heidrich and others 2020), soil properties (von Hoermann and others 2018), and land-use type (Babcock and others 2020; Dekeirsschieter and others 2011). Furthermore, an increasing use of fertilizers, as a consequence of intensified land use, leads to a decrease in soil microbial diversity (French and others 2017). Soil microbes, however, substantially contribute to nutrient cycling and accelerate decomposition processes (Dubey and others 2019; Lauber and others 2014). During decomposition, microbes emit volatile organic compounds that can vary among habitats and substrates and mediate carrion decomposition by attracting necrophagous insects (Cammack and others 2015; Dekeirsschieter and others 2009). Different odor bouquets potentially influence necrophagous beetle communities and hence decomposition rates.

The way this complex interplay of climate change, land-use intensification, and the decline in insects influence the decomposition of necromass has not yet been studied in the field. To disentangle the abiotic effects of a macroclimate (elevation) gradient, local temperatures, habitat and landscape, and the biotic effects of insects on dung and carrion decomposition, we conducted a landscape scale experiment using 179 study sites along an elevation gradient and across local and regional land-use types in Central Europe. Specifically, we tested the following three hypotheses: (i) Decomposition of dung and carrion in near-natural environments is faster compared to highly transformed land-use types; (ii) warmer climates and higher local temperatures are related to faster decomposition; and (iii) insect exclusion slows necromass decomposition.

## MATERIAL AND METHODS

### Study Sites

This study was conducted in southeast Germany within the federal state Bavaria. We selected 60 study regions ( $\sim 5.8 \text{ km} \times 5.8 \text{ km}$ ) along a climate gradient divided into five climatic zones based on multi-annual mean temperatures from 1981 to 2010 (Deutscher Wetterdienst, 2020), and among three regional land-use types (near-natural, agricultural, and urban landscapes) (Figure 1). All climate and regional land-use combinations were represented four times. Within each study region, we established study sites ( $3 \text{ m} \times 30 \text{ m}$ ) in the three most dominant local land-use types (habitats) out of four possible (that is, forest, grassland, arable

fields, and settlements). In total, there were 179 study sites (a single region out of the 60 study regions contained two study sites instead of three). The final selection of study sites covered a spatial extent of about 400 km as well as 1000 m in elevation. Additional details of the study site selection are described in Redlich and others (2021).

### Study Design and Data Collection

In May 2019, two pats of European bison dung ( $\acute{a}$  450 g) and two rat carcasses ( $\acute{a}$  200–250 g) were exposed on each of the 179 study sites. Upside down bicycle baskets protected all dung pats and rat carcasses from vertebrate scavenging. At each study site, one basket of each necromass type was additionally covered with mosquito netting (mesh size 1 mm) to limit arthropod access. The rats were placed 30 m apart from each other, while the two dung pats were placed in the middle of the study site adjacent to each other. To separate the soil from the dung and to facilitate the collection, small meshes (mesh size 1 mm) were placed underneath the dung at the beginning of the experiment.

Dung was collected in March 2019 from European bison in the National Park Bavarian Forest's animal enclosure, from defecating animals that had not been treated with antibiotics or anthelmintics. We intended to choose dung from a species, which functionally represents the current dominant domestic animal in agriculture, which is cattle. Bison is evolutionary close to the domesticated cattle and the advantage of bison is that from an evolutionary perspective, European bison were widely distributed across Europe until the twentieth century (Kuemmerle and others 2011; Svenning 2002) and organisms like insects and microbes were able to adapt to its dung. Contrary to domesticated cattle, bison prefer forests as well as herbaceous vegetation (Kuemmerle and others 2011), which makes them a suitable study organism for decomposition and land-use studies like this. We formed approximately 450 g pats for our experiment, weighed them, and stored them frozen. Dung pats were thawed one day prior to the beginning of the experiment. Decomposition of dung was measured by calculating the remaining dry weight after one month. Of 358 dung pats, 357 were collected after an average exposure of  $29 \pm 2$  (mean  $\pm$  SD) days and each pile was dried for five days at  $100 \text{ }^\circ\text{C}$ . Dung pat dry weight before exposure was analyzed by calculating the dry weight/wet weight ratio of 14 control samples (wet weight ranging between 96 and 449 g) from the same defecating animals (Appendix A). Temperature

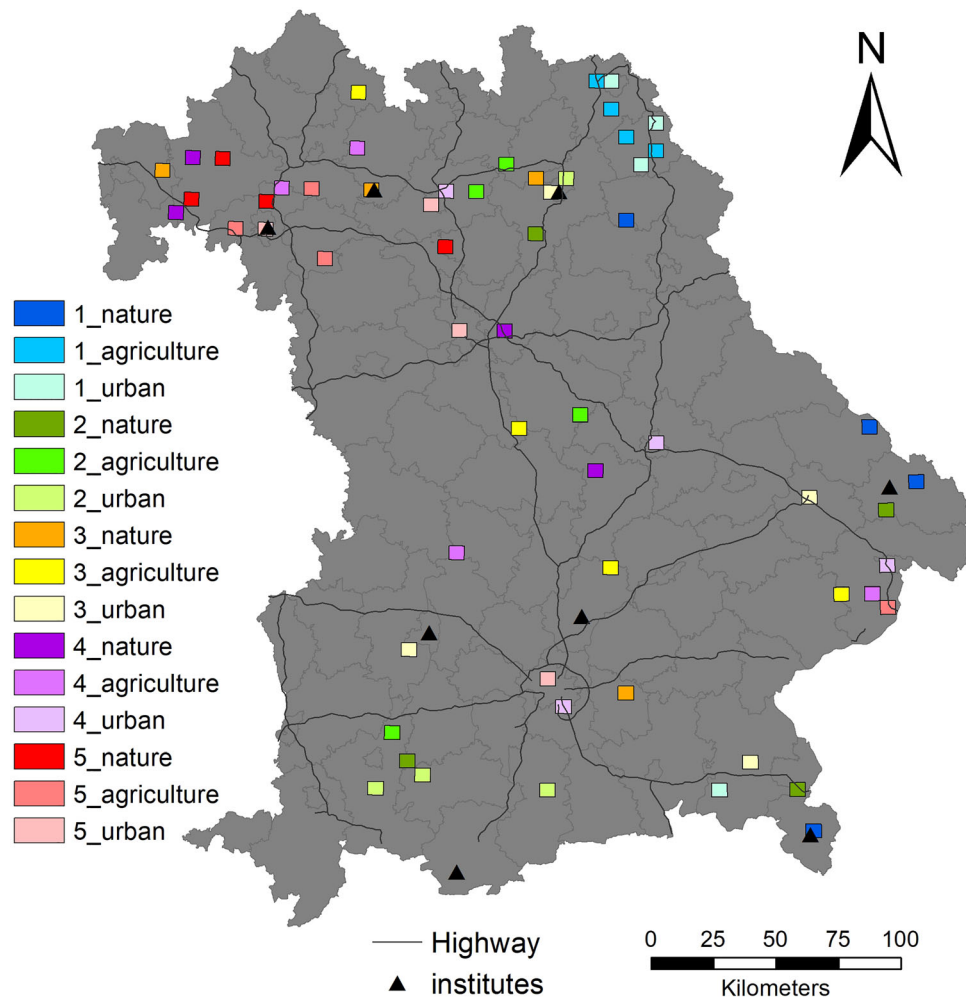


Figure 1. Location of study regions across Bavaria. Numbers (1–5) indicate climate zones; landscapes are defined as nature (near-natural), agriculture, and urban.

data loggers failed on four study sites, leaving 349 data points for the final statistical analysis.

Representing a functionally important group (rodents) across many habitats, we decided to choose feeder rats as a domesticated form of the brown rat (*Rattus norvegicus*) for our experiment. Considering that small animal carrion is naturally occurring in higher densities than carrion of larger animals (Barton and others 2019), an important proportion of the carrion in ecosystems can be assigned to rodents and makes them an ideal study organism even in higher elevations. Frozen rats were obtained by an online shop for snake food and thawed one day prior to the beginning of the experiment. The decomposition stages of rats were assessed by photographs. Photographs of both rats, with and without insect access, were taken on the day of exposure, two days after exposure to capture early changes in decomposition, and then every

14 days until mid-August (c. 90 days in total). Images of the carrion were then assigned to decomposition stages using the description by Dekeirsschieter and others (2012), and early and late active decay stages and mummification and unexpected disappearance as additional categories (Table 1). Due to our biweekly sampling frequency, we were not able to record the exact date of final decomposition for every carrion (as some would be gone between sampling points). Hence, we used an interval from the last sampling day on the study site when the carrion was not fully decomposed until the day the photograph of the fully decomposed rat was taken. By this, we got the interval with the first potential date of full decomposition and the day the decomposed rat was photographed. Only the onset of the final decomposition stages (stages 6 and 6b) was relevant for subsequent statistical analysis. Despite anti-scavenger cages protecting the carrion,

**Table 1.** Description of Carrion Decomposition Stages

Decomposition stage	Description
(1) Fresh	From death until first signs of bloating
(2) Bloated	Swelling of the body, first in the abdomen
(3) Early active decay	Deflating, skin is darkening
(4) Late active decay	Skin breaks up, leaking of liquids
(5) Advanced decay	Only some (wet) remains of flesh and skin
(6) Dry remains	Only bones and hair remaining
(6b) Mummification	Skin and organs are mummified
(7) Unexpected disappearance	Disappearance of the carrion by mammal scavengers or burying beetles

*Adapted from Dekeirsschieter and others (2012)*

98 rats were taken by vertebrate scavengers over the course of the study. At four study sites, the data loggers failed to measure local temperature, and six rats (one with, five without insect access) did not reach one of the final decomposition stages of 6 or 6b within the study period. Thus, data from 247 out of 358 rats were included in the final analysis (118 with insect access, 129 without).

Additionally, since no direct weight loss of the rats could be measured during the field experiment, we added another experiment with ten rat carcasses (five carcasses with insect access and five without). Here, pairs of carcasses (with/without insect access) were exposed successively after 3, 8, 14, and 21 days on a meadow adjacent to our institute, and weight loss was measured every 3–5 days. To facilitate handling of the carcasses during weight measurements, a mesh wire (mesh size *c.* 2 cm) was placed underneath each rat. To assess the weight loss each rat was lifted with the mesh wire and placed in an aluminum bowl (to capture leaking body fluids and to avoid the disintegration of the carcass). Wet weight was then measured and subtracted from the initial weight to get the weight loss in gram and %. This allowed us to compare weight loss over time with the decomposition stage classifications estimated from the photographs. Measurements on rainy days ( $n = 2$ ) were excluded from the analysis since measurements would be distorted by the wet fur.

### Environmental Parameters

We used elevation as a surrogate for a long-term macroclimatic gradient, which was highly correlated with multi-annual mean temperature and precipitation over the past 30 years (Spearman  $\rho = -0.84$ ;  $p < 0.05$  and  $\rho = 0.74$ ;  $p < 0.05$ , respectively). Information on multi-annual mean temperature and precipitation data for individual

study plots were extracted from gridded monthly datasets with a horizontal resolution of 1 km using a nearest source to destination approach. Subsequently, long-term averages thereof were calculated for the period 1991 to 2020. The raw input datasets are provided free of charge by the German Meteorological Service (DWD) and are described in Kaspar and others (2013).

To capture small-scale variation in local temperature across the sampling period and the different habitats, we used ibutton thermologgers (type DS1923, Hygrochron iButton<sup>®</sup>, Whitewater, WI, USA) on each plot. Each data logger was mounted on a wooden pole at 1.10 m height, facing north and with a roof panel to protect against direct sun exposure.

Land use was assessed in a nested design of local land-use types (habitats: forest, grassland, arable fields, settlements) within regional land-use types (landscapes: near-natural, agricultural, urban).

The role of flying and ground-dwelling insects was estimated by experimental exclusion.

### Statistical Analysis

We modeled the effects of local habitat, regional landscape, local temperature, elevation, and insect access on the decomposition rates of dung (final dry weight) and carrion (time until final decomposition). All models were built using R, version 4.0.2 (R Core Team 2021).

To allow for different response variables, namely ‘final dry weight’ for dung and ‘time until final decomposition’ for carrion, two separate generalized additive models (GAMs) (package *mgcv* by Wood 2006) were built to make both data sets comparable and to model nonlinear relationships. To account for each response variable, ‘final dry weight’ and ‘time until final decomposition,’ we used the families Gaussian and Cox.ph, respec-

tively, the latter implying a Cox proportional hazards model (Cox 1972). Because local temperatures measured by the data logger and elevation were only moderately correlated (Spearman  $\rho = -0.43$  and  $p < 0.05$ ), both were included in model building to have adequate surrogates for macroclimate and local temperature gradients. Elevation ranged from 168 to 1122 m a.s.l., so we scaled it by dividing by 100 (elevation100) to have comparable elevation and temperature scales.

In both models, habitat, landscape, local temperature, and insect access were included as environmental variables, with smoothness estimations for elevation100 as fixed effect and study site as a random effect for replicated measurements. To allow for variation in initial dung dry weight ( $108 \pm 0.01$  g (mean  $\pm$  SD)) and days of dung exposure ( $29 \pm 2$  days (mean  $\pm$  SD)), both parameters were included in the offset of the Gauss model. In both models, potential interactions of insect presence/absence with habitat, landscape, local temperature, and elevation were evaluated by Akaike's information criterion (AIC) comparison.

Although a higher value of the final dung dry weight would mean a lower weight loss (lower decomposition), an increase in the hazard rate indicates an increase in carrion decomposition so that the response variables of dung and carrion act in different directions (Figure 2). Thus, in the dung model output, algebraic signs of the estimates were inverted since this response variable is less intuitive to interpret than the Cox model results. By this, the

results are provided and interpreted as effects on carrion and dung decomposition rates.

Although long-term data on precipitation and temperature (multi-annual mean precipitation and precipitation over 30 years) were highly correlated with elevation (Spearman  $\rho = -0.84$ ;  $p < 0.05$  and  $\rho = 0.74$ ;  $p < 0.05$ , respectively), we additionally fitted both GAMs (dung and carrion) with the long-term precipitation and temperature data instead of elevation to account for both options as potential surrogates for macroclimate, and to compare their AICs. According to the AICs, models including elevation instead of long-term temperature and precipitation data gave a better fit (Appendix B). Therefore, elevation was chosen as a surrogate for macroclimate.

In the GAM analysis, only the right-censored day of final carrion decomposition could be included as response variable because of the model structure. Therefore, we additionally fitted a mixed-effect parametric Cox regression utilizing interval-censored data of the carrion decomposition (packages *survival* by Therneau and Grambsch 2001 and *tramME* by Tamási and Hothorn 2021). The mixed-effect parametric Cox regression included the period from the day when the carrion was last seen until the day when the carrion was finally decomposed, which led to a more precise result. For this model, landscape, habitat, local temperature, insect access, and elevation100 were included as independent variables and study site as a random factor (Appendix C).

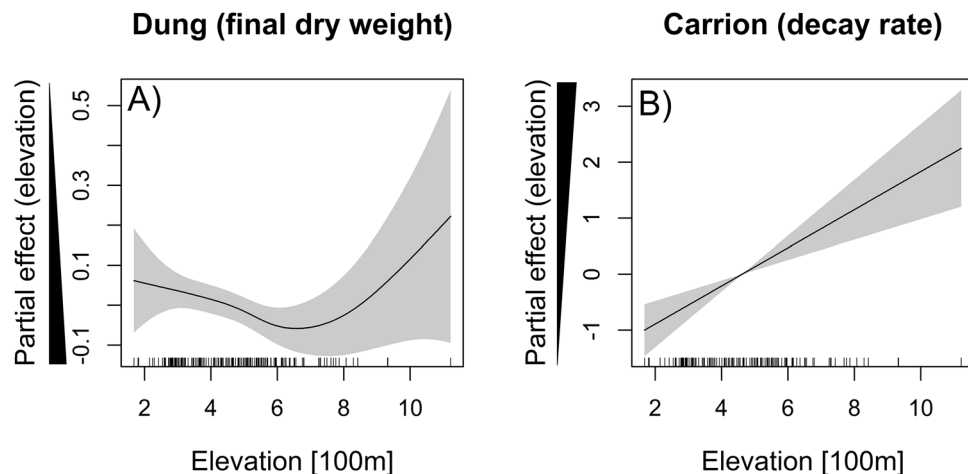


Figure 2. Partial plots for the smooth term  $s(\text{elevation100})$  for both GAMs with confidence intervals indicated by the gray-shaded areas. **A** Unimodal relationship for the final dry weight of dung along elevation with a minimum dry weight at about 700 m. **B** Linear relationship for the decomposition of carrion along elevation. High y-values for dung decomposition indicate high final dry weights and consequently slower decomposition rates, while high y-values for carrion decomposition indicate faster decay. Triangles on the left-hand side of each plot indicate the direction of increase (broad base) of decomposition along the y-axis.

For a more intuitive access to the partial effects of predictors on dung, we calculated the relative effect on dung weight for a change in local temperature or elevation by 1 °C or 100 m, respectively, as well as for a change in the factor levels of insect exclusion, habitat, or landscape type (Appendix D).

Coefficients in the Cox model represent the linear effect of the corresponding predictors on the hazard rate, that is, the temporal rate of transition events from the non-decomposed to the decomposed stage of the carcass. Interpretation of the survival analysis coefficient is thus less self-evident than for linear or additive models. We illustrated the isolated effects of single predictors by cumulative distribution functions indicating the probability of decomposition over the course of time and allowing for estimation of the delay caused, land use, insect exclusion, or decreases in temperature (details in Appendix D). All tables were created using the package *stargazer* by Hlavac (2018).

Datasets for carrion and dung and the R code for both GAMs and the mixed effect parametric Cox regression are provided as supplementary material.

## RESULTS

### Dung Decomposition

Dung decay followed a unimodal relationship with elevation described by the local curve minimum marking the lowest final dry weight. Hence, the highest weight loss across all study sites was between 600 and 700 m a.s.l. (Figure 2A, black triangles next to y-axis labels indicating the partial

effect of elevation on the dung weight loss/carrion decomposition rate). We found a marginal effect of elevation on dung decomposition, while local temperature, insect access, landscape, and habitat had no significant impacts (Table 2). We could improve the model without interactions by adding the interaction between elevation and insects, while any other combination of candidate interactions performed worse than the model with exclusive insect-elevation interaction. In that case the nonlinear effect of elevation (Figure 2A) was significantly influenced by insects increasing dung decomposition at high elevation and reducing decomposition at low elevation, but not changing the overall unimodal pattern (Appendix E).

### Carrion Decomposition

Higher carrion decomposition was associated with higher elevation (Figure 2B). Further, carrion decomposition was accelerated by six and about four days with insect access and an increase in local temperature by 1 °C, respectively (Table 2, Appendix D). Although not significant, the estimates of all non-forest habitats and non-natural landscapes were generally negative (Table 2). Additional potential interactions between presence/absence of insects and habitat, landscape, local temperature, and elevation did not improve the model (results not shown). The results of the mixed-effects parametric Cox regression (interval-censored time to decomposition) were commensurate with the GAM results (right-censored only) and revealed significant positive effects of insect

**Table 2.** Summary Statistics for Generalized Additive Gauss and Cox.ph Models

Predictors	Dung weight loss (family = Gauss)			Day of final carrion decomposition (family = Cox.ph)		
	Estimates	std. Error	<i>p</i>	Estimates	std. Error	<i>p</i>
(Intercept)	0.71	0.23	<b>0.002</b>			
Insects [yes]	− 0.01	0.01	0.664	0.56	0.15	< <b>0.001</b>
Habitat grassland versus forest	0.07	0.05	0.155	− 0.16	0.30	0.589
Habitat arable field versus forest	− 0.01	0.05	0.903	− 0.50	0.31	0.102
Habitat settlement versus forest	0.04	0.05	0.490	− 0.52	0.36	0.146
Landscape agriculture versus near-natural	− 0.06	0.04	0.165	− 0.33	0.27	0.229
Landscape urban versus near-natural	0.03	0.04	0.560	− 0.21	0.28	0.452
Local temperature in °C	− 0.02	0.02	0.150	0.56	0.12	< <b>0.001</b>
Smooth term (elevation100)			0.097			< <b>0.001</b>
Random effect (study site)			< <b>0.001</b>			< <b>0.001</b>
Observations	349	253				
<i>R</i> <sup>2</sup>	0.606	0.564				

*Insects, habitat, landscape, local temperature, and elevation100 were included as predictors in both models and study site as a random term. Algebraic signs of the estimates for final dung dry weight are inverted; by this, results can be read as estimates for dung weight loss. Significant p-values in bold.*

access, local temperature, and elevation on carrion decomposition (Appendix C).

The survival curves resulting from the mixed-effect parametric Cox regression describe the probability of complete carrion decomposition with and without insect access over time. At almost any timestamp, the probability of complete decomposition was higher for carrion with allowed insect access (Figure 3). This was supported by our additional experiment: After 31 days, carrion with insects allowed showed about 90% weight loss, whereas carrion without insects decreased by 50% (Figure 4).

## DISCUSSION

The overall aim of this study was to investigate the effects of local and regional land-use intensity, climate change (local temperature and macroclimate), and the decline in insects on the decomposition processes of dung and carrion.

Dung and carrion decomposition responded differently to land-use intensification, local temperature, macroclimate gradients represented by elevation, and insect access. Local and regional variation in land use did not affect the decomposition of carrion and dung. Neither was dung decomposition influenced by local temperature or macroclimate (elevation). However, dung decomposition followed a unimodal pattern with increasing elevation. Carrion decomposition, in

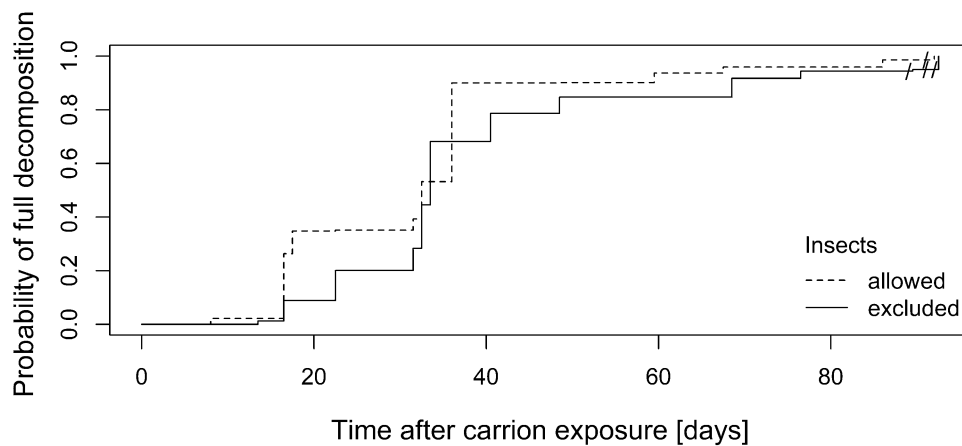


Figure 3. Survival curve for the probability of full carrion decomposition (onset of mummification or dry remains) with and without insect access over time. The dashed line indicates insect access, while the solid line displays no insect access.

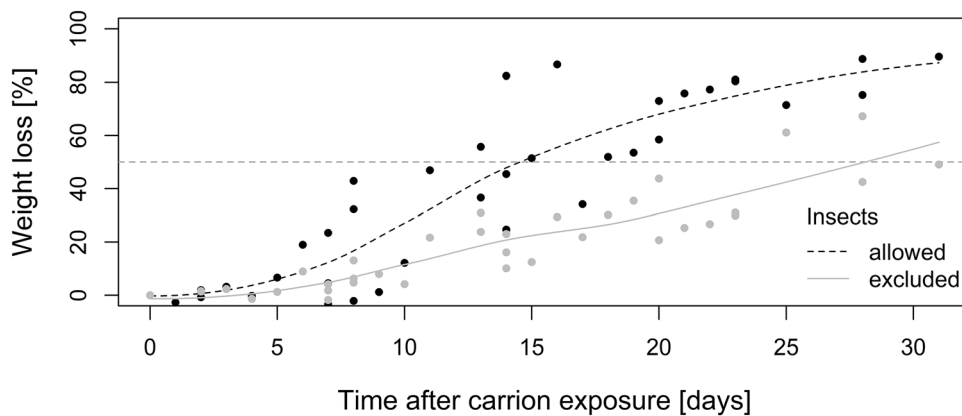


Figure 4. Weight loss of rat carrion with and without insect access ( $n = 5$  for each treatment) measured in weight loss in percentage over time. Gray and black dots indicate individual measurements, and curves represent the associated regression lines. Rats with allowed insect access are depicted in black and rats without insect access in gray. Horizontal gray line indicates 50% weight loss.



contrast, strongly responded to increasing local temperatures and elevation. Insect access only enhanced carrion decomposition, not dung, although insect diversity is widely known to affect both dung and carrion decomposition processes (Lee and Wall 2006; Pechal and others 2014). Our findings indicate that necromass decomposition, particularly carrion, in temperate regions is more affected by climate and the presence of insects than by land-use intensity.

## Land Use

We expected highest necromass decomposition rates in near-natural habitats and landscapes. Our results, however, show that decomposition processes are robust against land-use intensification. Hence, we suggest that decomposition is driven by other factors that are independent of habitat and landscape, although intensified land use has been reported to have significant effects on copro-/necrophagous beetles, soil-inhabiting invertebrates, and microbes (French and others 2017; Lauber and others 2008; Lumini and others 2010; Minor and Cianciolo 2007; Nichols and others 2008; Polasky and others 2011; von Hoermann and others 2018; 2020).

Land-use change and new agricultural practices, for example, the use of anthelmintics, can negatively affect dung beetles (Carpaneto and others 2007), whereas grazing-continuity of grasslands and a low habitat complexity positively affect dung beetle abundance and richness (Buse and others 2015; Romero-Alcaraz and Ávila 2000). Moreover, dung beetle functional diversity is highly variable among different regions, resulting in varying dung decomposition rates (Milotić and others 2019). Although the literature reports that diversity and abundance of decomposer communities vary across land-use types, our results suggest that for resources mainly decomposed by soil-inhabiting organisms (nematodes, arthropods, microbes), for example, dung, the absence of one functional or taxonomical group of decomposers may be replaced by other groups with similar functions, independently of the community composition across land-use types. Comparable results were found for leaf litter decomposition, where the exclusion of mesofauna ( $> 1$  mm) had no influence on decomposition rates (Barajas-Guzmán and Alvarez-Sánchez 2003), which highlights the importance of a species rich decomposer community.

Although necrophagous beetle abundance and richness are reported to be determined by land-use characteristics (von Hoermann and others 2018;

Wolf and Gibbs 2004), we found no significant effect of habitat or landscape on carrion decomposition. Other studies on necrophagous insects and microbes, however, would suggest distinct decomposition patterns among habitat types. Dekeirsschieter and others (2011), for instance, reported highest carrion beetle abundance in agricultural sites, compared to forest and urban sites. Furthermore, flies are the primary competitors of carrion beetles and benefit from open habitats and forest fragmentation (Gibbs and Stanton 2001). Besides insects, microbial communities and their activity substantially contribute to carrion decomposition (Crippen and others 2015; Weatherbee and others 2017), and microbial counts increase from woodland to pasture sites, accompanied by faster decomposition rates of carrion (A. S. Wilson and others 2007).

Taken together, our results suggest other factors than insect abundance and diversity, or microbial counts, are the primary drivers of decomposition processes across different land-use types. Barton and Evans (2017) assume that habitat effects are only relevant for generalist arthropods, while specialists, such as some flies, consider the carrion as their habitat and neglect the surrounding habitat.

## Local Temperature

Our findings show that the effect of local temperature on decomposition can be highly variable among necromass types and potentially depends on other factors like humidity, and insect access.

In Milotić and others (2019), dung beetle richness and abundance are increased with higher temperatures and decreased with higher precipitation, whereas the dung removal ratio responds the opposite way. Our result, however, is in line with an experimental study that observed no local temperature effects on dung removal and suggests humidity as a more important factor positively influencing dung beetles' activity and preventing dung from desiccation (Holley and Andrew 2019). Due to the absence of an additional layer (or skin), dung is more prone to desiccation, which may lower microbial decomposition activity, whereas carrion is covered by a skin that serves as a protection layer and maintains a moist milieu which is fundamental for decomposition processes, for example, by microbial decomposers and fly larvae (Carter and others 2007).

As expected, carrion decomposed faster with increasing local temperatures. This might be an indirect effect of increased microbial activity (Pechal and others 2013) and higher emission rates of

volatile organic compounds, which enhances the attraction of beetles and other necrophagous insects. Further, temperature increases insect activity and metabolic rates, which in turn may lead to overall great insect activity (Uhler and others 2021), and higher necrophagous insect abundances and feeding rates at carcasses (Barton and Bump 2019; von Hoermann and others 2018). These findings corroborate several other studies, where carrion decomposed faster in sunlit habitats, compared to shaded or forested sites due to higher temperatures (Sharanowski and others 2008; Shean and others 1993). Nevertheless, warm and dry climatic conditions may also slow the carrion decomposition by desiccation (Parmenter and MacMahon 2009).

## Elevation

We assume that the ideal temperature–precipitation ratio for efficient dung decomposition in our temperate study region is best represented at mid-elevations, considering decreasing temperatures and increasing precipitation along an elevational gradient. This is supported by Milotić and others (2019), where dung removal was reduced at higher temperatures, but higher precipitation favored the breakdown process. Taken together that local temperature had no effect on dung decomposition, and elevation only a marginal effect, we suggest that since climate change may not lead to increasing temperatures in all regions, it may potentially result in changes in precipitation that could impact dung decomposition processes. However, precipitation forecasts are often uncertain and site specific. Hence, to test for precipitation effects a broad-scale study across Europe would be needed to get reliable results. Moreover, the most commonly observed pattern for biodiversity along elevational gradients is a unimodal curve (Rahbek 2005), which was also reported for dung beetle abundance (Gebert and others 2020) and richness (Herzog and others 2013). Furthermore, soil microbial diversity (Shen and others 2015) and copro-/necrophagous beetle abundance and diversity are often negatively correlated with elevation (Martín-Piera and Lobo 1993), which would explain reduced decomposition at elevations above 700 m. Increasing temperatures due to climate change, however, are likely to cause a shift of dung beetles to upper elevational ranges (Menéndez and others 2014), which could potentially result in higher dung removal rates at upper elevations.

Since we found that flying and large ground-dwelling insects did not play a significant role in

dung decay, we speculate that the diversity and richness of other soil-inhabiting detritivores may peak at medium elevations. Earthworms, for instance, account for up to 50% of dung decomposition (Holter 1979), and their diversity and abundance tend to be higher with increasing latitude and in temperate regions, respectively (Phillips and others 2019). Furthermore, Collembolans (springtails) contribute considerably to the decomposition processes (Wang and others 2009) and were found to reach highest abundance at medium elevation in a mountain study in China (study sites were located between 3800 and 5000 m a.s.l.) (Jing and others 2005). Consequently, in future investigations earthworms and other soil-arthropods should be evaluated as an important component of the invertebrate necrobiome as well. Interestingly, in the presence of insects, decomposition at low elevations was slowed down, while at higher elevations decomposition happened faster. Assuming that dung resources become rare at higher elevations, it is likely that decomposers at higher elevations colonize and decompose this rare and valuable resource faster than on lower altitudes. Interactions where the main effects were not significant, however, should be handled with caution. An interaction of insects and climate has also been observed for the decomposition of another necromass type, namely deadwood (Seibold and others 2021). The underlying processes of this interaction in deadwood, however, are not transferable to dung, where the mechanisms behind this interaction are still unknown.

Carrion decomposition responded positively to increasing elevation, although temperature was lower at higher elevation study sites, indicating that temperature was not the driving factor for decomposition along the elevational gradient. Our findings are contrary to the results of other studies where carrion decomposition did either not directly respond to temperature changes along elevation (Farwig and others 2014) or was slower with increasing elevation (De Jong and Chadwick 1999; Richards and Goff 1997).

At lower temperatures, body size of dung and carrion-feeding beetles was found to be smaller than on warmer sites and lower altitudes (Farwig and others 2014; Herzog and others 2013), which might influence the decomposition process as reported by Farwig and others (2014). Lower temperature (and associated slowing microbial activity; Pechal and others 2013) and reduced larger beetle abundance at higher elevations provide plausible

explanations of slower decomposition processes at higher altitudes.

Small carrion exposed at lower altitudes is more prone to negative desiccation effects on associated microbes (Crippen and others 2015), and constrained insect larval growth (Bass 1997). Despite the presence of potentially larger carrion-feeding beetles, higher temperatures, and the increased risk of desiccation at lower altitudes, we found significantly faster carrion decomposition at higher elevations.

The complex interplay of ecological variables (for example, vegetation, microclimate, forest stands) leads to elevational effects on decomposition (De Jong and Chadwick 1999). Thus, we assume that at a macroclimatic scale there are other factors than temperature affecting decomposition along the elevational gradient in our study, such as the participation of edaphic invertebrates or the moisture regime dictating microorganisms' activity.

Elevation reflects climatic conditions on a broader temporal and spatial scale, compared to local temperature variation, which may explain the different decomposition patterns among these two variables. Our study, hence, suggests disentangling elevational and local temperature effects in future decomposition studies.

## Insects

Although exclusion or delayed access of insects leads to substantial reduction in decay and the subsequent insect population size and community composition (Lee and Wall 2006; Pechal and others 2014), in our study, only carrion decay, not dung decomposition, was strongly influenced by insects.

In general, dung decomposition happens rather slowly compared to carrion decomposition, due to the complexity of the substrate and the absence of a skin, that keeps moisture higher in carrion (Carter and others 2007). While carrion, besides microorganisms, is mainly decomposed by carrion-feeding beetles and flies (Merritt and De Jong 2015), dung serves as a resource for a wide variety of invertebrates. Along with dung beetles and flies, soil-inhabiting invertebrates are major contributors to necromass decomposition processes (Holter 1979; Wang and others 2009). These invertebrates were not excluded by our cages. Therefore, it is likely that dung breakdown in both dung pats was equally mediated by soil-inhabiting invertebrates, particularly earthworms, rather than by flying or ground-dwelling insects; even though the removal efficiency of earthworms is lower than that of dung beetles (Holter 1979; Rosenlew and Roslin 2008),

emphasizing the important contribution of diverse detritivore insects for rapid necromass turnover rates.

Within hours to days, carrion is inhabited by insects and their larvae, which feed on tissue and significantly contribute to the biomass loss during putrefaction and active decay (Benbow and others 2015; Richards and Goff 1997). This is supported by our large-scale study and the small carrion-experiment, where carrion with insect access lost 40% more weight compared to caged carrion, which is comparable with other studies (Barton and Evans 2017; Kočárek 2003; Payne 1965).

Despite cages, 27% of our rats were scavenged, which highlights the importance of vertebrates in decomposition processes under real world conditions. Insects and microbes, however, colonize carcasses within hours to days (Spicka and others 2011), whereas for scavengers it can be challenging to find this ephemeral resource in a spacious area before decomposition by insects and microbes has proceeded too far (Putman 1983). Focusing on insects' contribution to decomposition processes, we would recommend the use of cages to avoid extensive loss of carcasses.

Moreover, the sum of our findings for the decomposition of dung- and animal-remains on a large spatial scale highlights the variability of detritus (E. E. Wilson and Wolkovich 2011) and the necessity to distinguish between different kinds of necromass.

## CONCLUSION

Our results demonstrate that the ecosystem service of 'carrion and dung decomposition' is rather robust against land-use intensification on both local and regional scales in a temperate region. Contrary to dung, carrion decomposition is strongly affected by local temperature, macroclimate, and the presence of flying and ground-dwelling insects. Hence, climate change and a decline in necrophagous insects could alter nutrient cycling and the self-regulation of ecosystems through changes in carrion decomposition. Moreover, different necromass forms in temperate regions react differently to global change drivers and the decline in insects and should be investigated separately.

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## DECLARATIONS

**Conflict of interest** The authors declare that they have no conflict of interests.

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